Phylogenetic and phenotypic divergence of an insular radiation of birds

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General Abstract

Evolutionary divergence of lineages is one of the key mechanisms underpinning large scale patterns in biogeography and biodiversity. Island systems have been highly influential in shaping theories of evolutionary diversification and here I use the insular Zosteropidae of the south west Pacific to investigate the roles of ecology and biogeography in promoting evolutionary divergence.

Initially I build a phylogenetic tree of the study group and use it to reveal the pattern of colonisation and diversification. My results suggest a complex history of dispersal with the observed pattern most likely a result of repeated bouts of colonisation and extinction. I then use the new phylogeny to quantify the diversification rates of the Zosteropidae. I find a very high rate of lineage divergence and suggest the most likely explanation relates to extensive niche availability in the south west Pacific. I also find evidence for an overall slowdown in diversification combined with repeated bursts of accelerated speciation, consistent with a model of taxon cycles. I do not find evidence for sympatric speciation, however. Finally I combine morphological and phylogenetic data to investigate the mode of evolution, evidence for character displacement and influence of biogeography on trait evolution. I find little support for the traditional theory of character displacement in sympatric species. I do, however, find some support for biogeographic theories.

Taken together my results do not support traditional theories on the ecological and biogeographical basis of divergence, even in those cases where *Zosterops* have been used as exemplars. This appears to be because those theories assume rather simple patterns of colonisation and a static ecological system. Instead, my results suggest that evolutionary diversification is dominated by recurrent waves of colonisation and extinction, which, viewed at any particular moment, tend to obscure any underlying ecological rules.

Declaration

I declare that all the work presented in this thesis has not been previously submitted for a university degree and is entirely my own work, with the following acknowledgements:

Chapter 2

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Chapter 1

General Introduction

1.1 Speciation and divergence

Species are a fundamental unit of biological organisation and the mechanisms by which they arise is a fundamental question in organismal biology. The importance of divergence and speciation to our understanding of the natural world is reflected by a vast historic and contemporary literature on the subject. Indeed, there is much ongoing research and debate surrounding even the most basic principles of the field (for recent reviews see Coyne & Orr 2004; Gavrilets 2004; Newton 2003; Price 2008; Sobel *et al.* 2009). In the context of this thesis, for instance, it is notable that intense debate continues concerning the roles of ecology (Lack 1947; Schluter 2000b; Sobel *et al.* 2009) and biogeography (Coyne & Price 2000; Mayr 1963) in promoting evolutionary divergence; the relative role of sympatric speciation in rapid adaptive radiations (Coyne & Orr 2004; Fitzpatrick *et al.* 2008; Gavrilets & Waxman 2002; Phillimore *et al.* 2008a; Savolainen *et al.* 2006; Schliewen *et al.* 2001; Sorenson *et al.* 2003); the temporal pattern of phylogenetic divergence in adaptive radiations (Crisp & Cook 2009; Gavrilets & Vose 2005; Givnish & Sytsma 1997; Harmon *et al*. 2003; Lovette & Bermingham 1999; Phillimore & Price 2008; Price *et al*. 1998; Ricklefs 2003; Schluter 2000b; Weir 2006); and the link between phenotypic innovation and phylogenetic divergence (Alfaro *et al.* 2009; Anker *et al.* 2006; Claßen-Bockhoff *et al.* 2004; Hodges 1997; Leinonen *et al.* 2008; McKay & Latta 2002; Merilä 1997; Nicholls *et al.* 2006; Phillimore *et al.* 2008b; Sæther *et al.* 2007). It is these broad ongoing questions that I aim to address in this thesis.

Traditionally, the empirical study of modes of evolutionary divergence and speciation have proceeded down two lines, that are perhaps best characterised as the (i) Dobzhansky and

(ii) Mayr approach. The Dobzhansky approach involves laboratory-based experiments of invertebrates, often using *Drosophila* species as model organisms (Dobzhansky 1951; Rice & Hostert 1993). This traditional approach has, of course, reaped many rewards including a detailed understanding of the genetics of isolating mechanisms in a series of species, the potential role of different evolutionary mechanisms in promoting divergence, and the consequences of hybridisation on the divergence process (Dobzhansky 1951). Indeed, it can be argued that this traditional experimental approach continues to provide the bedrock for much of our understanding of the process of speciation, as demonstrated by its influence in recent major reviews and textbooks (Coyne & Orr 2004; Futuyma 1998; Mallet 2006; Noor & Feder 2006; Ridley 1996; Swami 2009; Willis 2009). It has, however, also been pointed out that the traditional approach is not without its limitations. For instance, the focus of laboratory-based experiments on a limited variety of species has been criticised for overemphasising the role of genetic isolating mechanisms at the expense of ecological and behavioural mechanisms (Coyne 1996; Moehring *et al.* 2006; Price 2008; Reed *et al.* 2008; Rice & Hostert 1993) and, more generally, for often failing to capture what actually happens in real populations (Florin & Odeen 2002; Odeen & Florin 2000; Price 2008).

Fortunately for the study of evolutionary divergence and speciation other modes of study are available and many of these have, in fact, been employed since the origin of interest in speciation. Several striking ‘natural experiments’ have led to highly influential field studies of Darwin’s finches (Grant 1999; Lack 1947), *Anolis* lizards (Losos 1994; Losos *et al.* 1997), old world leaf-warblers, genus *Phylloscopus* (Irwin *et al.* 2001; Richman & Price 1992), *Ficedula* flycatchers (Alatalo *et al.* 1990a; Alatalo *et al.* 1990b) and sticklebacks (Hatfield & Schluter 1999; McKinnon & Rundle 2002), but these remain relatively rare cases. A study method that has been particularly influential in the context of speciation is the use of the comparative methods (Bennett & Owens 2002; Harvey & Pagel 1991). These were used informally by both Darwin (1859; 1868) and Wallace (1858; 1891) in their original formulation of ideas regarding evolution and divergence. The Mayr approach is a type of comparative approach that draws comparisons among species from different islands or between island and mainland forms (Bennett & Owens 2002; Grant 1968; Lack 1970; Mayr 1942). Island-based systems hold particular attraction in the context of studies of divergence and speciation because they are commonly home to a high proportion of endemic forms (Orme *et al.* 2005), which potentially makes it easier to identify phylogenetically independent observations (Bromham & Woolfit 2004). This field of study has advanced rapidly in recent years with an explosion of statistically-robust methods for analysing phylogenetic patterns of divergence and a series of studies of island-dwelling systems (Emerson & Kolm 2005; Filardi & Moyle 2005; Harmon *et al.* 2003; Losos 1990; Losos *et al.* 1997; Moyle *et al.* 2009). One of my aims in this thesis is to extend this body of work by constructing a new molecular phylogeny of another well-studied insular group, the white-eyes (Zosteropidae) of the South west Pacific, and to use this to address a series of questions regarding diversification and speciation in an island setting. It is particularly appropriate that this is a bird group because studies of insular avian systems have played a high profile role in many areas of ecological and evolutionary study (Diamond & Mayr 1976; Freed *et al.* 1987; Grant 1966; Lack 1947; Lack 1971; Mayr 1940).

1.2 Phylogenetic and phenotypic divergence in island birds

Phylogenetic analysis of island species relationship patterns is a classic tool in ecology and evolution (Darwin 1859; Lack 1969; MacArthur & Wilson 1967; Mayr 1942; Simberloff 1976; Wallace 1880; Whittaker 2006). In large part this is probably because islands systems are thought to be relatively simple compared to their continental counterparts and therefore to represent relatively tractable systems that are nevertheless outside the laboratory. For instance, in island-dwelling species population limits are often clearly delimited by water, making comparisons between independent units relatively easy and making it more straightforward to identify geographic barriers between populations (Lack 1947; Mayr 1963; Rosenzweig 1978). In addition, island populations are usually small promoting short-term random genetic drift and thought to be exposed to strong selection pressures, providing ideal conditions for both neutral and adaptive divergence and speciation (Mayr 1942; 1963). Finally, insular systems are often particularly well studied, partly because of their interesting geographic context and partly because of the high proportion of distinct species, which means that data are often readily available for large-scale comparative analyses (e.g. (Clegg & Owens 2002).

Birds are excellent colonisers of islands because the combination of relatively large body size and power of flight make them good dispersers, and as a result they have often been used in comparative island studies (e.g., Fleischer *et al.* 1998; Lack 1947; Lovette *et al.* 1998; Ricklefs & Bermingham 1999). Compared to most taxa, birds are also easy to observe and as a result they are one of the best studied and understood groups in terms of ecological, morphological, behavioural and phylogenetic data (Price 2008). It can therefore be argued that birds have inspired theories on diversification and speciation from the earliest works on natural selection (Darwin 1859; Wallace 1871) to many classic works of the new synthesis and beyond (Lack 1947; Mayr 1942; 1963; Mayr & Diamond 2001). Having said this, it is also notable that, while the study of insular bird species has led to many theories about speciation and trait evolution, comparatively few of the predictions emerging have been tested with extensive data sets backed up with comprehensive and robust phylogenies (Price 2008). Recent advances in molecular phylogenies and analytical tools therefore provide a new opportunity to test these predictions.

1.3 The major themes

There are three major themes that I will explore in this thesis and different aspects of each are covered in the various chapters. These are: the mode of evolution, the origins and consequences of sympatry and the effects of biogeography on divergence of species and traits.

1.3.1 Mode of Speciation

1.3.1.1 The Geography of Speciation

Allopatric speciation is believed to be the predominant geographic mode of speciation (Coyne & Orr 2004; Mayr 1963). Evidence for birds, based on the phylogenetic patterns and geography of contemporary species, conforms to expectations of allopatric speciation (Coyne & Price 2000; Phillimore & Price 2008; Price 2008). Trait evolution is also predicted to be most rapid in allopatry, that is in the absence of gene flow from other populations (Price 2008; Rosenzweig 1995). However divergence with gene flow has been repeatedly documented (e.g., Danley *et al.* 2000; Emelianov *et al.* 2004; Freeland & Boag 1999; Liou & Price 1994). The importance of gene flow as a hindering process in trait evolution of geographically separated populations depends on the strength of selection (Postma & van Noordwijk 2005), and populations connected by even moderate levels of gene flow can still diverge if selection is sufficiently strong (Hedrick 1983). Indeed when previous separate species come into allopatry and hybrids are unfit gene flow can actually increase the strength of selection (Liou & Price 1994). Hence, the consensus view is that this allopatric speciation is driven by natural and sexual selection (Coyne & Orr 2004; Price 1998; Price 2008; Schluter 2000b). Potentially neutral drift may play a role (Dobzhansky 1951; Mayr 1942) but overall the evidence suggests that evolution and therefore speciation is dependent on intrinsic ecology and drift alone is not sufficient to explain observed rates of trait divergence (Clegg *et al.* 2002b; Merilä 1997).

1.3.1.2. Dispersal and Speciation

Mayr (1947) identified range expansion as a crucial part in the process of speciation. Recently there has been a shift in emphasis towards the importance of dispersal as a means of increasing the range of available niches leading to the changes in ecological and morphological traits that eventually may result in speciation (Sobel *et al.* 2009). Allopatry can potentially operate at very small scales if dispersal ability is poor and yet paradoxically, only species with good dispersal ability are likely to encounter the new ecological opportunities that make speciation likely. Therefore it is predicted that rapid speciation will often be the result of widely dispersing species swiftly becoming adapted to new environments and, perhaps as part of that adaptation, losing dispersal ability (Cody & Overton 1996; Diamond 1981; Diamond *et al.* 1976; Moyle *et al.* 2009). Widely dispersing vagile species may therefore act as drivers of speciation and reproductively distinct species may evolve from a particular subspecies within a widely dispersed species.

1.3.1.3 The Temporal Pattern of Diversification

Temporal patterns of diversification within species groups can be assessed in the light of molecular phylogenies using lineage through time plots and associated statistical tests (Harvey *et al.* 1994; Nee *et al.* 1994b; Nee *et al.* 1992). Often the statistical null model is that at any moment in time all lineages have an equal probability of speciating per unit time (the Yule model or birth-death process). This process will tend to yield a linear relationship between time on the x-axis and the log number of lineages in the reconstructed tree on the y axis. Related to this is the birth-death model where every lineage has a constant probability of going extinct, this process typically leads to an upturn toward the present in the lineage through time plot. In a model of an adaptive radiation, speciation is expected to occur more frequently early in the radiation as the group spreads into new ecological niches and adapts to them. Speciation rates are then expected to decline through time as the available niche space is filled (Schluter 2000b; Schluter & Ricklefs 1993; Simpson 1953). Many recent phylogenetic studies show evidence for a slowdown in diversification rates toward the present on a lineage through time plot (Phillimore & Price 2008; Weir 2006), which is consistent with the adaptive radiation explanation. Since slowdowns are unlikely under a birth-death model where extinction is high or increases through time, these findings imply that extinction rates are low.

1.3.1.4 Trait evolution

Understanding the mechanisms that underlie trait diversification rates and the temporal variation of those rates is central to evolutionary biology (Rabosky & Lovette 2008a; Ricklefs 2007). In particular the processes that lead to high rates of morphological diversification and rapid radiations in some lineages have generated much interest (e.g., Baldwin & Sanderson 1998; Hughes & Eastwood 2006; Schluter 2000b). Both adaptive and non-adaptive models have been proposed to account for trait differences in congeneric species, according to the role of selection in the diversification process.

The two principal non-adaptive or ‘neutral’ models of evolution are drift and founder effects neither of which invoke selection. Drift is a neutral process whereby traits diverge by chance because only a random assortment of the available genetic variation in a population is passed on to succeeding generations (Huxley 1938; Kaneshiro 1989; Wright 1931; Wright 1940). Theoretical models have shown that non-ecological trait evolution and speciation proceed only slowly unless the mutation rate is exceptionally high (Kondrashov 2003). Founder effects, the other type of non-adaptive model, were proposed by Mayr (1954) whose ‘genetic revolution’ model explained differentiation in small outlying populations through novel gene combinations being created through rapid genetic drift as a result of the founding of a new population by a very small number of colonists. Such founder effect models can potentially lead to rapid evolutionary change but there is little evidence they are common in natural populations (Coyne *et al.* 1997; Lande 1980).

Adaptive models, on the other hand, allow for rapid speciation because adaptation via natural selection leads to divergent selection in related traits (Rundle & Nosil 2005; Sobel *et al.* 2009). It is in these situations, where ecological specialisations for unique environments are evident in divergent characters and the imprint of a common ancestor can be deduced from shared characters, that the signature of Darwin’s “descent by modification” can be most clearly seen. Indeed the Darwin’s finches of the Galápagos, a classic example of rapid, adaptive speciation, influenced Darwin's original theory of natural selection (Darwin 1859). Mayr (1944) considered that since all environments are in some sense unique, all geographical races are also ecological races. Therefore the adaptive model is expected to be very common especially as it allows some gene flow where selection is strong enough to overcome it (Price 2008).

Among the Galápagos Finches for example, the two species of warbler finch (*Certhia olivacea* and *C. fusca*), which fill similar ecological niches, have been separated for more than two million years yet are so similar morphologically that they were only recognised as distinct species after molecular study (Petren *et al.* 1999; Petren *et al.* 2005) and show only weak premating isolation (Grant & Grant 2002). By contrast the small, medium and large Ground Finches (*Geospiza fuliginosa*, *G. Fortis* and *G. magnirostris*) are indistinguishable based on mitochondrial DNA (Freeland & Boag 1999; Sato *et al.* 1999) and yet occupy distinct ecological niches, display assortative mating and are clearly separate on the biological species concept (Mayr 1942; Mayr 1982).

Commonly then ecological trait evolution is expected to happen simultaneously with speciation events as morphological adaptation to new niches drives diversification. Typically trait evolution is expected to happen quickly and early in a radiation as taxa adapt to new niches and then slow down as the niche space fills (Nee *et al.* 1992). Species may divergence enough in allopatry to subsequently co-exist in sympatry following range expansion (Mayr 1947), as appears to have happened in the genus *Geospiza* (Grant & Grant 2008b). Potentially this could result in a further burst of speciation if character displacement is re-enforced in sympatry by competition that causes later arriving species to diverge from their founding populations.

1.3.2 The origin and consequences of sympatry

Sometimes closely related species are found inhabiting the same island this can be explained either by sympatric speciation or by multiple colonisation events (Coyne & Price 2000; Kondrashov *et al.* 1998). In theory, speciation could happen in sympatry if selection were sufficiently strong in two different directions, especially early in an island colonisation (Dieckmann & Doebeli 1999; Kondrashov *et al.* 1998). Comprehensive phylogenies combined with information on species geographic ranges are an important first step in testing for possible examples of sympatric speciation (Barraclough & Vogler 2000; Lynch 1989). However little evidence for sympatric speciation has emerged to date and if, as is generally agreed, sympatric speciation is rare in birds (Coyne & Price 2000; Futuyma & Mayer 1980) then it follows that congenerics must diverge sufficiently in allopatry to occupy substantially different niches before they can come into sympatry (Coyne & Orr 2004). Species in the same genus tend to have similar ecological requirements so competition between them will be more severe (Mees 1969). If two congeneric forms have not differentiated enough ecologically, then one or the other will be driven to extinct by competition in sympatry. Furthermore, post-zygotic reproductive isolation is slow to evolve in birds (Grant & Grant 1992; Lijtmaer *et al.* 2003; McCarthy 2006). If two congenerics have not become pre-zygotically reproductively isolated hybridisation could result in fusion of the two forms if there is no selection against the hybrids. Rates of trait evolution may be important in determining the feasibility of sympatry, particularly if there is a minimum distance that must separate congenerics in morphospace in order for them to survive in sympatry. Typically, where congenerics are found in the same area they are expected to differ morphologically and in a way that is related to the ecological differences between them (Losos 1990). This is particularly true if they are differentiated by the size or type of food they take rather than by differences in habitat, although the requirements of different habitats are also likely to result in morphological differences. For example highland species are typically larger than their lowland counterparts for reasons of heat conservation but this size difference may also be important in areas of overlap.

1.3.3 Biogeographical effects on divergence

Island systems have been shown to be important in the formation of endemism in birds (Orme *et al.* 2005) as many islands have unique subspecies or species which have, presumably evolved *in situ* (Mayr & Diamond 2001). However biodiversity is known to have a negative correlation with islands that are progressively smaller and more isolated. Species exchange is therefore thought to be heavily directionally biased, regularly flowing from continents to islands but seldom in the opposite direction (MacArthur & Wilson 1967), although are notable exceptions such as mainland recolonisation by *Anolis* lizards (Nicholson *et al.* 2005). In the south west Pacific for example, colonisation is predicted to be primarily eastwards from the large land masses of Asia and Australia, with the proximity of these biodiversity sources explaining the absence of adaptive radiations in the region (Price 2008). Indeed Mayr and Diamond (2001) emphasize geographic isolation as the primary cause of speciation in Northern Melanesia and downplay the role of morphological and ecological divergence.

Biogeographical attributes of islands can have important consequences for trait evolution, and hence speciation. For example, continental islands that were once part of a major land mass are likely to have retained fauna that reduce invasion success. In contrast, oceanic islands that have emerged from the sea, offer a “clean slate” and early arriving species may be able to exploit niches that would normally be closed to them, and hence evolve in unexpected directions (Barton 1989; Cox & Ricklefs 1977; Lack 1969). The ability of birds to adapt to fill vacant niches is well documented. This may be a niche normally occupied by a bird group absent from the area in question such as the woodpecker niche filled by woodpecker finches, *Camarhynchus pallidus*, on the Galápagos (Millikan & Bowman 1967) or a niche normally occupied by other taxa such as in New Zealand where Kiwis (Genus *Apteryx*) replace insectivorous mammals (Burbidge *et al.* 2003). Other characteristics, apart from island origin, which are potentially important for the evolution of novel traits are area, available habitats, elevation and prevailing weather conditions. Isolation is another important factor as this determines how easy an island is to colonise and the type of species that are likely to colonise it. A small island alone in the ocean is only likely to be colonised by very vagile species whereas a larger island connected to the mainland by an island chain may eventually be colonised by many species (MacArthur & Wilson 1967).

The number of species and the order in which they arrive can be very important in island settings. A newly arriving species on a species-poor island can have a major impact on the balance of the ecosystem. This is particularly true of vagile continental species which are hypothesised to have high competitive ability as a result of having evolved in competitive environments (Mayr & Diamond 2001). One possible consequence of this is that widespread vagile species drive colonisation and that endemic species arise from them (Mees 1961; 1969). Hence species with continental distributions are responsible for the generation of biodiversity. Isolated islands have low rates of colonisation and extinction as under the theory of island biogeography extinctions balance arrivals at equilibrium (MacArthur & Wilson 1967). Although these isolated islands may produce many endemic species, islands have not traditionally been thought to be biodiversity sources (Cowie & Holland 2006; Orme *et al.* 2005). Recently however this view has been questioned and it has been suggested that the contribution of island fauna to continental regions may be underestimated (Bellemain & Ricklefs 2008; Filardi & Moyle 2005). This remains to be evaluated for many groups with both continental and insular distributions.

1.4 The requirements of a model system

Investigating questions relating to modes of evolution, ecological speciation and biogeography in the context of island colonisation requires an unusual study system. An ideal study system would demonstrate the following attributes: (i) replicated system where multiple invasions have resulted in closely related forms inhabiting different islands, (ii) a natural pattern of colonisation that has not been greatly affected by human intervention, (iii) substantial variation in morphology and ecology across taxa, (iv) both allopatric and sympatric patterns of occurrence across related forms, (v) rapid recent diversification such that the effects of extinction are minimised, and (vi) detailed knowledge of the species designation, taxonomy, and geographic distribution of all forms within the study region. From a practical point of view it is also necessary to be able to sample all forms with the region of study and quantify variation in traits of potential ecological relevance.

Taxonomic groups that satisfy all of these requirements are likely to be rare. One such group, however, are the Zosteropidae of the south west Pacific, which not only show the above characteristics but have also been repeatedly invoked in theories of evolutionary divergence and speciation (Coyne & Price 2000; Diamond & Marshall 1977; Grant 1965; Lack 1971; Mayr 1963; Moreau 1964). It is this group that is the focus for my work in this thesis.

1.5 The family Zosteropidae

The white-eyes are an almost exclusively tropical group of passerine birds (Mees 1957). Their phylogenetic affinities have been uncertain for a long time but a recent molecular study of passerine families suggests that they are most closely related to the babblers (Timaliidae) (Barker *et al.* 2004). There are 12 genera in the family of which the most speciose genus is the nominate *Zosterops*, which contains between 60 and 70 species according to Mees (1957), and in excess of 70 according to more recent treatments (Dickinson 2003; Sibley & Monroe 1990). *Zosterops* is therefore the second largest avian genus and its natural distribution covers the range of the entire Zosteropidae family from Africa eastwards to the Pacific Ocean islands of Western Samoa and Macquarie Island (Mayr 1965; Mees 1957). Many of the species in the family are remarkably similar morphologically, which makes it difficult to resolve relationships using phenotypic characters alone (Lack 1971; Mees 1969), but they are known to have speciated relatively rapidly for an avian clade with the age of the entire family placed at only two million years in some estimates (Moyle *et al.* 2009). This is approximately the same as the average time taken for neotropical sister taxa to diverge to the level of recognised species (Weir & Hey 2009).

The white-eyes are the most prolific island colonists of all the species-rich avian families (Baille 2001; Clegg *et al.* 2002b; Clements 2000; Moreau 1964). The Indo-Australian Zosteropidae, in particular, have a high frequency of insular occupation (Mees 1969) in comparison with the African Zosteropidae (Moreau 1967). There are also multiple cases of different *Zosterops* species inhabiting a single island, making them an obvious candidate group to focus questions about both speciation and character displacement (Coyne & Price 2000; Grant 1965). Moreover, they contain two wide-ranging superspecies groups which are potential candidates for drivers of speciation in the region, the *Zosterops griseotinctus* group (Mees 1957) and the *Zosterops lateralis* group (Mees 1969). The rate of extinction in the group prior to historical times is thought to be low and museum specimens survive of the recently extinct species (Steadman 2006).

Perhaps not surprisingly given their abundance in island avifanuas, white-eyes have been a classic study system for ideas about the role of islands in promoting speciation (Clegg 1999; Clegg *et al.* 2002b; Lack 1971; Mayr 1965; Mayr & Diamond 2001; Mees 1957; 1961; 1969; Moyle *et al.* 2009). Particularly they have been instrumental in forming ideas on island colonisation (Mayr 1963), ecological isolation (Lack 1971), the rarity of sympatric speciation (Coyne & Price 2000; Mayr 1942; Mayr 1963), interspecific competition (Diamond 1977) and founder effects (Clegg *et al.* 2002a; Mayr 1954). More recently, the south west Pacific Zosteropidae have proven valuable in investigating the roles of the microevolutionary processes that underlie population divergence and potentially result in speciation (Clegg *et al.* 2002a; Clegg *et al.* 2008; Estoup & Clegg 2003; Frentiu *et al.* 2007; Mayr 1954; Phillimore *et al.* 2008b; Robinson-Wolrath & Owens 2003; Scott *et al.* 2003).

1.5.1 The Zosterops of the south west Pacific

The *Zosterops* of the south west Pacific are ideal for this study, forming a replicated natural system where multiple invasions have resulted in related forms living in allopatry and where these forms display variation in morphology and ecology (Figure 1). Many islands in the region have two or even three forms of *Zosterops* showing diverse morphologies and behaviours. It is this pattern that has led to the group being invoked in discussions on the relative role of ecological speciation (Mayr 1947; Moyle *et al.* 2009; Warren *et al.* 2006) and sympatric speciation (Coyne & Price 2000; Emerson 2008). In addition, members of the *Zosterops lateralis* species complex have frequently colonised islands where a congeneric is already present (Mees 1969). The dispersal abilities of one subspecies (*Z. l. lateralis*) are well documented (Higgins *et al.* 2006; Mees 1969). This subspecies has colonised New Zealand and adjacent islands within recorded history (Mees 1969; North 1904) and the occurrence of distinctive endemic subspecies testify to older dispersal events (Mees 1969). It is this subspecies that has been invoked in theories of founder effects (Clegg *et al.* 2002a) and more recently used in a series of tests of microevolutionary mechanisms (Clegg *et al.* 2002b; Estoup & Clegg 2003; Scott *et al.* 2003).

While the origins of the Zosteropidae of the south west Pacific has usually been assumed to be in the Australasian region (Mees 1969), there has been considerable debate on the proximate origins for different species and populations. Lack (1971) suggested that the distribution of the insular Zosteropidae is not the result of extensive speciation and further colonisation on the islands but rather of multiple colonisations waves from the mainland. In contrast, Mayr (1967) suggested that species from New Caledonia (*Z. xanthochrous* and *Z. minutus*), Fiji (*Z. explorator*) and Vanuatu (*Z. flavifrons*) represent a single superspecies and therefore must also represent a separate radiation from Australia, rather than successive colonisation waves. Although the origins of *Z. lateralis* are less disputed, with both Mees (1969) and Mayr (1965) proposing that *Z. lateralis* originated in Australia and spread into the South Pacific in waves of colonisation, the specifics of direct versus island-hopping colonisation mechanisms remain unclear and the contribution of different subspecies to island speciation has been speculative. For instance, based on plumage similarities, Mees (1969) concluded that *Z. strenuus*, *Z. tenuirostris* (Norfolk Island) and *Z. l. tephropleurus* (Lord Howe Island) evolved not simply from *Z. lateralis* but specifically from the *Z. l. cornwalli* subspecies and that *Z. albogularis* (Norfolk Island) evolved from the *Z. l. lateralis* subspecies. Lack (1971) likewise suggested that *Z. inornatus* (New Caledonia) evolved from the widespread *Z. l. lateralis* based on its similar colouring.

The species and subspecies names that are used in this thesis are shown in Appendix 2.1, Table1 A and B. For the most part I follow the nomenclature of Mees (1957; 1961; 1969), particularly regarding the delineation of subspecies groups. In one case, however, I depart from the stance adopted by Mees (1961) and use the nomenclature preferred by Mayr (1965; 1967). Controversy exists over the application of the names *Z. kulambangrae*, *Z.ugiensis* and *Z. rendovae* to species in the Solomons (see discussions in Mees 1961; and Sibley & Monroe 1990). Mees applies the name *Z. rendovae* to the group of birds, from San Cristobal, Guadalcanal and Bougainville that Mayr (1967) refers to as *Z.ugiensis*. Mayr uses *Z. rendovae* for the species group, found on Kolombangara, New Georgia, Vangunu, Nggatokae, Rendova and Tetepare, which Mees names as *Z. kulambangrae*. Note that only the names are different, both authorities agree on the delineation of the two species. Here I use the nomenclature applied by Mayr (1967), which was also preferred in a recent molecular phylogeny of the Zosteropidae (Moyle *et al.* 2009). Thus the name *Z. rendovae* is applied to the species that actually occurs on Rendova, which I believe reduces the potential for confusion. Mayr regards *Z. r. rendovae* from Rendova and *Z. r. tetiparus* from Tetipari as a megasubspecies, distinct from *Z. r. kulambangrae*, and it may be that these two groups are better treated as full species. Moyle *et al.* (2009) agree that there is a clear split between *Z. r. kulambangrae*, on the one hand, and the other two subspecies on the other but they further imply that all three subspecies may be worthy of species status. Additionally their tree shows the northern and southern forms of *Z. ugiensis* as phylogenetically distinct strongly suggesting that this should be split into two species. Subspecific names remain the same as in Mees except that the nominate species of *Z. ugiensis* from San Cristobel, *Z. rendovae rendovae* in Mees, becomes *Z. ugiensis ugiensis* and the form of *Z. rendovae* on Rendova, *Z. kulambangrae paradoxa* in Mees, becomes *Z. rendovae rendovae*. I also include one species unknown to Mees and therefore not included in his monograph*, Zosterops gibbsi*, which was described only recently (Dutson 2008).

Although much work has been done on the Zosteropidae, and on those of the Indo-Australasian region in particular (Lack 1971; Mayr 1965; 1967; Mees 1957; 1961; 1969), it is notable that these earlier studies were not informed by a molecular phylogeny. Relationships within the Zosteropidae are known to be difficult to resolve using traditional taxonomic techniques due to the comparative morphological uniformity of the family (Lack 1971; Mees 1969). New techniques of tree building and tree analysis mean that these questions are worth revisiting in the light of a comprehensive molecular phylogeny and this is one of the key differences between my work and that which has gone before. This tree resolves relationships at a finer taxonomic level, roughly to subspecies, than the recent phylogenetic analysis by Moyle *et al.* (2009), which covers a broader range of species than I examine here but is therefore inevitably less complete in terms of the proportion of taxa included.

1.5.2 Modes of evolution in the Zosteropidae

Zosterops have been used as the basis for the study of founder effects in island populations (Clegg *et al.* 2002a; Grant 2002). Clegg (2002a) showed that founder effects have little effect on genetic diversity due to large founding populations but repeated island hopping leads to decline in genetic diversity. Reporting on this study, Grant (2002) concluded that multiple immigration events would obscure changes initially caused by founder effects.

I predict that Zosteropidae of the south west Pacific should follow the early-burst model of phenotypic and lineage divergence. This is because they are a young species group spreading into a new region of unoccupied niche space such that genetic and phenotypic (particularly of ecologically relevant morphological traits) change is expected to be rapid as new colonists evolve to exploit the novel environment. In particular, the formation of new species is expected to occur with arrival on an island, as implied from the number of endemics in the region. Following colonisation and niche-filling, rates of both speciation and phenotypic evolution should decline. An emergent outcome of the expected concurrent divergence in genes and traits is that most morphological change should be concentrated at speciation events and hence follow a form of punctuated speciation. I test these ideas in Chapter 4 of this thesis.

1.5.3 Origins and maintenance of sympatry in *Zosterops*

The Zosteropidae of the south west Pacific have been instrumental in forming many of the hypotheses about trait evolution (Lack 1971; Mayr 1965; Mayr & Diamond 2001). Island *Zosterops* are commonly sympatric and have often been used as examples of character displacement (Diamond *et al.* 1989; Grant 1972b). Some sympatric *Zosterops* are segregated by habitat either completely, such as on Kulambagra (Mayr & Diamond 2001) or partially, such as on Grande Terre where *Zosterops xanthochrous* is more numerous in the highlands and in the native forest whereas *Zosterops lateralis griseonatus* is more common in cultivated land and on the coastal lowlands (pers.obs, Mees 1969). More typically, however, sympatric *Zosterops* are thought to be separated along a size gradient with most islands having two or three species separated either on overall body size or bill size and shape (Grant 1968; Grant 1972a; Lack 1971; Mayr 1967; Mees 1957; 1961; 1969). The classic theory is that the earlier arriving species grew in size to exploit a greater range of foods which allowed a later arriving more typically sized individual to co-exist with it (Lack 1971). Sympatry is one of the themes that I return to several times in this thesis, quantifying first the phylogenetic affinity of sympatric species in Chapter 2 and then testing for non-random patterns of phylogenetic variation among sympatric forms in Chapter 3.

1.5.4 Biogeography of the Zosteropidae

The Zosteropidae of the south west Pacific are thought to have had an Australian origin and to have subsequently spread across the region following a relatively simple ‘stepping stone’ pattern of west to east colonisation.

Many insular white-eye species, such as *Zosterops inornatus* on Lifou or *Zosterops albogularis* on Norfolk Island, are single island endemics. Several single island endemics, such as *Zosterops splendidus*, are separated from other islands by water gaps of only a few kilometres. Others species such as *Zosterops xanthochrous* and the dark and yellow clades of *Zosterops flavifrons* (Chapter 2) are confined to a single archipelago but found on more than one island and have, in some cases, been shown to migrate between islands (Clegg & Phillimore 2010). At the extreme end the vagile species *Z. lateralis* has colonised many of the islands and archipelagos in the region. The *Z. lateralis* forms on many of these islands show distinct morphological differences from more typical mainland forms. There should be a correlation between distribution and wing length in the Zosteropidae.

I also test for evidence for the ‘island rule’, which predicts that insular forms of large species should become smaller whereas insular forms of small species should become larger (Forster 1964; van Valen 1973). Although the island rule remains controversial, especially in birds (Blondel 2000), Clegg and Owens (2002) demonstrated that birds with a body size of less than approximately 100g tend towards larger body size on islands and species larger than 100g tend towards smaller body size. Since the Zosteropidae are passerines and have a mass substantially less than 100g they are therefore expected to be, on average, larger on small land masses than they are on large ones. I also investigate the long-standing associated prediction that passerine birds on small islands tend to have more robust bills than their relatives on larger land masses (Grant 1965; Lack 1947), which again is thought to be a consequence of niche expansion (Blondel 2000; Clegg & Owens 2002).

1.6 Aims and predictions

I aim to construct a phylogenetic hypothesis of the relationships between island white-eye populations in the south west Pacific. This will be used to investigate questions regarding the taxonomic rank of these species and the history and timing of colonisation events in these islands. The focus will be the widespread and very subspecies rich *Z. lateralis* species complex. At the broader level the phylogeny will include samples from all the named species of Zosteropidae in the south west Pacific except *Z. santaecrucis* and *Woodfordia lacetosa*, which I was unable to obtain. This will enable me to test proposed colonisation timings of these islands and place the diversification that followed in a phylogenetic context.

I will then use this phylogeny to address the importance of modes of phylogenetic and phenotypic evolution and interspecific competition in *Zosterops* species that have colonised the islands of the south west Pacific. Based on the system and on the prevailing theories for each of these themes I make the following simple predictions for the Zosteropidae in each of the principal themes that I have indentified.

(i) Speciation was rapid and early in the history of the Zosteropidae with trait change concentrated at speciation events.

(ii) Sympatric *Zosterops* are unlikely to have speciated while in sympatry. Therefore they should prove to be more distantly related than expected by chance, to allow time for reproductive isolation to have developed in allopatry. They are also expected to occupy distinct ecological niches and therefore should be more distinct with respect to key morphologically traits than expected by chance.

(iii) The prediction for the effects of biogeography in the Zosteropidae is that colonisation routes are from the continents eastwards, that endemics lose dispersal ability, and that the geographical distribution of the islands is important for both speciation and trait evolution.

Chapter 2

Insular Evolution in Pacific Island Birds:
Multiple Colonisations and Mosaic Distribution

2.1 Abstract

Diversification of groups among islands and archipelagos is thought to play a significant role in determining large scale patterns in biogeography and biodiversity. Here I reconstruct the molecular phylogeny of a classic study system for insular evolution, the white-eyes of the south Pacific, and use this to address a series of long standing questions regarding insular evolution. Earlier taxonomic treatments of this group, based on phenotypic characters, have typically favoured a relatively simple model of insular phylogeography, including an Australian origin for the group, colonisation from west to east driven by wide spread vagile species and intra-archipelago, and possibly sympatric, speciation. My results conflict with several aspects of this simple model, with little support for an Australian origin, a simple pattern of west to east colonisation or for endemic species arising from currently widespread forms. Phenotypic variation is, therefore, typically a weak indicator of broad patterns of phylogenetic affinity. I also find no support for sympatric speciation, with co-occurring species typically being the result of multiple invasion waves. Instead, phylogenetic relationships suggest multiple invasions of the region with the most recent of these, the supertramp Silvereye (*Zosterops lateralis*) showing little phylogenetic structure. Taken together my results suggest that the history of colonisation is more complicated than the traditional scenario with the mosaic diversity of the region potentially the result of leapfrog colonisation events but most likely the result of repeated bouts of colonisation followed by extinction.

2.2 Introduction

The mechanisms of insular evolution and speciation and their impact on the world's biogeography and biodiversity in general and on birds in particular have been central to evolutionary thought since the earliest days of the discipline (e.g. Darwin 1859; Wallace 1891) and remain the subject of ongoing study (e.g. Grant & Grant 2008b; Losos & Ricklefs 2009a; Losos & Ricklefs 2009b; Mayr & Diamond 2001; Whittaker & Fernández-Palacios 2007). Inferences about insular colonisation and divergence patterns have traditionally been based on the distribution of morphologically determined species and subspecies (Mayr & Diamond 2001). However molecular studies are challenging traditional interpretations of the evolutionary history of insular forms, often revealing that current colonisation patterns have resulted from complex colonisation dynamics (Bellemain & Ricklefs 2008; Filardi & Moyle 2005). In a molecular study of Pacific monarchs, for instance, Filardi and Moyle (2005) found evidence of intra-archipelago divergence, colonization among archipelagos and colonization in the 'upstream' direction, that is from small remote islands to continents. This is a far more complicated pattern than the simple stepping stone colonisation and divergence pattern described by Mayr (1942) based on morphology and distributional patterns. Here I focus on three issues where molecular phylogenetic information can substantially improve our understanding of island colonisation dynamics and subsequent speciation events. These are (i) elucidating the predominant direction of colonisation, (ii) quantifying the frequency of intra-archipelago speciation and its role in generating regional biodiversity, and (iii) establishing whether sympatric distributions of congeners are the result of sympatric speciation or multiple colonisations.

Islands and archipelagos have been identified as hotspots of endemism (Orme *et al.* 2005; Stattersfield *et al.* 1998) and have been suggested to be of high importance to the generation of biodiversity through *in situ* speciation (Whittaker & Fernández-Palacios 2007). However exchange between continental and island faunas is thought to be largely biased in a "downstream" direction where waves of colonisation proceed from areas of higher to progressively lower biodiversity (i.e. from continental areas to large islands and from large islands to small islands), based on the well-documented gradual reduction of species diversity with increasing distance from continents (MacArthur & Wilson 1967; Mayr 1941; Wallace 1855). A predominance of downstream colonization is expected because of the vulnerability of small island populations to stochastic events (Sæther *et al.* 2007), that presumably result in frequent extinctions and increased niche availability (Diamond & Marshall 1977; Ricklefs 2003), the increased competitive ability, or faunal dominance, exhibited by species that have evolved in more highly competitive environments (Mayr & Diamond 2001) and the greater source pool of continents due to their area. Hence it is generally considered that species with continental distributions possess a greater potential for contributing to the generation of future biodiversity, via colonization of new areas, than insular species do. In this context, insular species, particularly those occurring on small isolated islands, are not considered as biodiversity sources. The distribution of faunal assemblages in the south west Pacific shows a strong bias for downstream colonisation in a west to east direction, from highly speciose regions of mainland Australia and New Guinea to successively more remote islands and archipelagos (MacArthur & Wilson 1967; Mayr 1942). Indeed, the distribution of avifauna in the region led Mayr (1941) to conclude that species exchange was so heavily biased in the downstream direction that no true Polynesian avifauna was recognisable. However recent molecular studies have found evidence of colonisation in the reverse “upstream” direction, including colonisation of continents by island forms (Bellemain & Ricklefs 2008; Filardi & Moyle 2005). Levels of upstream colonisation and the contribution of island fauna to continental regions may therefore be underestimated, and remains to be evaluated for many groups that have both continental and insular distributions.

The colonisation of archipelagos rather than single isolated islands sets the stage for intra-archipelago speciation, and may result in adaptive radiation due to the opportunity for sympatry following stages of allopatric divergence (Grant & Grant 2009; Ricklefs &

Bermingham 2008). The colonisation of isolated archipelagos has produced spectacular examples of intra-archipelago speciation and adaptive radiations, such as the Darwin’s finches (Geospizidae) of the Galápagos (Grant & Grant 2008b; Lack 1945; Lack 1947), the *Anolis* lizards of the Greater Antilles (Losos *et al.* 1998) and the silversword alliance (Compositae) of Hawaii (Baldwin & Sanderson 1998). In cases where there are significant barriers to movement between archipelagos, intra-archipelago diversification may be particularly important in generating diversity within a group (Mayr & Diamond 2001). Furthermore, these groups of sister-species may subsequently provide a rich source for colonists over a broader region if they go through stages of expansion, thereby producing complex patterns of colonization and divergence. One potential outcome that may arise out of complex colonisation patterns including intra-archipelago divergence and further rounds of colonization is that several species may arise from different subspecies within a larger species group. This means that reproductively isolated species evolve while their parent taxa remain part of a wider population that is not reproductively isolated. This situation has been suggested for several insular *Zosterops* species in the south west Pacific (Lack 1971; Mees 1969).

Although colonisation patterns can result in sympatrically distributed congeners, this condition can, theoretically, also arise via sympatric speciation. Coyne and Orr (2004) regarded the idea that speciation can occur within a freely interbreeding population as the most controversial aspect of speciation theory. High-profile papers have since shown cameo examples where sympatric speciation is the best explanation for the origin of certain species (Savolainen *et al.* 2006) but these are often the special case of host shifts by parasitic species (Feder *et al.* 2005; Sorenson *et al.* 2003). However despite widespread interest it is notable that very little evidence has been found for sympatric speciation in island birds (Coyne & Price 2000; but see Friesen *et al.* 2007). The alternative is that sympatric congeneric distributions on islands arise from multiple colonisation events. If these colonisations are sourced from the same population/species, then *in situ* speciation is required to occur prior to the next colonisation wave in order for a subsequent colonist to be reproductively isolated. Therefore, for highly vagile species that regularly colonise islands, speciation must occur quickly for sympatry to result, although it is possible that speciation could be completed via reinforcement.

Here I take a phylogenetic approach to examine island colonisation dynamics using the white-eyes (Family Zosteropidae) of Australia and the south west Pacific, a group that has emerged as a classic study system for insular evolution,(Clegg *et al.* 2002b; Diamond 1977; Diamond & Marshall 1977; Lack 1971; Mayr 1963; Moyle *et al.* 2009). The morphological similarity of many white-eye species renders the taxonomy of the family particularly difficult to resolve using phenotypic characters (Lack 1971; Mees 1969) and thus a molecular phylogenetic approach is essential for understanding species and population relationships and the colonisation dynamics that contributed the divergence patterns. The difficulties in resolving the taxonomy may be further complicated by the high rate of speciation, estimated at 2.24 taxa per million years (Moyle *et al.* 2009). This is remarkable in a vertebrate, more than twice that estimated for any other bird group studied to date (Baldwin & Markos 1998; Lovette *et al.* 2002; Weir & Schluter 2007) and only exceeded among published studies by certain groups from ‘continental islands’ such as montane lupins (Hughes & Eastwood 2006) and cichlids in African lakes (Meyer 1993; Seehausen 2000). The white-eyes are a highly speciose bird family, having more successful island colonisers than any other passerine group (Clegg *et al.* 2002b; Moreau 1964) with insular forms comprising 63% of currently recognised species and 78% of all subspecies (Baille 2001; Clements 2000). The high frequency of insular occupation is particularly evident in the Indo-Australian Zosteropidae, where the majority have insular distributions (Mees 1969), in comparison to the African Zosteropidae (Moreau 1967).

Within the region shown in Figure 2.1, white-eyes form a replicated natural system of ecologically and subtly morphologically variable forms, where multiple invasions have resulted in numerous cases of sympatric and allopatric distributions. One of the curiosities of the family Zosteropidae is that mainland forms are usually allopatric whereas it is common to find two or even three sympatric congenerics on even quite small islands (Lack 1971). In the south west Pacific, sympatric *Zosterops* distributions have frequently arisen following colonization by a member of the *Z. lateralis* species complex to an island where a congener was already present, while in other cases the origins of sympatry and dynamics of colonization are not clear (Mees 1969). Cases of sympatric species e.g. *Z. tenuirostris* and *Z. albogularis* on Norfolk Island, continue to be presented as potential instances of sympatric speciation (Emerson 2008), a possibility considered unlikely by Coyne and Price (Coyne & Price 2000) in their comparative study of sympatric island birds. An alternative explanation for sympatric congenerics is that the Zosteropidae are frequent and early colonists on islands and are able to adapt quickly to local conditions allowing successive colonisations to occupy niches that would be closed to them on the mainland (Mayr 1963). The fast speciation rates (Moyle *et al.* 2009) and excellent dispersal abilities (Higgins *et al.* 2006; Mees 1969; North 1904) of the Zosteropidae are consistent with this alternative.

Here I generate a phylogeny of the Zosteropidae of the south west Pacific using mitochondrial and nuclear DNA and building on previous work on *Z. lateralis* subspecies (Phillimore 2006) and *Z. flavifrons* from Vanuatu (Phillimore *et al.* 2008b). Moyle *et al.* (2009) investigated the expansion of the white-eyes on a hemispheric scale using an approach that included most currently recognised species but did not address intra-specific, inter-island relationships. Most other previous phylogeographic work on this family has focused on small geographic portions of the clades overall distribution, covering the Indian Ocean (Warren *et al.* 2006), Micronesia (Slikas *et al.* 2000a), Australia (Degnan & Moritz 1992; Degnan *et al.* 1999) and Pacific Ocean islands (Clegg *et al.* 2002a; Clegg *et al.* 2002b; Estoup & Clegg 2003). This is the largest phylogeographic study to date, combining a greater breadth of species sampled with intensive intraspecific sampling of populations from different islands.

This phylogeny will enable me to use the Zosteropidae to test a number of questions about insular biogeography. First I investigate if the predominant direction and incidence of colonisation; specifically whether the origins of island species are continental or insular, whether there is evidence for upstream versus downstream colonisation and if this occurred in multiple colonisation waves. If *Zosterops* diversity in the south west Pacific is mostly due to colonisation waves from mainland Australia, rather than separate insular radiations, then a phylogeographic signal of distinct but geographically overlapping clades would be expected. If the origins of the Zosteropidae of the region are continental and descendents of the ancestral form survived in the original location, then Australian taxa should be basal. If the origins are insular the pattern will be more complex. If migration waves spread from west to east (downstream) then more easterly distributed species should generally be younger. If there was more than one colonisation wave, this pattern should appear in successive layers, each with older taxa in the west and younger in the east.

Second I will examine more complex colonisation scenarios. I test the prevalence of intra-archipelago speciation and its role in generating regional biodiversity through the secondary colonisation of other areas. Intra-archipelago speciation would be supported by the occurrence of sister species within the same archipelago. If these species groups have not been the source for new species in other areas, then the sister-species within the archipelago will form a monophyletic group. If new species on neighbouring islands are sourced from an archipelago, the new species should be more closely related to the archipelago group than to the mainland or other groups. In particular, upstream dispersal has occurred, some young species whose sister species are on eastern islands should appear on western islands or on the mainland. I then investigate if endemic species have arisen from a subset (or subspecies) of a widespread species. If endemic species have arisen from within widespread species then clades of widespread species should be paraphyletic and include lineages recognised as distinct species.

Third I will test whether there is support for sympatric speciation as an explanation for sympatric forms of the Zosteropidae. If sympatric speciation has occurred then sympatric taxa on single islands should form monophyletic clades.

In addition to the main questions I will also examine whether island populations of the widespread *Z. lateralis* show phylogenetic structure. If described subspecies form monophyletic clades this would be suggestive of a reduction in dispersal propensity in some populations. Finally, I test if phenotypic classification of species and subspecies agree with phylogenetic clades. If phenotypes describe phylogenetic clades then the topography of the molecular phylogeny should correspond to traditional morphological taxonomy. In particular I focus on *Z. flavifrons* from the Vanuatu Archipelago to examine the congruence between phylogeny and plumage types and subspecies (Mayr 1942; Murphy 1929).

2.3 Methods

2.3.1 Taxon sampling

My overall sampling strategy was to obtain samples from as many species and subspecies as possible of the Zosteropidae (following the classification of Mees 1969) of a core region bounded by Australia to the west, Chatham Island and Fiji to the east, the Santa Cruz Islands to the north and Tasmania and New Zealand to the south (Figure 2.1). This region was selected as the range of the widespread *Z. lateralis* species complex, which provided a comparison with insular endemics.

Particular attention was paid to sampling *Z. lateralis*, which has been the subject of several previous studies (Clegg *et al.* 2002a; Clegg *et al.* 2002b; Clegg & Phillimore). According to Mees (1969) the *Z. lateralis* species complex consists of 18 morphological types, including five distinct species, distributed in Australia and the south west Pacific. All species within this complex, including two probably extinct forms (*Z. strenuus* and *Z. albogularis*), were sampled. In addition thirteen of the fourteen subspecies of *Z. lateralis* recognised by Mees

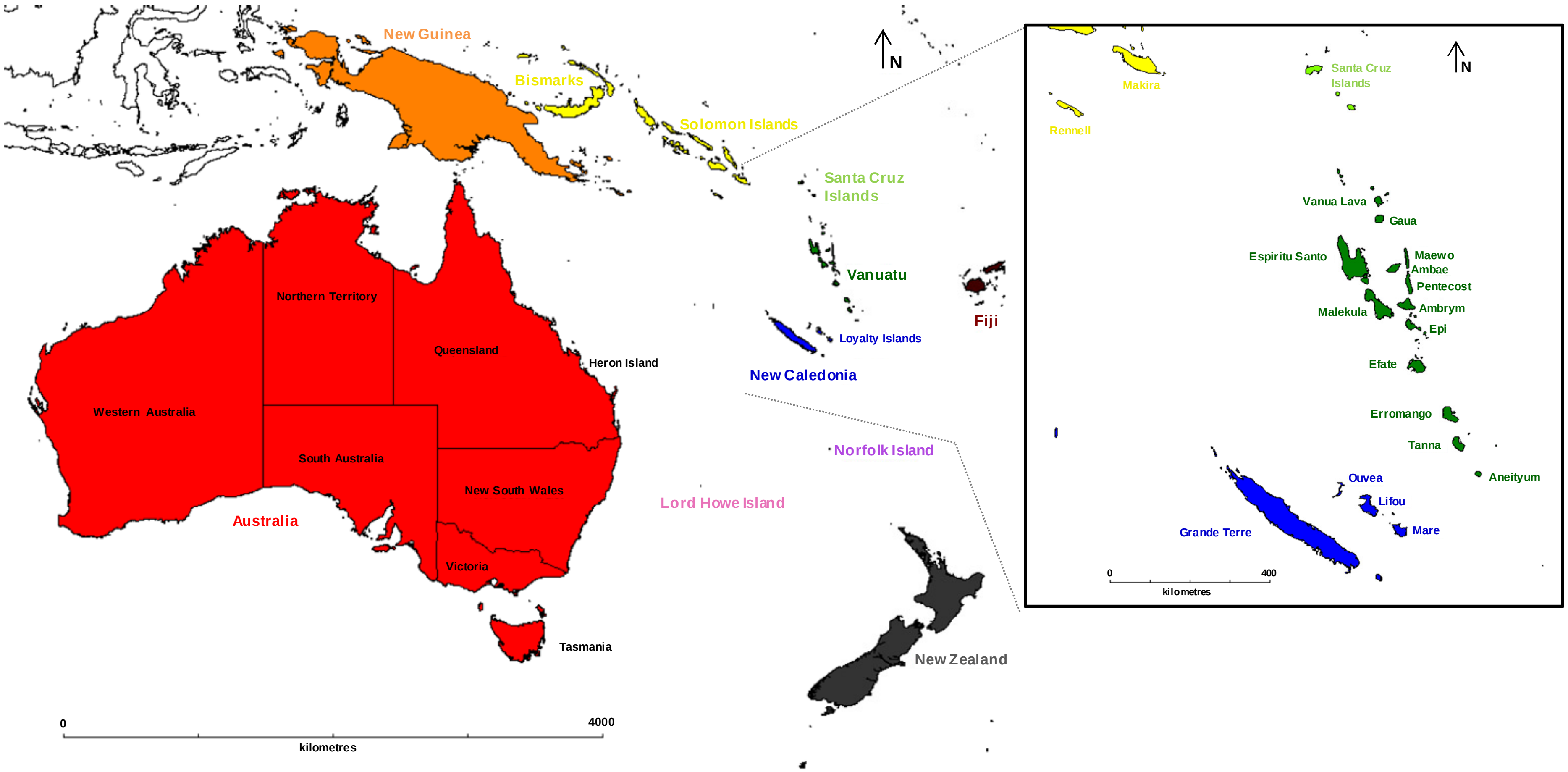


Figure 2.1. The study region of interest in the South West Pacific. Australia (Red) and New Guinea (Orange) are traditionally considered to be likely sources of the regions avifauna. The Bismarks and the Solomons (Yellow) are potentially important in west to east migration. The Santa Cruz Islands (Light Green), Vanuatu (Dark Green), New Caledonia (Blue), Norfolk Island (Purple), Fiji (Brown), Lord Howe Island (Pink) and New Zealand (Dark Grey) are the principal islands in the study. The insert names individual islands in the New Caledonian, Vanuatu and Solomon archipelagos.

(1969) were sampled. The omitted subspecies *Z. l. valuensis* is found only on Mota Lava in Vanuatu and is considered by Mees (1969) to have diverged peripatrically and recently from nearby *Z. l. tropica* populations. *Z. l. tephropleurus* is sometimes regarded as a distinct species (Clements 2000; Hindwood 1940; Sibley & Monroe 1990) but here retain it as a subspecies. Note that the abbreviation *Z. l.* always refers to *Zosterops lateralis*. Potentially confusing species, such as *Z. luteus*, are written in full. Field sampling was supplemented with museum material provided by the Natural History Museum at Tring (hereafter referred to as Tring), to produce a virtually complete representation of the forms of Zosteropidae in the region. This enabled me to add to the phylogeny species that are either extremely difficult or, in the case of the two extinct species, impossible to collect by means of fieldwork. Sampling covered an extensive geographic area including mainland Australia, Australian islands, New Zealand, New Caledonia, Vanuatu and Fiji (Table 2.1).

Live specimens were caught in mist-nets during field trips I made to New Caledonia and Vanuatu covering a total duration of eight months. Blood samples were collected by exposing the brachial vein of each bird and piercing it with a fine gauge needle (26 G, 0.45 x 10 mm). The resulting blood droplet was drawn up with a capillary tube and transferred to a microfuge tube containing EDTA buffer or 90% ethanol (Clegg *et al.* 2002b; Clegg & Phillimore 2010; Phillimore *et al.* 2008b). For a subset of samples a drop of blood was also absorbed on a filter paper which had been prepared with a drop of 0.5 M EDTA (Clegg & Phillimore; Petren 1998). My samples were combined with those collected by other field workers during previous trips.

As multiple individuals are required if relationships between closely related species are to be accurately recovered (Melnick *et al.* 1993; Ruano *et al.* 1992), I obtained toe-pad samples from four museum specimens where possible. However small numbers of voucher specimens meant that in some cases it was only possible to obtain two. In addition, because the DNA of some of these specimens was old and therefore degraded, it proved impossible

Table 2.1.The species and subspecies sampled, their origin and the number of mitochondrial and nuclear regions sequenced. Collectors were Dr. Sonya Clegg (SMC), Dr. Albert Phillimore (ABP) and Richard Black (RAB). *Z. rennellianus* was kindly provided by C. Smith (Burke Museum). Abbreviations are New Caledonia (N.C.), north (N), south (S), east (E) west (W) and central (C).

Part A: Modern blood samples

Taxon			**Collection details**			**No. Of samples sequenced**			
Genus	**species**	**subspecies**	**Location**	**Date**	**Initials**	**CB1**	**ND3**	**ATPase**	**TGFB2**
Zosterops	*flavifrons*	*brevicauda*	Santo	2004/06	APB/SMC	5	5	3	5
Zosterops	*flavifrons*	*efatensis*	Efate	2004/06	APB/SMC	5	5	2	5
Zosterops	*flavifrons*	*efatensis*	Erromango	2004	ABP	4	4	1	4
Zosterops	*flavifrons*	*flavifrons*	Tanna	2004	ABP	5	5	1	5
Zosterops	*flavifrons*	*gauensis*	Gaua	2004	ABP	5	5	2	4
Zosterops	*flavifrons*	*macgilivrayi*	Malekula	2004	ABP	5	5	3	5
Zosterops	*flavifrons*	*majuscula*	Aneityum	2004	ABP	5	5	2	5
Zosterops	*flavifrons*	*perplexa*	Ambae	2006	SMC	5	5	5	5
Zosterops	*flavifrons*	*perplexa*	Ambrym	2006	SMC	5	5	4	5
Zosterops	*flavifrons*	*perplexa*	Epi	2004	ABP	4	4	1	4
Zosterops	*flavifrons*	*perplexa*	Maewo	2006	SMC	5	5	5	5
Zosterops	*flavifrons*	*perplexa*	Pentecost	2006	SMC	5	5	2	5
Zosterops	*flavifrons*	*perplexa*	Vanua Lava	2004	ABP	4	4	1	4
Zosterops	*inornatus*	-	Lifou	2006	RAB	5	5	3	5
Zosterops	*lateralis*	*chlorocephalus*	Heron	1996/97	SMC	5	4	0	1
Zosterops	*lateralis*	*familiaris*	Brisbane	1996	SMC	4	4	0	2
Zosterops	*lateralis*	*griseonatus*	North N.C.	2006	RAB	5	4	5	5
Zosterops	*lateralis*	*griseonatus*	South N.C.	2006	RAB	5	4	5	5
Zosterops	*lateralis*	*lateralis*	New Zealand	1997	SMC	2	2	1	2
Zosterops	*lateralis*	*lateralis*	Norfolk	1998	SMC	2	2	1	1
Zosterops	*lateralis*	*lateralis*	Tasmania	1996/97	SMC	3	4	0	0
Zosterops	*lateralis*	*melanops*	Lifou	2006	RAB	5	4	4	5
Zosterops	*lateralis*	*nigrescens*	Mare	2006	RAB	5	5	5	5
Zosterops	*lateralis*	*tropica*	Ambae	2006	SMC	3	3	3	3
Zosterops	*lateralis*	*tropica*	Gaua	2004	ABP	3	2	1	3
Zosterops	*lateralis*	*tropica*	Pentecost	2006	SMC	5	5	5	5
Zosterops	*lateralis*	*tropica*	Santo	2004/06	ABP/SMC	6	7	4	8
Zosterops	*lateralis*	*tropica*	Vanua Lava	2004/06	ABP/SMC	3	4	2	4
Zosterops	*lateralis*	*vatensis*	Ambrym	2004	ABP	5	5	5	5
Zosterops	*lateralis*	*vatensis*	Efate	2004/06	ABP/SMC	5	5	3	5
Zosterops	*lateralis*	*vatensis*	Epi	2004	ABP	4	4	1	4
Zosterops	*lateralis*	*vatensis*	Erromango	2004	ABP	3	4	1	4
Zosterops	*lateralis*	*vatensis*	Malekula	2004	ABP	5	5	1	5
Zosterops	*lateralis*	*vatensis*	Tanna	2004	ABP	5	4	2	5
Zosterops	*minutus*	-	Lifou	2006	RAB	5	5	4	4
Zosterops	*rennelianus*	-	Rennell		C.Smith	1	1	1	0
Zosterops	*tenuirostris*	-	Norfolk	1998	SMC	2	2	1	2
Zosterops	*tephropleurus*	-	Lord Howe	1998	SMC	2	2	1	2
Zosterops	*xanthochrous*	-	Mare	2006	RAB	5	5	5	5
Zosterops	*xanthochrous*	-	North N.C.	2006	RAB	5	5	5	5
Zosterops	*xanthochrous*	-	South N.C.	2006	RAB	5	5	5	4

Part B: Museum toepad samples

Taxon			**Collection details**			**No. Of samples sequenced**			
Genus	**species**	**subspecies**	**Location**	**Date**	**Museum**	**CB1**	**ND3**	**ATPase**	**TGF-B**
Woodfordia	*superciliosa*	-	Rennell	1954	Tring	2	2	0	0
Zosterops	*albogularis*	-	Norfolk	1939	Tring	4	4	0	0
Zosterops	*explorator*	-	Fiji	1898/1966	Tring	2	2	0	0
Zosterops	*gibbsi*	-	Vanikolo	1997	Tring	1	1	0	0
Zosterops	*lateralis*	*flaviceps*	Fiji	1888/98	Tring	4	2	0	0
Zosterops	*lateralis*	*gouldi*	CS Australia	1965/66	Tring	4	4	0	0
Zosterops	*lateralis*	*halmaturinus*	E,SE Australia	1965	Tring	2	2	0	0
Zosterops	*lateralis*	*ramsayi*	Australia	1964	Tring	4	4	0	0
Zosterops	*luteus*	*balstoni*	W Australia	1966/69	Tring	3	3	0	0
Zosterops	*luteus*	*luteus*	N Australia	1964/69	Tring	5	5	0	0
Zosterops	*strenuus*	-	Lord Howe	1919	Tring	4	4	0	0

to extract usable sequences from them. Consequently for some species I was only able to use sequence from one or two individuals in the phylogeny. The Tring samples used and the regions they were sequenced at are summarised in table 2.1 (Part B) and full details of all the individuals sequenced can be found in Appendix 2.1 (Appendix Table 2.1.A).

The phylogeny was supplemented with sequences obtained from GenBank (accession numbers given in Appendix 2.1, Appendix Table 2.2.B) to place the south Pacific *Zosterops* into a wider geographic context of species relationships. These included African *Zosterops* sequenced at the *cyt-b*, ND3 and ATPase regions (Warren *et al.* 2006), and Asian *Zosterops* sequenced at the ND3 region (Moyle *et al.* 2009).

2.3.2 DNA extraction

DNA extraction from fresh blood (modern) samples followed an ammonium acetate precipitation method (Nicholls *et al.* 2000). All ancient DNA work was performed within an Ultraviolet (UV) cabinet in a laboratory free of PCR product. All work surfaces and plastics, including pipettes, were cleaned with bleach and sterilised with UV radiation daily. Double distilled water was autoclaved and also sterilised with UV-radiation. DNA was extracted from the museum toe pad samples using an adapted Qiagen DNeasy Kit (Qiagen Ltd., Crawley, UK). The toe pad sample was finely sliced to aid digestion, placed in a microcentrifuge tube with 180µl Buffer ATL, 20µl 1M DTT and 20µl of Proteinase K, vortexed and incubated at 56^{0}C for twelve hours. I followed standard protocol for ancient DNA extraction described by Qiagen, except that where the protocol calls for a 3 minute centrifuge at 14000rpm I centrifuged at 13000rpm for 3 minutes and 30 seconds and the amount of buffer was reduced from 75µl to 50µl in the in the final stage of the process.

Quantification of DNA was performed using a Nanodrop 8000 (Thermo Fisher Scientific, 2009). Extractions were diluted with Siegen Buffer AE to 20ng/ul for blood sample extractions and 10ng/ul for toe-pad sample extractions.

2.3.3 DNA amplification

Three mitochondrial regions and one nuclear DNA region were amplified via polymerase chain reaction (PCR). These regions were selected to complement published *Zosterops* sequences (Moyle *et al.* 2009; Phillimore 2006; Phillimore *et al.* 2008b; Warren *et al.* 2006).The three mitochondrial regions were: a 308 base pair (bp) fragment of *cytochrome b* (primers CB1 and CB2, (Palumbi 1996)); a 393 bp fragment of the ND3 gene (primers L10755 and H11151, (Chesser 1999)); and a 951 bp fragment of ATPase 6 and 8 (primers CO2GQL and CO3HMH, (Phillimore 2006)). The nuclear DNA region was a 582 bp fragment of Introns 5 and 6 of the TGFB2 gene (primers TGF5 and TGF6, (Primmer *et al.* 2002)).

Modern DNA samples were amplified at all mitochondrial and nuclear regions. Amplifications were performed in 20µl volumes. Each PCR included 20ng of template DNA, 0.5µM of each primer, 0.25µM dNTPs, 1x reaction buffer (Bioline), 2mM $MgCl_2$, 0.1 units of *Taq* Polymerase and was made to volume with water. A drop of oil was added to the well. The thermal cycling reactions were performed in a PCR machine (MJ Research DNA engine Tetrad) with the hot lid off.

Restrictions on the amount of material and difficulties with sequencing meant that ancient DNA samples were amplified at the *cytochrome b* and ND3 regions only. Due to the degraded nature of DNA sourced from museum samples, additional primers were designed to amplify each region as two smaller sized fragments. I designed new primers (Table 2.2) to be used in combination with the standard forward and reverse primers (Table 2.3). Ancient DNA samples were amplified using a Qiagen multiplex kit (Qiagen Ltd., Crawley, UK). A primer mix of forward and reverse primers (each at 5uM final concentration) and double distilled autoclaved water was prepared in the ratio 1:1:23. An equal volume of the Qiagen master mix was added to the primer mix to create the final master mix. Each reaction contained 10ng DNA template (evaporated in each well) and 15 µl of the final mastermix was then added to each well. The reaction plate was sealed with a silicon lid that had been cleaned with bleach, dried and UV-sterilized. Thermal cycling was performed with a heated lid to minimise evaporation.

Table 2.2. New primers designed to amplify smaller sections of the cyt-b and ND3 regions. The primers were paired with the forward and reverse already available for CB1 (Palumbi 1996) and ND3 (Chesser 1999).

Name	Sequence	Annealing Temp (°C)	Used with
CB1strR	GCAGATGAAGAAGAATGAAG	52.55	CB1
CB1endF	ACCTAGCCTTTGCTTCAG	53.09	CB2
ND3strR	ATGGGAGTGGAAGGAGTAG	54.63	L10755
ND3endR	TTTCTTCCTAGTAGCAATCC	51.43	H11151

Thermocycling conditions varied for different primer sets (see Table 2.3 for variations). An initial denaturation of 94^0C for 180 seconds was followed by 35 or 40 cycles of: 94^0C for 30 seconds, annealing temperature and duration as specified, 72^0C for 35 to 45 seconds, followed by a final incubation at 72^0C for 600 seconds

The quantity of PCR product was determined by comparison against a standardized 100 bp ladder (Bioline) on a 1.5% agarose gel, stained with SYBR® Safe (Invitrogen Corporation). Products were diluted for sequencing to approximately 3.3ng per 100bp of PCR fragment. PCR products were cleaned prior to sequencing using the ExoSAP (USB Corporation) protocol, where 2µl of ExoSAP was mixed with 5µl of each PCR product and incubated in a sealed plate on a PCR thermocycler at 37^0C for 15 minutes then 80^0C for 15 minutes.

Cycle sequencing reactions were conducted in 10 µl total volumes, comprising 1.0µl BigDyeTerminator mix (v3.1 was used for ATpase 6 & 8 and v1.1 for all other sequences), 1.5µl of sequencing dilution buffer, 1.6µl of Primer (0.5µM), 4.9µl of ddH_2O and 1.0µl of the cleaned DNA template. A control plasmid (pGEM-3Zf(+)) and forward primer (-21 M13) were included on each plate as a positive control. The cycle sequencing profile included an initial denaturation of 96^0C for 60 seconds, followed by 30 cycles of 94^0C for 10 seconds, 50^0C for 5 seconds and 60^0C for 240 seconds. The PCR machine hot-lid was set to on.

Table 2.3. PCR thermal cycling conditions for the primers. † denotes the temperature and duration of annealing. ‡ denotes the duration of the elongation step. The total number of cycles used is also given for each primer. ¥ denotes the primers used to split the cyt-b and ND3 regions into smaller sections. The newly designed primers were paired with the forwards and reverses already designed for CB1 (Palumbi 1996) and ND3 (Chesser 1999).

Primer Pair	Annealing†		Elongation duration‡	
	(°C)	(Seconds)	(Seconds)	# of cycles
L10755 & H11151	54	30	35	35
CB1 & CB2	52	30	40	40
C02GQL & C03HMH	56	30	45	35
TGFB2	64	30	45	35
CB1 & CB1strR¥	55	45	40	40
CB1endF & CB2¥	55	45	40	40
L10755 & ND3strR¥	54	30	35	35
ND3endF &H11151¥	54	30	35	35

Cycle sequencing products were precipitated using a standard ethanol precipitation. Briefly, 2µl of 125mM EDTA, 2µl 3M sodium acetate (pH 5.2), 10µl ddH_2O and 52.5µl 95% ethanol were added to the 10µl sequencing reaction. Following a 15 minute incubation period in dark conditions, the samples were centrifuged for 15 minutes at 3220g, the liquid removed and then centrifuged upside down for 30 seconds at 190g. The DNA pellets were washed by adding 70% ethanol, centrifuging for 5 minutes at 3220g and removing the liquid as described earlier. The plate was allowed to dry for two minutes before 10µl Formamide was added to each well and mixed. The plate was then sealed with a clean rubber Septa and placed on a PCR block at 95^{0}C for three minutes to denature the DNA. The products were then run on an ABI 3730 sequencer (Applied Biosystems).

Bases were scored using the program Codon Code Aligner version 3.7.0 (CodonCode Corporation, USA). Sequences were aligned by Clustal Analysis, using the default parameters, and by eye using the program BioEdit version 7.0.9 (Hall 1999).

2.3.4 Model Testing

The best model (lowest AIC) of sequence evolution for a given gene was determined using jModeltest v. 0.1.1 (Guindon & Gascuel 2003; Posada 2008). Trees were constructed using neighbour joining and model choice was based on minimisation of the Akaike Information Critera. Each of the three mitochondrial genes was tested separately and the models used both for the individual trees and within the partitioned multi-gene trees. As not all of the models tested were available as standard in the BEAST program that I used for phylogenetic reconstruction (Drummond & Rambaut 2007), I selected the available model with the lowest AIC score (Sullivan & Joyce 2005).

2.3.5 Phylogenetic construction

In order to generate as complete a tree as possible, sequence from all three genes was considered together in an analysis that included all taxa for which there was sequence for at least one gene. Hereafter this tree is referred to as the ‘All Evidence Tree’. For all trees, if multiple individuals shared the same haplotype only a single representative was included.

Additionally phylogenetic trees were reconstructed separately for each gene individually. Partitioned analyses were also conducted by combining information from the *cyt-b* and ND3 genes, hereafter referred to as the ‘Two Gene Tree’, and from the *cyt-b*, ND3 and ATPase 6 & 8 genes, hereafter referred to as the ‘Three Gene Tree’. In the partitioned analyses parameters were allowed to vary between the different genes and only samples with sequence for all the genes in question were used.

Using substitution models identified in jModeltest, a Bayesian relaxed clock inference approach (Drummond *et al.* 2006) was implemented in BEAST v. 1.4.8 (Drummond & Rambaut 2007) and UPGMA was used to construct a starting tree and a birth-death prior was placed on branching times (Gernhard 2008). A relaxed clock approach was used because it allows the tree to be rooted without an outgroup (Drummond *et al*. 2006). I used a lognormal distribution to model rate variation across adjacent branches. Substitution was assumed to occur at a rate of 1% per lineage per million years (Weir 2006; Weir & Schluter 2008). For each analysis four independent chains were run for 20 million generations. The four runs generated log and tree files which were combined using LogCombiner v1.4.8 (Drummond & Rambaut 2007). Two million generations were removed from each chain as burn-in. Tracer v. 1.4.1 was used to assess convergence and whether the four chains were sampling from the posterior distribution. In all cases the chains converged and the combined results for the four independent chains had an estimated sample size (ESS) of greater than 200 for all parameters. TreeAnnotator v. 1.4.8 (Drummond & Rambaut 2007) was used to estimate the maximum clade credibility tree across the posterior distribution of 14400 trees.

2.3.6 Predictions and tests

The Predictions of this study are therefore as follows:

- If the *Zosterops* of the south west Pacific are the result of a single ancient colonisation, they should form a single monophyletic clade in the phylogeny.
- If the origins of the Zosteropidae of the region are continental and descendents of the ancestral form survived in the original location, then Australian taxa should be basal. If the origins are insular the pattern will be more complex.

- If migration waves came from west to east then more easterly species should generally be younger. If there was more than one wave this pattern should appear in successive layers, each with older taxa in the west and younger in the east. In the extreme version of this scenario, where each species originates in Australia and then colonises an island, Australian taxa would appear to be recent and the tree would appear unbalanced.
- If intra-archipelago speciation is prevalent then all the species in an archipelago should fall within the same clade. If there is back stream migration some young species whose sister species are on eastern islands should appear on western islands or on the mainland.
- If endemic species have arisen from within widespread species then clades of widespread species should be paraphyletic and include lineages recognised as distinct species.
- If sympatric speciation has occurred then sympatric species endemic to a single island should be sisters.
- If recent colonists diverge rapidly at the mitochondrial DNA level then described subspecies of *Zosterops lateralis* should form monophyletic clades within the phylogenetic tree.
- If phenotypes describe phylogenetic clades then the topography of the molecular phylogeny should correspond to traditional morphological taxonomy.

2.4 Results

I obtained sequence data from a region of *cyt-b* that ranged in size from 287 to 308 bp, a region of ND3 that ranged in size from 195 to 393 bp, a region of ATPase 6 & 8 that ranged in size from 573 to 951 bp and a region of TGFB2 that ranged in size from 560 to 958 bp (See attached CD for sequence files).

For *cyt-b* 217 sites (70%) were invariable and 76 sites (25%) were parsimony-informative. For ND3 the corresponding figures were 223 (57%) and 212 (34%) and for ATPase 6 & 8 they were 544 (56%) and 247 (34%). The nuclear gene, introns 5 and 6 of the TGFB2 gene, despite the fact that it evolves relatively quickly for an avian intron (Primmer *et al.* 2002) unfortunately proved to have no useful variation in the Zosteropidae. Neither subspecies or species group together on the tree, as shown by the phylogeny in Appendix 2.3., and no nodes have a posterior support of greater than 0.2. This is not surprising given that the sequences were almost all identical and the variation was not species specific.

2.4.1 The phylogeny of the Zosteropidae – Origins of the main clades

The three single gene trees for *cyt-b* (Appendix Figure 2.2.A), ND3 (Appendix Figure 2.2.B) and ATPase 6 & 8 (Appendix Figure 2.2.C) show broad structural agreement with one another although in the single gene trees relatively few nodes have strong Baysian posterior support (>90%). Well supported nodes are consistent across trees. Some individual samples do appear in slightly different places in different trees, particularly in the single gene genes however these always have poor Bayesian support and I do not attempt to draw major conclusions from them. In the results and discussion presented below, I generally focus on the ‘All Evidence Tree’ (Figure 2.2) to interpret phylogenetic relationships with support from the ‘Two Gene Tree’ (Appendix Figure 2.2.D) and the ‘Three Gene Tree’ (Appendix Figure 2.2.E) due to the higher Bayesian support in these trees.

The African Zosteropidae have reasonable Bayesian support as monophyletic in the All Evidence Tree (Bayes support = 0.85) and this deep split with the rest of the family was evident in all phylogenies. The positions of the Asian and Indian Ocean *Zosterops* groups are less consistent across trees, however both groups show deep divergence from the south west Pacific Zosteropidae. The All Evidence Tree has strong Baysian support for the Asian group as the sister group south west Pacific Zosteropidae. These two groups have strong support together as a monophyly (Bayes support = 0.93) and both groups are themselves strongly supported as monophyletic. Where a monophyletic clade has high support and consists of two further highly supported nodes these two lower clades can be considered sister groups. Bayes posterior support is 1 for the Asian group and 0.96 for the south west Pacific.

2.4.2 Origins of the south west Pacific Zosteropidae – Insular or continental affinities

None of the phylogenetic reconstructions indicate that mainland Australian forms are basal to the south west Pacific *Zosterops* species, as would be expected if the origins of that clade were continental. The south west Pacific clade itself is composed of three distinct clades. The first of these, which contains the New Caledonian endemics, I will term the ‘New Caledonian Clade’. I will term the second the ‘*Zosterops lateralis* Clade’ because it contains the many forms of that species. The third I will term the ‘Vanuatu Clade’ because it contains the majority of forms of the Vanuatu endemic *Zosterops flavifrons*. The exception is *Z. f. majuscula* and the All Evidence Tree supports the suggestion of Phillimore *et al.* (2008b) that this a cryptic species and evidently not part of the *Z. flavifrons* clade. Phillimore *et al.* (2008b) suggested that the affinities of the Aneityum *Zosterops* lie with *Z. lateralis*, although the weak support for this affinity was acknowledged. The ‘New Caledonian Clade’ is well supported as a monophyly in the All Evidence Tree (Bayes support = 1) as is the main part of the ‘Vanuatu Clade’ (Bayes support = 1). The partitioned trees both show strong support for the monophyly of *Zosterops lateralis* (Bayes support > 0.9). However the relationships between the clades are unclear as are the true positions of particular species, notably *Zosterops explorator*, *Zosterops luteus* and *Z. f. majuscula*.

2.4.3 Waves of colonisation West to East

The lack of support for a continental origin is not consistent with a single wave of colonisation from the mainland from west to east. However there is some phylogenetic signature of downstream colonisation from west to east and north to south. Two species from islands upstream, that is north and west, of Vanuatu are sisters to the two colour clades of *Z. flavifrons* clade. *Z. gibbsi*, from Santa Cruz, is basal to the dark clade and *Woodfordia superciliosa*, from the Solomon island of Rennell, is sister to the yellow clade. Both relationships are well supported in the All Evidence tree. In the larger ND3 gene (Appendix 2.2.B) there is support that Solomon island species from further west again, *Z. metcalfi*, from Choisel and *Z. stresemanni*, from Malita are part of a monophyly that includes the Vanuatu clade (Bayes support = 0.92). The All Evidence Tree suggests, with strong posterior support, that this whole south Pacific group is the sister group of Asian species from further west again. This would seem to be consistent with a pattern of west to east migration.

Nevertheless, overall the patterns are too complex to conform to a simple west to east model of colonisation. For example *Z. rennellianus* from Rennell in the Solomons appears as the sister species of *Z. xanthochrous* from New Caledonia. Since these species are separated by several archipelagos and numerous other species this a pattern inconsistent with a single simple east west dispersal event. The ND3 gene in isolation suggests that *Z. explorator* and *Z. luteus balstoni* may be within a group of Asian species that also includes the majority of Solomon Island white-eyes and *Z. olegineus* from Yap and *Z. cinerus* from Palau Island (Appendix 2.2.B). If so this would add to the general pattern of different phylogenetic clades having geographically overlapping distributions, a pattern that suggests several separate waves of colonisation. On a smaller geographic scale Phillimore *et al.* (2008b) concluded that the genetic structure of *Z. flavifrons* suggests that this morphospecies is the perhaps result of three or perhaps even four separate migrations into the archipelago. Certainly it is clear from the phylogeny that it does not form a single superspecies with *Z. xanthochrous*, *Z. minutus* and *Z. explorator* as suggested by Mayr (1967). These four species are well separated on the tree with only *Z. xanthochrous* and *Z. minutus* found in the same clade and even then these two are not sister species as, unexpectedly, *Z. rennellianus* from the Solomon Islands is well supported as the sister species to *Z. xanthochrous* in the Three Gene Tree (posterior support = 0.91). This New Caledonian clade, distinct from those previously described (Mees 1969), may represent further evidence for multiple waves of colonisation.

2.4.5 Intra-archipelago speciation and upstream migration

Evidence for intra-archipelago speciation requires the occurrence of species from the same island groups to appear together within well supported clades. Although two archipelagos might appear to match this criterion they are clearly not true examples of intra-archipelago speciation. The dark and yellow clades of *Z. flavifrons* from Vanuatu are found in the same clade and the New Caledonian species *Z. xanthochrous, Z. inornatus* and *Z. minutus* are also in a single clade. However, these clades also contain birds from islands outside these archipelagos and the species from the same archipelago are often not sisters. The Vanuatu clade that encompasses three of the four *Z. flavifrons* subclades, also includes *Z. gibbsi* from the geographically adjacent Santa Cruz Islands and *W. superciliosa*, from Rennell Island. The more basal position of these latter two species within the clade does not support a scenario of recolonisation out from Vanuatu. Similarly, although all of the New Caledonian endemics occur within the same, well supported, clade, there are, again, birds from other islands within the clade. The Three Gene Tree shows *Z. inornatus*, from Lifou, strongly supported as being the sister group to a clade containing both *Z. minutus*, also from Lifou, and *Z. xanthochrous* the other New Caledonian endemic. There appears to be little phylogenetic structure within *Z. xanthochrous* itself with populations from different parts of the main island and from Mare being paraphyletic. However this clade also includes *Z. albogularis* and *Z. tenuirostris* from Norfolk Island, *Z. strenuus* from Lord Howe and *Z. rennellianus* from Rennell Island in the Solomons. The phylogenetic relationships among this set of species show that their distribution has arisen out of a complex series of colonisation and recolonisation events. In particular, it appears that the species on the isolated islands of Lord Howe and Norfolk have contributed to the fauna of New Caledonia, providing an example of upstream migration.

2.4.6 Sympatric speciation

Two of the four criteria for sympatric speciation as defined by Coyne and Orr (2004) are that the two species must be largely sympatric and that they must be sister species. The phylogenetic reconstruction provides no evidence of sympatric speciation. In no case are sympatrically distributed species (*Z. strenuus* and *Z. l. tephropleurus* on Lord Howe Island; *Z. albogularis*, *Z. tenuirostris* and *Z. lateralis* on Norfolk Island; *Z. inornatus*, *Z. minutus* and *Z. lateralis* on Lifou, New Caledonia; *Z. xanthochrous* and *Z. lateralis* on New Caledonia; *Z. flavifrons* and *Z. lateralis* on Vanuatu; *Z. explorator* and *Z. lateralis* on Fiji) found to be sister species in the All Evidence Tree (Figures 2.2), nor indeed in any of the single-gene or other combined trees (Appendix 2.2.A, 2.2.B, 2.2.C, 2.2.D, 2.2.E). Instead sympatric species are always from relatively more distantly related clades.

2.4.7 Phylogenetic structure in recent colonists

Both the Three Gene and Two Gene trees show a strongly supported monophyletic clade containing the majority of the south Pacific *Z. lateralis* and the majority of the Australian *Z. lateralis* (Bayes support >0.92 in both trees, Appendix Figures 2.2.D and 2.2.E). The same clade appears in the All Evidence Tree, albeit with low support. The age of this clade, based on the molecular clock, suggests that the spread of *Z. lateralis* into the Pacific began just under one million years ago. However there is very little phylogenetic structure evident in the Pacific *Z. lateralis* clade itself, with even very different looking forms, such as the strikingly dark-headed Lifou form (*Z. l. melanops*) proving to be non-monophyletic. An older monophyly (Bayes support = 0.9 on the Two Gene Tree) suggests a deeper split between some individuals from the Australian *Z. lateralis* subspecies *gouldi* (south west Australia), *ramsayi* (northern Queensland) and *halmaturina* (south eastern Australia) and the rest of the clade. This split is clearly driven by the ND3 gene as this is seen in the ND3 gene tree but not the *cyt-b* gene tree (Appendix Figure 2.2.B). The All Evidence Tree also shows this split but most *Z. lateralis* nodes have poor Bayesian posterior support and subspecies from

Australia, Norfolk Island, Lord Howe Island and New Caledonia are interspersed among the Vanuatu *Zosterops*.

The *Z. lateralis* picture is complicated by a relatively small number of *Z. lateralis* haplotypes, including *Z. l. cornwalli* from Queensland and *Z. l. tropica* from Espiritu Santo, in Vanuatu, which appear as basal to the main *Z. lateralis* clade. Although this has poor support in the All Evidence Tree some of the same individuals from these same Vanuatu islands are strongly supported as being distinct from the rest of the *Z. lateralis* clade in the Three Gene Tree (Bayes support = 0.92). Additionally, in all the trees , one *Z. luteus* subspecies, *Z. luteus luteus* from Queensland and Northern Territory is contained within the *Z. lateralis* clade.

2.4.8 The evolution of endemic species from widespread subspecies

One of the curiosities of the phylogeny shown in Figure 2.3 is that it does not follow expected relationships predicted by taxonomies based on patterns of phenotypic similarity (Lack 1971; Mayr 1945; Mees 1969). This is particularly true of some of the large-bodied endemic species. Based on plumage similarities Mees (1969) concluded that *Z. strenuus*, *Z. tenuirostris* and *Z. l. tephropleurus* evolved not simply from *Z. lateralis* but specifically from the *cornwalli* subspecies. Similarly Mees (1969) concluded that *Z. albogularis* evolved from the *Z. l. lateralis* subspecies. Lack (1971) likewise suggested that *Z. inornatus* of New Caledonia evolved from the widespread *Z. l. lateralis* based on its similar colouring. Were this the case we would expect those species to come out within the *Z. lateralis* group and moreover to be sister species to the *Z. lateralis* subspecies named. Instead, these species are all found within the New Caledonia clade and appear to be quite distinct from *Z. lateralis*. Only *Z. l. tephropleurus* resides within the *lateralis* clade and, counter to the prediction, it does not emerge as the sister group to from the *cornwalli* subspecies.

2.4.9 The correlation of phenotypes and phylogenetic clades in the Zosteropidae

The traditional divisions of *Zosterops* on the basis of morphological similarity (Mees 1969) are not well supported by mtDNA gene trees. This is most clearly illustrated in the paraphyly of the *Z. flavifrons* clade. Mayr (1945) identified a split, based on plumage colour between "Yellow" and "Dark" forms of *Z. flavifrons*. The uniqueness of the cryptic species *Z. flavifrons majuscula* has already been demonstrated. *Z. f. majuscula* was thought by Mees (1969) to be part of the Yellow clade, this is not supported here. With the exception of this form however, the split on the basis of plumage colour holds true in all the trees and is very well supported in the most comprehensive tree, the All Evidence Tree. Bayes support is 1 for the monophyly of the Yellow clade and 0.91 for the monophyly of the dark clade. There is, however, reason to question the current subspecies designations. The Yellow clade, found mainly in the more southerly islands and Gaua in the north, consists of the subspecies *efatensis*, *gauensis* and *flavifrons*. *Z. f. flavifrons* appears to be coherent and monophyletic but *Z. f. efatensis* and *Z. f. gauensis* are paraphyletic. The Erromango population of *Z. f. efatensis* is monophyletic and the sister group of *Z. f. flavifrons*. However the *Z. flavifrons* white-eyes from Efate and Gaua are phylogenetically indistinguishable in the All Evidence Tree. This is interesting given that Gaua is in the northern part of the archipelago and the only island north of Efate that contains a member of the Yellow clade. The Dark clade is mainly found in the north including all the islands between Efate and Gaua. There is a similar pattern in the Yellow clade, where *Z. f. brevicauda* from Espiritu Santo is monophyletic but the other two subspecies are paraphyletic. However within that paraphyly the population from Epi is well supported on the All Evidence Tree as monophyletic (Bayes support = 1). In addition there is strong support for a deep split within the Dark clade with the *Z. flavifrons* populations from Espiritu Santo and Vanua Lava shown to be a monophyletic clade separate from the other Dark forms (posterior support = 1 on the All Evidence Tree). As noted by Phillimore *et al.* (2008b) this splits the subspecies Z. f. *perplexa*. So while some of the morphologically based assumptions hold up in the phylogeny there are also notable departures from orthodox taxonomy.

Interestingly, and perhaps significantly, the All Evidence Tree strongly suggests that the two main *Z. flavifrons* clades are not even sister groups. *Z. gibbsi*, a recently described species from Santa Cruz (Dutson 2008), is strongly supported as the sister group to the northern Dark clade (Posterior = 0.99) and *Woodfordia superciliosa* is almost as strongly supported (posterior 0.87) as the sister group for the Yellow clade. The latter finding agrees with the results of Moyle *et al.* (2009) who, working with a different, but partially overlapping, set of markers, found that *W. superciliosa* was the sister group to their *Z. flavifrons* specimen. *W. superciliosa* looks so different to other Zosteropidae that it has been placed in a different genus but there seems, on a phylogenetic basis, very little justification for this. However it is important to note that, due to the difficulty of obtaining specimens we were unable to include *W. lacertosa*, of the Santa Cruz group, in any of our gene trees. It would be instructive to learn if this is, as commonly supposed (Mees 1969) the sister species to *W. superciliosa* or whether it might reasonably be considered to fall outside the genus *Zosterops*.

The grouping of the *Z. lateralis* species complex identified by Mees (1969) based on morphological similarities is likewise also only partially supported by the phylogeny. As noted above, while the subspecies of *Z. lateralis* itself form a coherent group, the other species named in the complex, *Z. strenuus*, *Z. tenuirostris*, *Z. albogularis* and *Z. inornatus*, do not appear to be particularly closely related to *Z. lateralis*.

Taken together, the non-validity of so many of the morphologically based taxonomic assumptions must call into question the validity of making higher level assumptions on the basis of morphology within the Zosteropidae.

Figure 2.2. (Overleaf) The All Evidence Tree. A maximum clade credibility tree of the Zosteropidae of the south west Pacific based on sequence from all three genes considered together in an analysis that includes all taxa for which there is sequence for at least one gene. Up to 393 bp of ND3, 308 bp of cyt *b* and 958 bp of ATPase are combined. Numbers adjacent to nodes represent Bayesian branching support. Numbers in curled parentheses indicate voucher numbers. Monophyletic island clades were collapsed. Coloured branches indicate the geographic location of different taxa using the same colour code as Figure 2.1. Grey branches indicate extant species from the African and Asian clades. For details of the collapsed African and Indian Ocean clades see Warren *et al.* (2006). For details of the *Z. flavifrons* groups see Phillimore *et al.* (2008b).


Z. albogularis (Norfolk Island) {All 4 samples}
Z. inornatus (Lifou) {All 5 samples}
Z. stenuus (Lord Howe) {All 4 samples}
Z. rennelianus (Rennell) {Z.rn1}
Z. xanthochrous (N.C.) {All 15 samples}
Z. minutus (Lifou) {All 5 samples}
Z. tenuirostris (Norfolk Island) {N125}
Z. l. gouldi (Australia) {1965.43.993}
Z. l. halmaturina (Australia) {1965.43.990, 1965.43.991}
Z. l. ramsayi (Australia) {1964.60.1014}
Z. l. gouldi (Australia) {1965.43.992}
Z. l. gouldi (Australia) {1966.21.269}
Z. l. ramsayi (Australia) {1964.60.1012}
Z. luteus luteus (Australia) {All 4 samples}
Z. l. lateralis (Tasmania) {TAS15}
Z. l. lateralis (Norfolk Island) {N103, N120}
Z. lateralis {See table 2.3.i}
Z. l. gouldi (Australia) {1966.21.270}
Z. l. cornwalli (Queensland) {B77}
Z. lateralis {See table 2.3.ii}
Z. l. ramsayi (Australia) {1964.60.999}
Z. l. tropica (Pentecost) {PEN08}
Z. l. cornwalli (Queensland) {B74}
Z. l. cornwalli (Queensland) {B83}
Z. l. tropica (Santo) {245}
Z. l. griseonatus (N.C.) {N091, S015, S020}
Z. l. melanops (Lifou) {L122}
Z. l. melanops (Lifou) {L002}
Z. l. nigrescens (Mare) {M071}
Z. l. melanops (Lifou) {L031, L088, L102}
Z. l. nigrescens (Mare) {M001, M027, M044, M089}
Z. l. vatensis (Tanna) {109}
Z. l. griseonatus (N.C.) {See table 2.3.iii}
Z. tephropleurus (Lord Howe) {Both samples}
Z. l. flaviceps (Fiji) {1898.9.30.186}
Z. l. flaviceps (Fiji) {1888.9.1.781}
Z. l. vatensis (Efate) {EF44}
Z. l. vatensis (Ambrym) {ABY07}
Z. l. vatensis (Efate) {155}
Z. l. vatensis (Ambrym) {ABY39}
Z. lateralis {See table 2.3.iv}
Z. l. vatensis (Ambrym) {ABY25}
Z. l. tropica (Santo) {222}
Z. l. vatensis (Malekula) {215}
Z. l. tropica (Pentecost) {PEN03}
Z. l. vatensis (Malekula) {178}
Z. l. vatensis (Epi) {415}
Z. l. vatensis (Efate) {174}
Z. l. vatensis (Efate) {153}
Z. l. tropica (Santo) {SAN7}
Z. l. cornwalli (Queensland) {B82}
Z. l. cornwalli (Queensland) {B76}
Z. l. tropica (Santo) {SAN2}
Z. l. vatensis (Ambrym) {ABY36}
Z. f. majuscula (Aneityum, Vanuatu) {All 5 samples}
Z. flavifrons 'Yellow Clade' (Vanuatu) {See table 2.3.v}
W. superciliosa (Rennell) {Both samples}
Z. gibbsi (Vanikolo) {Z.gi1}
Z. flavifrons 'Eastern Dark Clade' (Vanuatu) {See table 2.3.vi}
Z. flavifrons 'Western Dark Clade' (Vanuatu) {See table 2.3.vii}
Z. explorator (Fiji) {Both samples}
Z. luteus balstoni (Australia) {All samples}
Z. montanus whiteheadi {ZMUC.O2662}
Z. japonicus {LSUMZ.B20880}
Z. at. atricapillus {LSUMZ.B36434}
Z. erythropleurus {ZMUC.O2776
Ancient Indian Ocean white-eyes
African and maderaspatanus white-eyes
0.76
1
1
1
0.93
0.98
1
1
1
1
1
1
0.86
1
1
0.96
0.87
0.99
1
1
0.87
1
1
0.99
0.91
1
1
1
1
0.93
1
1
1
1
0.86
0.85
0.6

Table 2.4. Voucher numbers of specimens included in tips representing more than one individual in Figure 2.2.

2.3.i

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	lateralis	cornwalli	Queensland	B79, C132
Zosterops	lateralis	gouldi	Australia	1966.21.270
Zosterops	lateralis	lateralis	New Zealand	D3, C132
Zosterops	lateralis	lateralis	Tasmania	TAS01, TAS04, TAS06
Zosterops	lateralis	ramsayi	Queensland	1964.60.1001

2.3.ii

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	lateralis	chlorocephalus	Heron Island	H1568, H1613, 9010, 9601
Zosterops	lateralis	cornwalli	Queensland	B71, 77

2.3.iii

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	lateralis	griseonatus	N.C.	N018, N024, N036, N109, S014, S030, S035

2.3.iv

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	lateralis	tropica	Ambae	AMB55, AMB56, AMB57
Zosterops	lateralis	tropica	Espiritu Santo	233, SAN9
Zosterops	lateralis	tropica	Gaua	251, 261, 267
Zosterops	lateralis	tropica	Pentecost	PEN16, PEN18, PEN33
Zosterops	lateralis	tropica	Vanua Lava	317, 319, VAN46
Zosterops	lateralis	vatensis	Ambrym	ABY26
Zosterops	lateralis	vatensis	Epi	412, 418, 423
Zosterops	lateralis	vatensis	Erromango	371, 373, 380
Zosterops	lateralis	vatensis	Malekula	176, 183, 199

2.3.v

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	flavifrons	efatensis	Efate	18, 25, 40
Zosterops	flavifrons	efatensis	Erromango	378, 385, 392, 405
Zosterops	flavifrons	flavifrons	Tanna	73, 110
Zosterops	flavifrons	gauensis	Gaua	269, 271, 285, 294

2.3.vi

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	flavifrons	macgilivrayi	Malekula	185, 193, 201, 211
Zosterops	flavifrons	perplexa	Ambae	AMB3, AMB4, AMB5, AMB7
Zosterops	flavifrons	perplexa	Ambrym	ABY09, ABY10, ABY12, ABY13
Zosterops	flavifrons	perplexa	Epi	420, 421, 427
Zosterops	flavifrons	perplexa	Maewo	MW03, MW06, MW07
Zosterops	flavifrons	perplexa	Pentecost	PEN17, PEN69, PEN70

2.3.vii

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	flavifrons	brevicauda	Espirtu Santo	227, 229, SAN6, D
Zosterops	flavifrons	perplexa	Vanua Lava	311, 320, 329

2.5 Discussion

The new phylogenies presented suggest that the origins and diversification of the Zosteropidae of the south west Pacific are more complex than traditionally assumed (Lack 1971; Mayr 1942; 1967; Mees 1957; 1961; 1969). For instance, the simplistic model of a single colonisation wave from west to east spreading in a linear pattern from continents to islands does not fit with the phylogenetic data. Instead, I find evidence consistent with multiple waves of colonisation and extinction. In addition there are a number of unexpected relationships between geographically distant or morphologically dissimilar species, which are inconsistent with the simple model and require more complex models of colonisation dynamics. There is possible evidence of upstream colonisation but no convincing evidence of intra-archipelago speciation. There is no evidence consistent with sympatric speciation. A widespread recent colonist *Zosterops lateralis* is shown to have little phylogenetic structure and is ruled out as the source species for many of the endemics of the region. Linked to this is the clear implication that traditional taxonomy based on phenotypes is a poor predictor of underlying phylogenetic relationships. Results must be approached with a certain degree of caution as factors such as incomplete lineage sorting and ancient hybridisations can cause errors in a mtDNA gene tree reconstruction (Funk & Omland 2003).

Australia has been suggested as the original source for the Zosteropidae of the south west Pacific, potentially via New Guinea (Mayr 1941; Mees 1969). For this to be the case, Australian taxa would be expected to be basal in the tree, assuming descendents of the ancestral form have survived in Australia. This prediction is not supported in my analyses with the basal clade suggesting an Asian origin for the south west Pacific white-eyes. The ND3 gene tree, which includes the most Asian species, suggests that *Z. luteus* may actually be within the Asian clade and, therefore, a candidate for the ancestor of the south Pacific radiation. However, in the All Evidence Tree both Australian forms (*Z. luteus* and *Z. lateralis*) appear to be within the general south Pacific clade. Of course, as in any phylogeographic study based on extant species, the possibility that an earlier, now extinct, Australian form was the ancestral species cannot be excluded.

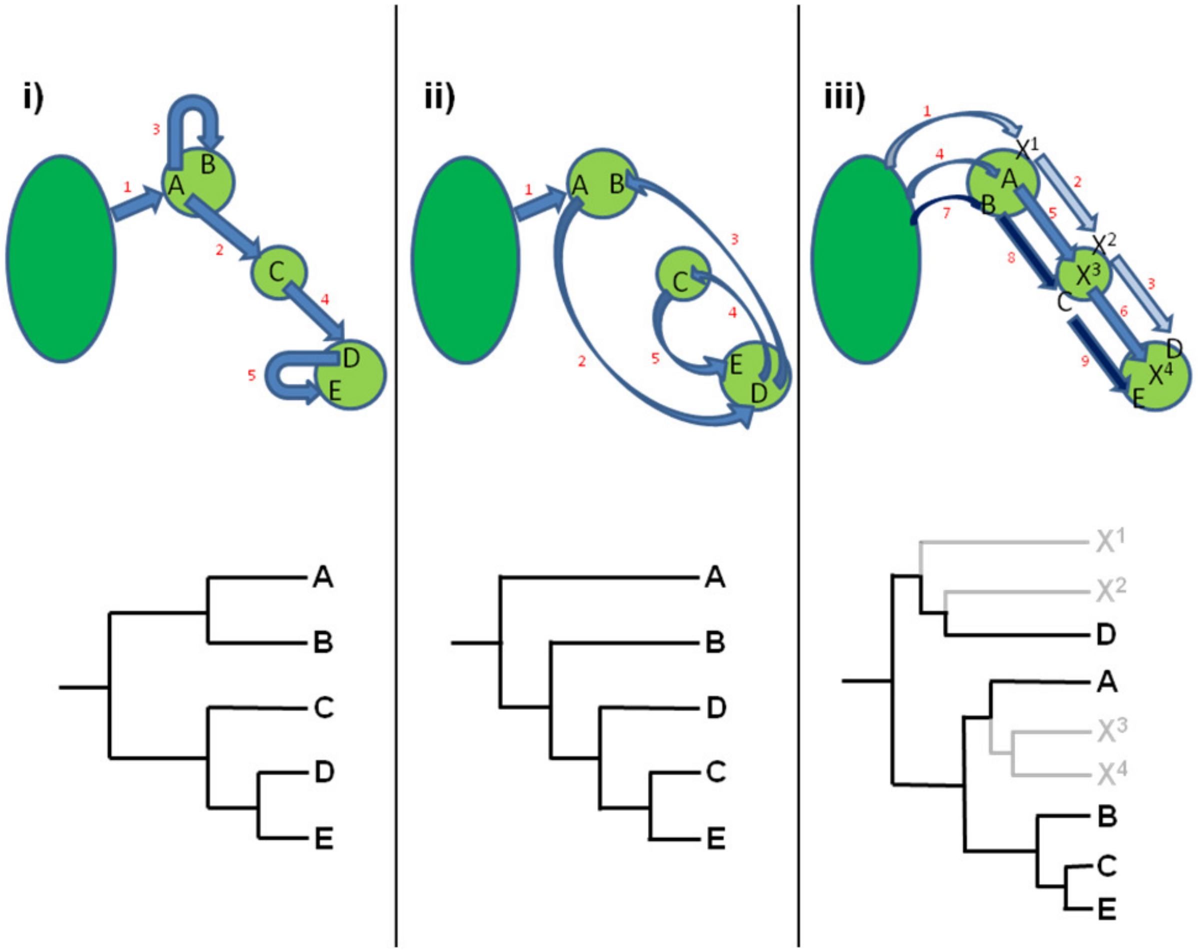


Figure 2.3. Three possible colonisation scenarios for island colonisation. The large dark green oval represents a continent and the smaller green circles represent archipelagos or islands of different sizes and at different distances from the continent. Red numbers indicate the order of the colonisation events. In scenario i) colonisation is in a single wave in one direction with intra-archipelago or possibly sympatric speciation. In Scenario ii) there are colonisation events between archipelagos in several directions and over large distances. In scenario three several waves of colonisation and extinction result in the same pattern. Importantly scenarios ii) and iii) are difficult to distinguish from their phylogenies without information on extinct species (greyed out in the trees).

Whatever the ultimate origin of the south west Pacific white-eyes there are three possible scenarios that might explain the colonisation pattern of the region, as shown in Figure 2.3. Scenario i) is the classic model of a single uni-directional colonisation wave with intra-archipelago speciation. In the mosaic model, scenario ii), there may be intra-archipelago speciation but crucially colonisation events take place in all directions and over large distances, often jumping over island groups. In scenario iii) the multiple wave and extinction model colonisation is also essentially unidirectional but occurs in several waves with extinctions leaving niches for forms in subsequent waves to exploit or subsequent waves causing extinctions.

The traditional model, (Scenario i in Figure 2.3), is clearly too simplistic as it predicts that the whole clade should be monophyletic with Australian taxa basal. The ND3 phylogeny suggests that the south Pacific Zosteropidae are not monophyletic and we have seen that the Australian taxa are not basal. This model would also predict that sister groups will be found on adjacent islands. Sister groups do not usually appear on nearby islands and cases where this does happen, such as the eastern and western groups of the Dark clade of *Z. flavifrons*, are the exception rather than the rule. Finally it would predict that old species should only be found close to the continent and that younger species should be on the more easterly and isolated islands. This is clearly not the case. There is no evidence that the eastern isolate *Z. f. majuscula* is a young species. Similarly the young *Z. lateralis* species is found on islands all over the region irrespective of distance from the mainland.

In the mosaic of colonisation model, (Scenario ii in Figure 2.3), there is an initial seeding of the region from a mainland source but the archipelagos themselves then act as drivers of speciation. Speciation takes place readily within archipelagos, possibly even sympatrically, and, crucially, the island groups then provide migrants to colonise other, often distant, islands within the region. Darwin’s finches (Geospizidae) are a classic example of adaptive radiation and evolved by intra-archipelago speciation. That is that islands within the archipelago were sufficiently easy to reach so that they could be colonised but sufficiently difficult to make colonisation events rare, allowing adaptation to local conditions and subsequent speciation (Grant & Grant 2008b; Lack 1971).

Mayr and Diamond (2001) suggest that significant barriers to movement between archipelagos mean that speciation is expected to occur within them. If this is the case we would expect species within archipelagos, especially ones that are large and remote, to form a clade. The ‘Vanuatu’ Clade and the ‘New Caledonia’ Clade both contain several species from the same archipelago, hence the clade names. However because both clades contain taxa that are found on islands outside those archipelagos they cannot be true examples of intra-archipelago speciation unless those outside taxa are the result of colonisation from the archipelago. I consider this unlikely because it would mean large dispersal jumps being made by endemic, and presumably sedentary, species but it cannot be completely discounted as a possibility. If it were true, this would represent a departure from the accepted orthodoxy of an essentially west to east Colonisation pattern and suggest that recolonisation events of islands of the mainland from more remote islands or archipelagos are not as rare as supposed. This would account for the patchy pattern seen within the region. In the absence of human interference the natural rate of vertebrate extinction on oceanic islands is thought to be very low (Steadman 1991; Steadman 2006). Scenario ii has the advantage that it would require relatively few extinction events within the time frame. Pockets of extinction would create vacant niches that might be colonised from islands from almost anywhere within the south Pacific, such as Norfolk Island being colonised by birds from Lifou and Rennell being colonised by birds from Vanuatu. Stattersfield *et al.* (1998) consider that high rates of ecological and allopatric speciation account for high levels of endemic species richness. The islands of the south west Pacific provide plenty of opportunity for both so that there may be no need to postulate colonisations from a species rich continent to explain diversity. With this interpretation the data would seem to support the hypothesis that, far from being an evolutionary dead end, islands do form a valuable source for speciation and colonisation (Bellemain & Ricklefs 2008). It has been suggested (Lack 1971) that white-eyes are among the first species of birds to colonise new islands in the Indo-Australian region. If this is so then islands are valuable sources for recolonisation and speciation and small island populations may be more valuable in evolutionary terms than often thought.

The third model is one of waves of extinction and colonisation (Scenario iii in Figure 2.3). Wilson (1959; 1961) described a cycle of colonisation with three stages. In stage I species have a large taxonomic range and little or no endemism, as *Z. lateralis* does now. In stage II endemic species evolve in the region but the group is still centred on the source region. In stage III the colonists evolve into endemic groups. During this cycle species undergo range contractions and local extinctions leave a scattered distribution. This leaves niche space for a newly evolving stage I species to occupy. Wilson (1961) based his ideas on the ant species of Northern Melanesia but Mayr and Diamond (2001) suggested that a similar process might be occurring in birds. It is certainly possible that *Z. lateralis* is a stage I species in an ongoing taxon cycle in the region.

Under scenario iii geographically distant relatives are the result of wide-spread colonisation followed by uneven extinction resulting in a patchwork distribution. For example the sister species *Z. albogularis* and *Z. inornatus* might represent a very early colonisation wave that left survivors on only more remote islands. Other islands were occupied by a new wave that resulted in the rest of the New Caledonian endemics as well as *Z. rennellianus, Z. tenuirostris* and *Z. strenuus*. This scenario would also typically result in very old taxa being found on remote islands, as is the case with *Z. f. majuscula.* The theory of taxon cycles would also predict the presence of a young and widespread form. Here, *Zosterops lateralis* a candidate for a stage I taxon cycle species. It has spread widely across the region and shows local adaptation in phenotype, for example the large *Z. l. chlorocephalus* on Heron and the black-headed *Z. l. melanops* and *Z. l. nigrescens* in the Loyalty Islands, but as yet shows little underlying phylogenetic variation (although it shows considerable population genetic structure, Clegg & Phillimore 2010). The genetic structure that there is, for example the monophyletic Tanna population, could be considered as the product of earlier but still recent waves, perhaps within the last 10,000 years. On this interpretation, this study suggests *Z. lateralis* as the most recent colonisation wave and, probably, three previous major colonisation waves. One very ancient wave, represented by *Z. f. majuscula*, and two others, represented by the New Caledonian and Vanuatu clades. There is also evidence of minor waves of colonisation within the larger waves, for example the multiple invasions of Vanuatu by *Z. flavifrons* detailed in Phillimore *et al.* (2008b). The difficulty with this interpretation is that, if it is true that for a new colonisation to take place an extinction of a previous species is required then it is questionable if there was sufficient time for the level of extinction and replacement required in this model. Our phylogeny estimates the split of the south west Pacific clade at about four million years. Ricklefs and Bermingham (2007) working in the Lesser Antilles, estimate that the 'average life span' of a population of an endemic form with a restricted distribution is about two million years. This is half the time estimated in our phylogeny and it might seem that this would mean that there would be too little time for so many waves of extinction and colonisation even for such a rapidly diversifying lineage as the Zosteropidae. However there is evidence that a new colonist can invade even where a previous congeneric already exists, as *Z. lateralis* has done on multiple occasions. It may even be that a new invader might contribute to the extinction of an endemic especially if its arrival coincides with some unusual environmental change such as a hurricane or invasion by a destructive mammal. The decline of *Z. albogularis* on Norfolk island is thought to have been caused by the introduction of black rats (*Rattus rattus*) in the 1940's combined with competition from *Z. l. lateralis*, which self introduced in 1904 (BirdLife International 2009). However *Z. lateralis* reached there shortly before the rats arrived and it may have outcompeted *Z. albogularis* under the new conditions. *Z. lateralis* is a relatively recent coloniser on many islands in the region and it may be that it is currently in direct competition with more specialised endemic *Zosterops*. It may be significant that *Z. lateralis* is more commonly found in disturbed areas of human habitation on many of these islands. Change is an on-going process and, whatever the cause or effect, new colonists may prove better competitors in such times than specialist endemics. Potentially, the coexistence of *Z.*

lateralis with other white-eye forms may not be an evolutionary stable state. Stage I species, by definition, are likely to be both competitive and vagile. Thus, colonisation by such species seems more plausible than extensive colonisation by island endemics which are known to have reduced dispersal ability. Taken together, it seems more likely therefore that a wave of colonisation and extinction (Scenario III) would leave closely related species on distant islands than that an island endemic would spontaneously cross a thousand kilometres of sea to colonise a remote island (Scenario II).

The *Z. lateralis* picture is complicated because of the deep split that occurs in the tree which suggests that certain lineages have been isolated for a long time. However this cannot be the case as other individuals from the same populations appear in the main *Z. lateralis* group. The most plausible explanation for this is that there was a period of isolation when there was little gene flow between populations and that, although gene flow has now resumed not enough time has passed to allow a complete homogenisation. An alternative explanation is that *Zosterops lateralis* picked up mitochondrial DNA through introgression with an earlier inhabitant of the area. Introgression is likely to be the explanation of the fact that *Zosterops luteus luteus*, actually appears within the main *Z. lateralis* clade. Degnan & Moritz (1992) found a similar result and concluded that this is a result of introgression between *Z. lateralis* and *Z. luteus luteus* where they meet in northern Australia. This is the most likely explanation despite the fact that *Z. luteus luteus* is not most closely associated on the phylogenetic trees with, the partially sympatric, *Z. lateralis ramsayi*. The pattern is, perhaps, consistent with an ancient introgression event, although this cannot be confirmed with the available data.

The main processes of avian speciation on oceanic islands are a matter of debate and sympatric speciation is especially controversial. Part of the problem of identifying sympatric speciation is that it is very difficult to prove that contemporary sympatrics did not have an allopatric origin (Coyne & Orr 2004) but the minimum evidence required is for two species with sympatric distributions to be sister species. I find no evidence for this occurring in the Zosteropidae of the south west Pacific. Indeed even the sympatric endemics *Z. albogularis* and *Z. tenuirostris*, which Coyne & Price (2000) conceded could be an example of sympatric speciation, are shown not to be sister species in the phylogenies presented here. I conclude then that speciation on the same island does not readily occur in white-eyes even where there is very divergent habitat, such as on Grande Terre in New Caledonia where there is both wet and dry forest at all elevations from sea level to 1628m yet there is only one endemic species. Many assumptions about speciation within the Zosteropidae have been made based on taxonomy. *Woodfordia superciliosa* is one of many white-eyes taxonomically assigned on the basis of plumage colour, in this case to a separate genus. My data seems to show conclusively that this species nested well within the Zosteropidae and should not be assigned its own genus. *Woodfordia superciliosa* is an extreme example of what would appear to be a general rule within the Zosteropidae, that morphological analysis and especially colour is likely to be a poor predictor of underlying relationships within the Zosteropidae.

It seems probable that the complex pattern of colonisation in the south west Pacific is the result of a concatenation of causes. Multiple waves of colonisation are the most likely cause of the major clades in the south west Pacific. Within that larger framework, however, the phylogenetic structure has included smaller, inter-archipelago colonisation waves, intra-archipelago speciation and, perhaps, some upstream dispersal events.

Chapter 3

Tempo and mode of an explosive diversification:

The white-eyes of the south west Pacific

3.1 Abstract

Rates of diversification often vary through time and theory predicts that the pattern of this variation may provide information on the underlying macroevolutionary processes. Species-level molecular phylogenies contain information regarding these temporal dynamics, expressed as the accumulation of lineage diversity through time. Here I quantify the rate of diversification of a rapidly diverging, predominantly island-dwelling group of birds, the Zosteropidae of the south west Pacific. I find an average rate of diversification of between 0.69 to 0.91 taxa per million years, which greatly exceeds the average rate found across avian lineages. I also find strong evidence for a slowdown in the rate of diversification through time and this result is robust with respect to the details of the underlying phylogenetic hypothesis. However, phylogenetic lineage-through-time plots reveal a pattern of repeated bursts of accelerated speciation, consistent with a model of repeated waves of island colonisation and insular taxon cycles. Finally, I show that *Zosterops* have diversified considerably faster in the south west Pacific than in the Indian Ocean, and suggest that the most likely explanation relates to the extensive availability of islands in the south west Pacific region. Taken together, these results suggest that temporal and geographical variation in the rate of diversification in this group is linked to waves of colonisation associated with extensive island and niche availability.

3.2 Introduction

The extent to which species diversification rates vary over time, and the processes that cause such patterns, are central questions in evolutionary biology (Barraclough & Nee 2001; Eldredge & Gould 1972; Gingerich 1983; Nee *et al.* 1992; Rabosky & Lovette 2008b; Ricklefs 2007; Simpson 1944). Island systems have often been used as models for understanding questions of lineage diversification with respect to both geographic and temporal variation (Clark *et al.* 2008; Lomolino 2000). The accepted view is that speciation in oceanic island lineages arises due to selection, either natural or sexual or possibly both (Coyne & Orr 2004; Price 2008; Uy *et al.* 2009). In birds, the conventional view is that divergence happens predominantly in allopatry or possibly parapatry, and is driven largely by selection, with the contribution of neutral processes, such as founder effects (Clegg *et al.* 2002b) or and drift (Gavrilets 2004; Merilä 1997), of lower consequence. Recently there has been a shift in emphasis from a focus on processes operating in allopatry to the importance of dispersal as a mechanism to increase ecological opportunity and subsequently speciation rates (de Queiroz 2005; Sanmartín *et al.* 2008). Certainly there is evidence for very high speciation rates in association with new ecological opportunities, for instance radiations of Darwin's finches (Geospizinae) on the Galapagos, honeycreepers (Fringillidae: Drepanidinae) in Hawaii and cichlids (Cichlidae) in the Great Lakes of Africa (Grant & Grant 2008b; Lovette *et al.* 2002; Seehausen 2006). Dispersal to new areas is one way that organisms may find opportunities to increase or shift their ecological niche space and expand into novel niches.

The tempo and mode of evolutionary diversification can be studied using time-calibrated molecular phylogenies (Nee *et al.* 1994a; Nee *et al.* 1994b; Ricklefs 2007). The information contained in these phylogenies can be represented by lineage through time plot which shows the known accumulation of lineages towards the present (Harvey *et al.* 1994). One approach for inferring the temporal pattern in diversification rates is the γ-statistic of Pybus and Harvey (2000), which utilises information on the interval between successive reconstructed speciation events on a phylogeny. Under a Yule process, where every species has an equal chance of speciating at any moment in time and there is no extinction (Yule 1925), the log number of lineages in the reconstructed tree is expected to increase linearly through time and the γ-statistic will follow a normal distribution centred on zero. If speciation rates have declined through time, then speciation events will tend to be clustered more densely in the early history of a clade and the lineage through time plot would show a downturn with the γ-statistic will tending to be negative. This pattern has often been reported for time-calibrated molecular phylogenies (Harmon *et al.* 2003; McPeek 2008; Phillimore & Price 2008; Weir 2006) and fits with theories of adaptive radiation; where speciation rates are high as lineages diversify to take advantage of multiple available niches but slow down later as niche space is filled (Schluter 2000b; Simpson 1953; but see McPeek 2008). Rabosky and Lovette (2008b) show that slowdown is highly unlikely under a birth-death model where extinction increases through time, or under a birth-death model where extinction rates are high.

There are a number of caveats to be kept in mind when inferring diversification rates using a lineage through time approach. Phylogenetic studies typically rely on extant or very recently extinct species because genetic material for ancient species is usually unavailable (Steadman 1995). In poorly fossilising groups, such as birds, there is often no evidence for pre-historical extinct species even where their existence can be inferred (Steadman 2006). This means that the number of reconstructed lineages will be an underestimate of the true numbers of lineages (Harvey *et al.* 1994; Nee *et al.* 1994a; Nee *et al.* 1994b; Nee *et al.* 1992). Another issue is the danger of mis-recording the number of taxa present in a lineage. Species are usually considered the basic units of biological organisation but their delineation is often problematic (Mallet 1995; Mallet & Willmott 2003). In particular, the rise in the popularity of variants on the phylogenetic species concept (Cracraft 1989), has led to an increased amount of taxonomic ‘splitting’ (Isaac *et al.* 2004) and the subsequent increase in apparent species numbers also has consequences for estimated rates of diversification. In the context of quantifying diversification rates and temporal patterns in diversification, Purvis *et al*. (2009) suggested that there is a risk that lineages that may in the future go on to become full species are excluded from macroevolutionary studies. Thus, given the potential effect of species definition on analyses of the temporal dynamics of phylogenetic diversification, it is prudent to employ a range of species definitions, ranging from conservative species concepts based on reciprocal monophyly to less conservative “incipient species” lineages.

The two principal aims of this study are to use the phylogenetic hypotheses for the *Zosterops* of the south west Pacific developed in Chapter 2 to: (i) investigate the temporal dynamics of the speciation process and determine which model best fits the data, and (ii) determine, given that the speciation of the group in the Pacific has been suggested to be exceptional, what stage of the speciation process departs most from that found elsewhere.

Zosteropidae are particularly suitable for the study of temporal patterns of phylogenetic diversification because the per-lineage diversification rate estimated for the *Zosterops* has been estimated to be 1.95-2.63 species per million years, (Moyle *et al.* 2009), which is considerably higher than has been reported for any other bird genus (Price 2008). Indeed, the highest reported rate for birds outside the Zosteropidae, which was for *Dendroica* warblers, was of the order 0.5 species per million years (Lovette & Bermingham 1999; Moyle *et al.* 2009). Using the standard 2% divergence to convert genetic distance into time, Wier and Schluter (2007) estimated that divergence times for sister species averaged about two million years in the tropics and other studies have suggested even slower rates (Gill *et al.* 2005; Marks *et al.* 2002). The entire radiation of the Zosteropidae is only two million years according to Moyle *et al.* (2009) estimate and, while I estimate an older age for the clade of 4.7 (Chapter 2, Figure 2.3), this still represents a very recent radiation. The reasons for this rapid diversification are yet to be verified making this an interesting study group for the investigation of diversification rates. Moyle *et al.* (2009) suggest a prominent role for taxon specific characteristics interacting with the geography and earth history experienced by the group. The taxon specific characteristics cited by Moyle *et al.* (2009) were sociality, rapid morphological speciation, short generation time, ecological generalism and plasticity in dispersal behaviour.

In order to examine why the speciation of the Zosteropidae has been so rapid and to understand temporal dynamics in diversification rates it is helpful to consider Mayr's (1947) stages in speciation. Phillimore and Price (2009) note that three of the stages identified by Mayr may be the limiting step in species formation and therefore ecological and nonecological factors that hinder any of these steps may thereby cause speciation rates to decline. In stage one, the frequency of barriers or dispersal events sets the stage for population divergence to begin. In stage two, traits diverge in response to natural selection, sexual selection or drift (Coyne & Orr 2004; Gavrilets 2004). Crucially, however, ecological models of speciation are expected to be faster than non-ecological models (Clegg *et al.* 2002b; Price *et al.* 2009; Rundell & Price 2009). In stage three, range expansion increases the opportunity for renewed speciation, although for species to expand their ranges they should be sufficiently divergent from other species, including congenerics, such that the two can coexist in sympatry. In the absence of range expansion, opportunities for speciation are expected to decay through time because ecological opportunities are limited by space, hence range expansion is the third rate-limiting step.

Zosterops are also interesting for the study of diversification because they show relatively high rates of insular sympatry (Lack 1971). In many groups, closely related species show limited overlap with respect to their geographical distributions, with the ranges of sister-species often either abutting or overlapping relatively narrowly (Allen 1907; Jordan 1905; Phillimore *et al.* 2008a). One factor that is thought to limit sympatry among closely related taxa is ecological competition (Hardin 1960; Lack 1944; Price 2008). This would appear to be the case for continental *Zosterops*, such as Z. *senegalensis* and *Z. poliogaster* on the

African mainland, which usually have allopatric distributions. However, many of the South Pacific islands have two or even three species of *Zosterops* each (Lack 1971; Mees 1961; 1969). Species rich avian families tend to be those with the strongest dispersive abilities (Phillimore *et al.* 2006) and this might be expected to apply to the Zosteropidae, which are one of the most speciose bird families in the world (94 species according to (Clements 2007)) with the *Zosterops* genus itself one of the two most species-rich genera.

The first stage of my analysis is to test if there has been slowdown in the lineage through time plots for the Zosteropidae that would be consistent with patterns for bird phylogenies in general (Phillimore & Price 2008). A pattern of slow-down in time calibrated molecular phylogenies is expected if as islands are colonised the available niches become filled (McKenna & Farrell 2006; Nee *et al.* 1992; Price 2008; Weir 2006). I will examine temporal dynamics of lineage diversification employing three interpretations of the number of *Zosterops* lineages, in order of decreasing stringency: (i) using only allospecies that are widely-held to be reproductively isolated, (ii) using *Zosterops* forms that are reciprocally monophyletic on the combined Four Gene Tree (see Methods) and (iii) using all populations that might be considered incipient species based on evidence from mitochondrial trees, microsatellite analysis, subspecies studies and known isolation from conspecific populations. I will use these three trees to test not only for slowdown in the rate of diversification but also for phylogenetic imbalance, where some lineages are more prone to speciate than others (Purvis & Agapow 2002). If diversification proceeds via a single source species colonising new islands and undergoing peripatric speciation, then I would predict that the resulting phylogenetic tree should be highly imbalanced and that the number of lineages in the reconstructed phylogeny should accumulate in a linear rather than exponential fashion.

In the second part of my analysis I will test competing theories on the mechanisms that may lead to high rates of diversification, focusing on the roles of geographic isolation, allopatry and sympatry that relate to the three stages of species formation in Mayr's model (1947). To determine the role of geographic isolation, I make a comparison of the number of available islands in different size and distance classes (Newton 2003) to see if there are significant differences between the Pacific region and another area of *Zosterops* speciation on Indian Ocean islands. Second, I estimate how allopatry influences divergence rates by estimating the ‘time to allopatry’ and the average duration required to produce an endemic taxon. A minimum estimate of time to allopatry can be obtained by measuring the age distribution of allospecies and then determining if it is shorter in areas with slower speciation rates (Weir & Schluter 2007). I will also look at the average duration required to produce an endemic taxon. It has been hypothesised that tropical birds often speciate over very small distances and if this is the case in the Zosteropidae then sister species in the tree should often be found on geographically adjacent islands (Mayr & Diamond 2001). The third step that limits the rate at which species form is range expansion and I will use age differences between sympatric species as a measure of the time required for species to expand their ranges post-speciation. If little time is required then sympatric species should be closely related but if a long time is required then sympatric species will tend to be connected by long branch lengths and be far apart on the phylogenetic tree.

3.3 Methods

3.3.1 Model Testing

The program jModeltest v. 0.1.1 (Guindon & Gascuel 2003, Posada 2008) was used to examine the best model of sequence evolution for the given data. The tree was constructed using neighbour joining and model choice was based on minimisation of the Akaike Information Critera. Not all of the models tested were available as standard in the BEAST program so I selected the available model with the lowest AIC score (Sullivan and Joyce, 2005).

3.3.2 Phylogenetic construction of The Four Gene Tree

In Chapter 2 of this thesis I was concerned with reconstructing the phylogenetic relationships of *Zosterops* species in my study region of the south west Pacific. In this chapter, however, it also important to include, not only species from my study area, but from the entire clade because I need to estimate overall rates of diversification. Moyle *et al.* (2009) demonstrated that the clade containing the south west Pacific *Zosterops* also included species from the Solomons and further afield. Since a study of diversification through time requires as complete a tree as possible (Doyle & Donoghue 1993; Ricklefs 2007) and sequence data was available for these species I constructed phylogenetic tree for the wider clade. A new phylogenetic tree was constructed by combining information from the *cyt-b*, ND2, ND3 and ATPase 6 & 8 genes.

Representatives of lineages were selected based on the gene tree in chapter 2 which used the *cyt-b*, ND2, ND3 and ATPase 6 & 8 genes and the gene tree of Moyle *et al.* (2009) which used ND2, ND3 and TGFB genes, with the latter sequences taken from GenBank. Although many of the same species were sequenced in these two trees, the individuals in all but one case were different. Where there was overlap in species sequenced in the two datasets, a sequence from each dataset was included to ensure that the two datasets gave the same result, i.e. the two individuals were sister species on the tree. The package APE (Paradis *et al.* 2004) in the statistical program R was used to alter trees and drop extra individuals so that only single representative of each taxon was included in the final tree. Sequence from all genes was considered together in an unpartitioned analysis. Using substitution models identified in jModeltest, a Bayesian relaxed clock inference method (Drummond *et al.* 2006) was implemented in BEAST v. 1.4.8 (Drummond & Rambaut 2007). The advantage of using a relaxed clock approach is a tree can be rooted without an outgroup (Drummond *et al.* 2006). UPGMA was used to construct a starting tree and a birth-death prior on branching times was applied (Gernhard 2008). I used a lognormal distribution to model rate variation across adjacent branches assuming a substitution rate of 1% per lineage per million years

(Weir 2006; Weir & Schluter 2008). For each analysis four independent chains were run for 20 million generations. The four runs generated log and tree files which were combined using LogCombiner v. 1.4.8 (Drummond & Rambaut 2007). Two million generations were removed from each chain as burn-in. Tracer v. 1.4.1 was used to assess convergence and whether the four chains were sampling from the posterior distribution. In all cases the combined results for the four independent chains had an estimated sample size (ESS) of greater than 200 for all parameters. TreeAnnotator v. 1.4.8 (Drummond & Rambaut 2007) was used to estimate the maximum clade credibility tree across the posterior distribution of 14400 trees. This methodology was repeated for each of the lineage datasets allospecies, reciprocally monophyletic groups and potentially incipient species.

3.3.3 Data selection

Moyle *et al.* (2009) showed that all the Zosteropidae species in the South Pacific region (Chapter 2, Figure 1) are contained with a single monophyletic clade, making the group amenable to the study of lineage diversification rates. Data selection for the different parts of this analysis is crucial. The region of the south west Pacific that seems to have high speciation rates stretches in an arc from the Solomons Islands down through the Santa Cruz Islands, Vanuatu and New Caledonia to New Zealand and adjacent islands. Included in this region are two of the superspecies as described by Mees (1961; 1969), namely *Z. griseotinctus* and *Z. lateralis*. Molecular studies now suggest that these two named superspecies groups do not, in fact, form natural clades (Chapter 2, Moyle *et al.* 2009) but nevertheless together they represent a group of unusually high species diversity. The Four Gene Tree shows that all the species in this core region fall within a monophyletic clade that also includes a number of forms from outside the region (see Appendix 3.1). I have at least one representative of every named species within the region except *Z. santaecrucis* and *W. lacertosa*, both of which are from the Santa Cruz Islands.

Analyses were performed on three interpretations of the Four Gene Tree. These were pruned to different criteria as follows:

(i) ‘Conservative’ species tree

The first tree employed was a conservative tree based on species that are generally accepted to be true species and reproductively isolated (Chapter 2, Figure 2.2). This tree is shown in Appendix 3.1.A.

(ii) ‘Reciprocally Monophyletic’ tree

The second tree is made up of *Zosterops* forms that represent monophyletic tips in the tree. This tree includes some forms referred to as subspecies that are highly likely to be true species but which, because they are not yet in sympatry with congeners cannot be shown to be so. There are four unsampled taxa that potentially could be included in the tree. However, due to the difficulty in classifying *Zosterops* based on morphological characteristics (Chapter 2), I did not attempt to fit these four taxa into the tree. It is therefore possible that the speciation rates are under-estimated. This tree is shown in Appendix 3.1.B.

(iii) ‘Incipient species’ tree

In the third tree I attempt to include, not only currently recognised species, but also potential incipient species. As far as possible I have attempted to deduce these incipient species from the molecular information. Subspecies that appear to be isolated based on molecular evidence are included as tips on the tree. For example, where monophyletic *Z. flavifrons* clades are coincident with island distributions I have designated them as incipient species, resulting in this species being divided into eight actual or potential species. Likewise, *Z. lateralis* of Vanuatu are divided into three distinct groups based on microsatellite DNA variation: the form on Tanna, the form on Efate and Erromango and the birds on all remaining islands (Clegg & Phillimore 2010), thereby adding three tips to the tree. Inevitably, gaps in genetic sampling below the species level introduce potential error to the tree, producing an underestimate of the number of species. Therefore, as far as is reasonably possible, I have followed the conclusions of Mayr (1967) and Mees (1957; 1961; 1969) in identifying morphological species and their likely relationships and included these as incipient species. For example one unsampled *Z. lateralis* subspecies, *Z. l. valuensis* form Mota Lava in northern Vanuatu was positioned as a sister taxa to *Z .l. tropica* following Mees (1969). Likewise, for Solomon Island taxa, I have included each named morphological subspecies in the tree. I also extrapolate from the relationships deduced by Mees (1969) to include species that occur within the clade of interest but outside the core geographical area of the study. Notably, there are four full species missing from the tree. These are two species from the genus *Rukia*, *R. ruki* and *R. longirostra*, and one from the genus *Woodfordia*, *W. lacetosa*. Molecular phylogenies (Moyle *et al.* 2009; Slikas *et al.* 2000b) show that both these genera are nested within the *Zosterops* clade and there is a case for both genera to be subsumed within the genus *Zosterops*. However, for the purpose of maximising the number of tree tips, I assumed that the current genus names reflect a close relationship between the species and add them into the tree accordingly. The only species within the region that I do not attempt to add to the tree is *Z. santacrucis* as its true position in the tree is ambiguous. Murphy and Mathews (1929) favoured a relationship with *Z. samoensis* from Samoa but this was rejected by Mees (1969).

Where sequence data was not available additional tips were built into the incipient species tree using the online program Phylowidget (Jordan & Peil 2008). The incipient species tree is shown in Appendix 3.1.C.

3.3.4 Lineages through time

Lineage through time plots and γ-statistics (Pybus & Harvey 2000) for the three phylogenetic trees were performed using the APE package (Paradis *et al.* 2004) in the statistical program R (R Development Core Team). The lineage through time plot showed how lineages accumulate over time and a negative value of the γ-statistic indicated a slowdown in the rate of speciation. The lineage axis in these plots is usually logged because an exponential increase in lineages is expected if there is an equal chance of each branch splitting. The statistical significance of the γ-statistics was tested in R under a one-tailed test.

3.3.5 Tree imbalance

Tree imbalance was tested using the package apTreeshape in R (Bortolussi *et al.* 2006). An Aldous graphical test was used to see if the data was a better fit for a Yule or a PDA (Proportional to Distinguishable Arrangements) model (Aldous 1996; Aldous). The shape of each phylogenetic tree was quantified using a Colless statistic (Kirkpatrick & Slatkin 1993). The larger the value of the Colless statistic the more unbalanced the tree (Blum *et al.* 2006).

3.3.6 Geographic isolation and species diversification rates

I calculated species net diversification rates (McCune 1997) as:

Rate = (ln(number of extant species) –ln(initial species diversity)/ time

Three estimates of per-lineage diversification rate were obtained, one for each of the interpretations of the Four Gene Tree. Species numbers were therefore based both on taxonomic divisions (Mees 1957; 1961; 1969; Sibley & Monroe 1990) and on mitochondrial data. I used crown group age for the time of diversification, which was in millions of years and was taken from the Four Gene tree. As crown group age was used initial species diversity was taken as being two (Klak *et al.* 2004; Magallón & Sanderson 2001). I also obtained three estimates of diversification rate from African and Indian Ocean taxa using the same sets of principles to select taxa. Species numbers were based on Sibley and Monroe (1990) and on the gene tree of Warren *et al.* (2006). Crown ages for the African and Indian Ocean Clade were taken from the Partitioned Three Gene Tree (Chapter 2, Figure 2.3).

3.3.7 Rates of divergence in allopatry and time scales to speciation

The node ages generated from the calibrated molecular tree were used for the ages of individual species. Species age was taken to be the age of divergence from the sister species. It is possible that this produced an overestimate of species age if the true sister species was an unknown extinct species. Where posterior support values were lower than estimates from previous trees, better supported ages from those trees were used (Chapter 2 and Warren *et al.* 2006). A list of the ages used is in Appendix 3.2. These ages were used to compare the times to allopatry between Zosteropidae from the south west Pacific and the Indian Oceans. Time to allopatry is used here as a measure of the second rate limiting step in Mayr's (1947) model, divergence under selection. I used Student's t-test to test if the values from the two regions were significantly different.

3.3.8 Sympatric species and time to range expansion

Since it is assumed that species cannot come into sympatry until they can ecologically coexist, time to sympatry is used as a surrogate for the average time required until range expansion. To test if sympatric species are less closely related to each other than expected by chance, I noted the age of all the ancestral node of all the sympatric pairs in the tree and calculated a mean value. For each of the three trees in turn, I generated random pairs of taxa for each island that contains sympatric species. Random pairs were generated in two ways: first by fixing one of the species as one that actually occupies the island concerned and then randomly selecting a second species; and second by allowing both species of the sympatric pairs to be selected randomly. I then obtained one- and two-tailed p-values to test if the observed mean age of sympatric species was significantly different from that expected under these two random scenarios.

3.4 Results

3.4.1 Lineages through time

The lineage through time plots for all three phylogenetic trees and the corresponding γ-statistics and p-values are shown in Figure 3.1. All three figures show a slowdown in diversification rate, a pattern supported by the negative γ-statistics, although the slowdown in the Incipient Species Tree is not statistically significant. The slowdown is statistically significant for the other trees, however.

3.4.2 Tree Imbalance

The Aldous plots (Figure 3.2) suggest that the Yule model is a better fit for the data than the PDA model, as there is a closer match between the line predicted from the Yule model and the green line, the median regression line, that predicted from the PDA model. All the trees are balanced as shown by low Colless statistics (negative in all three cases).

3.4.3 Speciation Rates

Estimated rates of diversification in taxa per million years for the whole Pacific clade were: i) 0.76 for the conservative tree, ii) 0.80 for the monophyletic tips tree and iii) 0.98 for the incipient species tree. Rates for particular clades on the incipient species tree were even faster, such as the Pacific *Z. lateralis* clade which had a rate of 3.70 taxa per million years. Rates for the African and Indian Ocean species were noticeably slower.

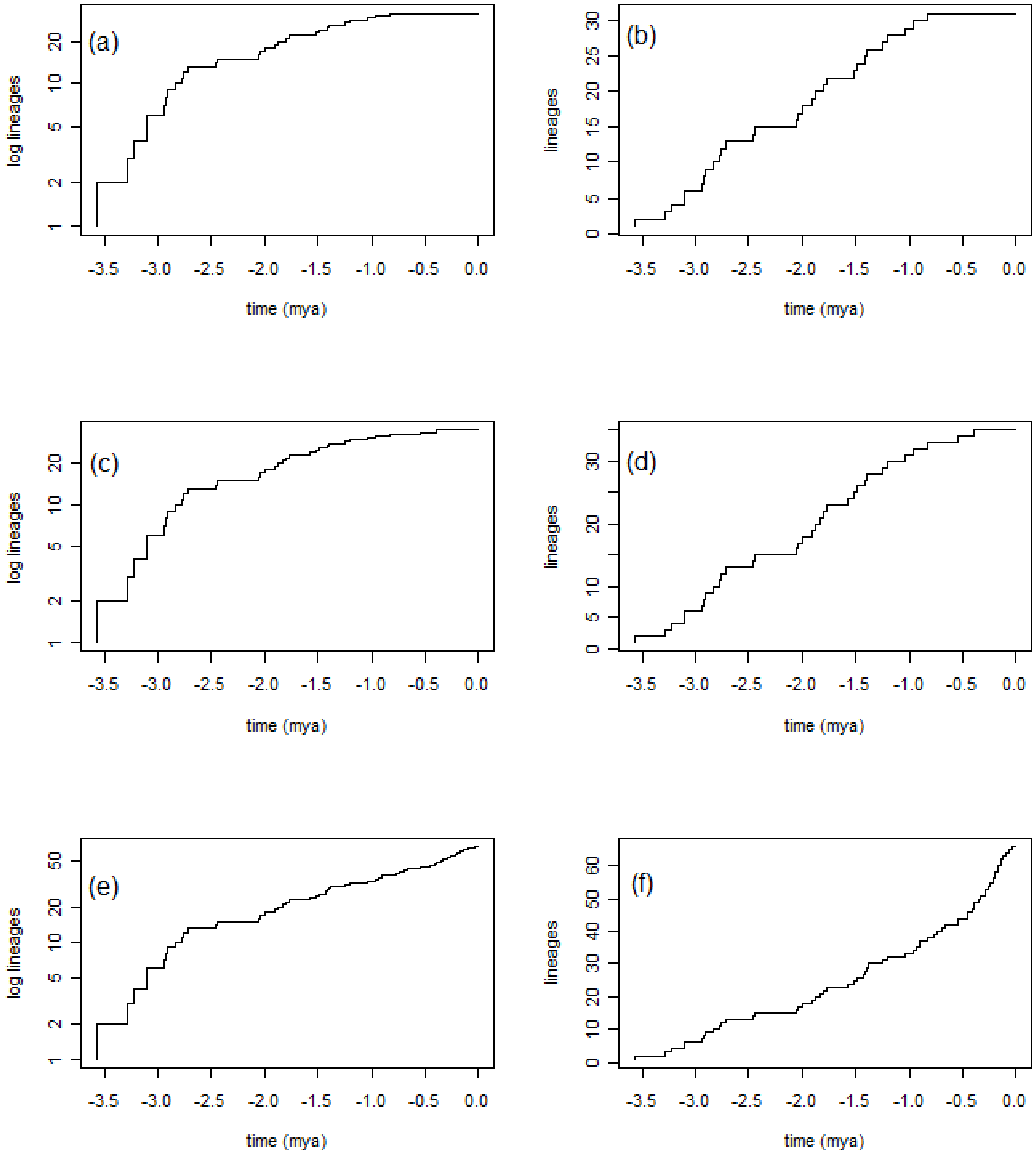


Figure 3.1. Lineage through time plots based on logged (a, c and e) and linear (b, d and f) data for the three phylogenetic trees: a) and b) are plots for the Conservative tree, c) and d) for the Reciprocally Monophyletic tree and e) and f) for the Incipient species tree. The γ- statistics for the three trees are: Conservative tree = -5.24 (p-value = 0.001); Reciprocally Monophyletic tree = -4.96 (p-value = 0.001); ; Incipient species tree = -1.47 (p-value = 0.07);

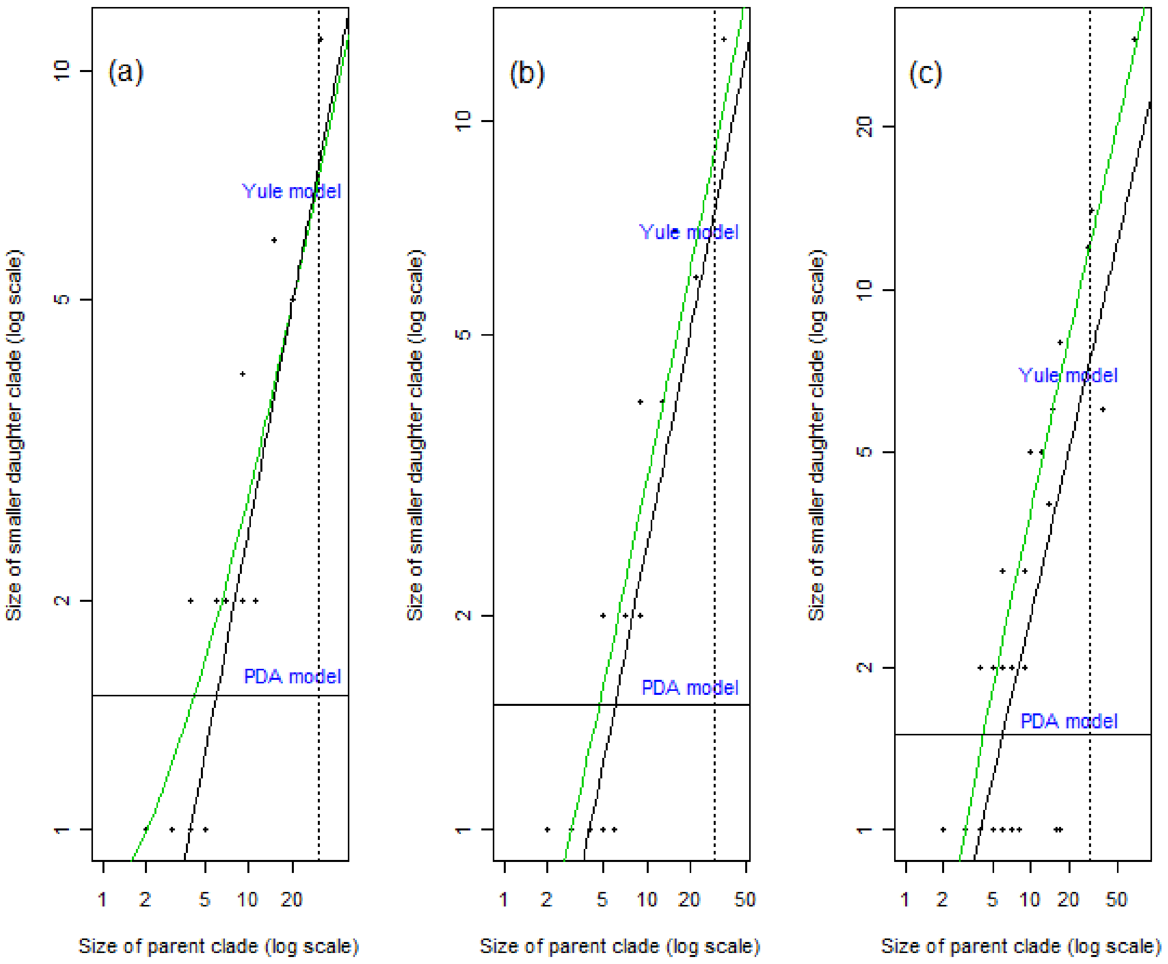


Figure 3.2. Aldous plots for the three phylogenetic trees: a) the Conservative tree, b) the Reciprocally Monophyletic tree and c) the Incipient species tree. The green line represents the median regression estimated from the tree data. The diagonal solid line represents the Yule model and the horizontal solid line represents the PDA model. The Colless statistics for the three trees: a) Conservative tree = -0.350, b) Reciprocally Monophyletic tree = -0.497 and c) Incipient species tree = -0.68 show that the trees are balanced in all cases.

Table 3.1 Estimated diversification rates for the Pacific clade and various subclades within it. Confidence intervals (CI) are also shown. *CI not available due to low confidence at the node. **The African and Indian Ocean islands clade (AIO) was aged on the Partitioned Three Gene Tree (Chapter 2, Figure 2.3).

	Conservative Species Tree		**Monophyletic Tree**		**Incipient species Tree**	
Clade Name	**No. taxa**	**Rate (CI)**	**No. taxa**	**Rate (CI)**	**No. taxa**	**Rate (CI)**
Pacific	31	0.77 (0.66 - 0.87)	35	0.80 (0.69 - 0.91)	66	0.98 (0.84 - 1.12)
Vanuatu*	20	0.70 (-)	22	0.73 (-)	37	0.89 (-)
New Caledonia	9	0.55 (0.46 - 0.67)	9	0.54 (0.46 - 0.67)	12	0.65 (0.55 - 0.80)
Lateralis	1	-	3	0.72 (0.48 - 0.83)	16	1.14 (0.90 - 1.85)
Pacific Lateralis	1	-	1	-	15	3.70 (2.48 - 5.71)
African Clade**	18	0.16 (0.13 - 0.20)	21	0.56 (0.45 - 0.69)	26	0.61 (0.49 - 0.75)

3.4.4 Geographic isolation and island comparison

Table 3.2 shows a comparison between two oceanic regions inhabited by the Zosteropidae. The south west Pacific has many more *Zosterops* species than the Indian Ocean. Total island area and average island area are both inflated by very large islands, Madagascar in the Indian Ocean and New Zealand in the south west Pacific. The UN isolation index is similar for both regions but the components comprising that differences are different. On average, Indian Ocean islands are twice as far from the nearest similar sized island as Pacific Ocean islands but twice as near to a large land mass. In particular, there are about five times as many islands in the south west Pacific.

Table 3.2. A comparison of the number of insular *Zosterops* species in two oceanic regions and the characteristics of the islands in the region in particular relating to the number, size and isolation of islands available for colonisation.

Region	SW Pacific	Indian Ocean
Number of islands of 5 km^2 or larger	126	24
Number of *Zosterops* species in the region	26	10
Number of endemic *Zosterops species*	25	10
Total island area in the region	346545.18	594792.7
Average island area	3039.87	23791.708
Average distance to nearest island of the same or larger size	76.42	137.64
Average distance to the next island group	581.67	577.2
Average distance to the nearest continent	1831.75	934.4
Average isolation index for the region	69.83	62.88
Average sea depth between the island and the nearest land	1501.22	2680

3.4.5 Rates of divergence in allopatry and time scales to speciation

The time taken to reach allopatry was marginally not significantly different between the African and Indian island *Zosterops* and those from the south west Pacific, although there was a trend towards a more rapid rate to allopatry in the Pacific region (Welch two sample t-test: t = 3.08, df = 14.7, p = 0.08). Similarly, rates of rate expansion, as represented by the time required to come into sympatry were not significantly different between the two regions (Welch two sample t-test: t = 0.81, df = 28.8, p = 0.42).

3.4.6 Sympatric species and of range expansion

The observed and expected ages for sympatric pairs of taxa for the three different trees are shown in Table 3.2. For the first two trees the age of sympatric species in no greater than would be expected by chance (two-tailed P-value >0.05 in all cases). However, the incipient species tree suggests that sympatric species are significantly more distantly related than would be expected by chance alone (two-tailed P-value = 0.002 for both the fixed and free randomisation types).

Table 3.3. The observed and expected ages for sympatric pairs of taxa for the three different trees. For each tree the mean and minimum observed and expected values are shown both for when the randomised species pair is 'fixed' to contain one of the actual species on the island and when it is 'free' to select all the sympatrics at random. Age is given in million years (my).

Tree type	**conservative**				**monophyly**				**incipient species**		
Randomisation type	**fixed**		**free**		**fixed**		**free**		**fixed**	**free**	
age type	**mean**	**min**	**mean**	**min**	**mean**	**min**	**mean**	**min**	**mean**	**min**	**mean**
observed age (my)	3.3	2	3.3	2	3.3	2	3.3	2	3.57	3.57	3.57
mean expected age (my)	3.27	2.02	3.24	1.98	3.25	1.86	3.23	1.91	3.01	0.99	3.15
median expected age (my)	3.29	2	3.25	2	3.27	1.83	3.25	1.91	3.04	0.54	3.13
one tailed P-value	0.458	0.543	0.397	0.516	0.418	0.444	0.378	0.492	0.001	0.001	0.001
two tailed P-value	0.916	1	0.794	1	0.836	0.888	0.756	0.984	0.002	0.002	0.002

3.5 Discussion

My results show that the Zosteropidae of the south west Pacific show the early-burst of phylogenetic diversification followed by a significant slowdown. Phylogenetic diversification rates were extremely rapid compared to other vertebrate groups (Johnson & Cicero 2002; Lovette *et al.* 2002; Roy 1997) but the pattern of phylogenetic branching was balanced suggesting that the result is not biased by particular speciose clades. In comparison to Indian Ocean island populations, the times required for range expansion or for allopatric species to develop was not significantly more rapid and nor did the average age of sympatric species depart significantly from that expected at random. Overall these findings are consistent with what would be expected under an adaptive radiation model, and the availability of island niches seems the most probable reason for the explosive diversification of the Zosteropidae of the south west Pacific.

3.5.1 Lineages through time and the mode of phylogenetic evolution

The lineage through time plots indicate a dramatic slowdown in the *Zosterops* of the south west Pacific. This agrees with the finding of Moyle *et al* (2009) that the whole *Zosterops* clade shows a rapid slowdown in lineage rates. However, although there is an overall slowdown across the tree, it is not clear that the rate of slowdown remains constant across the constituent sub-clades of that tree.

As expected from previous studies of white-eyes (Moyle *et al.* 2009), lineage through time plots show an initial burst of speciation irrespective of the precise phylogenetic hypotheses underpinning the analyses. Presumably this corresponds to the early rapid diversification of the group as they expanded into a new area. Following this initial expansion there is an asymptote in the log plot and diversification rates slow. Interestingly in all three lineage through time plots seem to show a second burst of rapid speciation at about two million years before the present is indicated. In fact, the log plots for the first two trees show two consecutive burst of speciation followed by slowdowns. There are two possible explanations for this. The first is that this burst of speciation relates directly to the formation of new land masses. Many of the islands of the region, particularly the islands of Vanuatu, the Loyalty group of New Caledonia and the New Georgia group of the Solomons, are of late Pliocene or early Quaternary volcanic origin. It is plausible therefore that a significant number of new island habitats were emerging at around the two million year mark. The second possible explanation, consistent with the phylogenetic pattern seen in the *Zosterops* of the region, is that it is the result of waves of colonisation, that are part of a taxon cycle as described by Wilson (1961). Taxon cycles are sequential expansions and contractions in the range of species (Ricklefs & Bermingham 2002; Wilson 1961). The two bursts of speciation, each followed by a slowdown, may represent two subsequent waves of colonisation by the *Z. flavifrons* clade and the New Caledonian clade respectively (Chapter 2). This idea is by no means incompatible with the idea of new island emergence but the timings of the second speciation burst do not seem to fit particularly well with known island emergence times.

The slowdown in lineage diversification shown by the Incipient Species Tree is not as extreme as found for phylogenies where more stringent species definitions were applied. Again, there appears to be a second speed up in the diversification rates at about the two million year mark but, in addition, there is a distinct suggestion of a third speed up of diversification rates as the plot reaches the present. This increase towards the present is expected in lineage through time plots because it represents lineage birth without lineage extinction whereas the flatter section in the middle of the plots represents birth minus extinction, as extinct species are not sampled in this part of the plot (Nee 2001; Nee *et al.* 1994a; Nee *et al.* 1994b). However, the apparent speeding up of speciation rates in the incipient species tree may represent the latest wave in a taxon cycle, in this case due to the relatively recent expansion of the *Z. lateralis* clade across the south west Pacific. Given that this is the least conservative tree, an alternative explanation for the observed pattern is that I overestimated the number of potential incipient species.

3.5.2 Lineage diversification rates

Per-lineage diversification rates estimated from the *Zosterops* in this study were faster than most bird genera examined to date (Price 2008; Slikas 1997; Voelker 1999) and comparable to some of the fastest diversifying groups from other taxa (Bell & Donoghue 2005; Hodges & Arnold 1994; McCune 1997). The complete clade rates were, however, less than half the rate estimated for the same species group by Moyle *et al.* (2009), who estimated a rate of 1.95 to 2.63 species per million years. This difference can be attributed to different calibration methods. Moyle *et al.* (2009) used a clock calibrated by geological evidence whereas I based my times on a molecular clock with a base substitution rate of 2% per million years (Weir & Schluter 2008). Both methods make assumptions and the ages on the molecular clock are subject to a certain amount of error. However, there are also reasons to be cautious about dating based on island emergence as it assumes that the emergence of the island is co-incident with the speciation event. A species may in fact be older than the island it currently inhabits if it evolved on a different island and dispersed to a newly available island before going extinct. A species may also be younger than the island it inhabits if it arrived and or diverged on the island long after the island formed. The fact that the younger *Z. rendovae* allospecies group is found on comparatively old islands is suggestive of the latter possibility. Ideally the problem would be solved by calibrating the clock with fossil evidence but unfortunately the fossil record for white-eyes is extremely poor (Steadman 2006).

The Pacific clade of *Z. lateralis* is very young with a crown age of only 0.55 million years. Despite the young age of the clade, ten island forms of *Z. lateralis* (*lateralis, chlorocephalus, tephropleurus, griseonatus, nigrescens, melanops, vatensis, tropica, valuensis* and *flaviceps*) are recognised on traditional taxonomic methods, translating to a lineage diversification rate of 4.23 taxa per million years. In comparison, there are only four mainland forms (*gouldi*, *halmaturina*, *cornwalli* and *ramsayi*) giving a diversification rate of 0.74 taxa per million years. The disparity in lineage diversification rates is even more distinct using the lineages identified from the incipient species tree rather than the morphological designations, with fifteen monophyletic island lineages compared to only two distinct mainland lineages. This translates to lineage diversification rates of 3.70 taxa per million years in insular *Z. lateralis* and 0.38 taxa per million years for mainland lineages. These later figures are upper estimates of lineage diversification rather than speciation as many of the groups are unlikely to be reproductively isolated as yet. Taking the average time to allospecies of 1.91 million years, calculated from the allospecies data for the south west Pacific as the divergence time to full species status, gives a rate of 1.38 taxa per million years for speciation in *Z. lateralis*. This is slightly faster than speciation rates on islands for the south Pacific clade as a whole. Again this is to be expected because there is, as yet, no extinction in this part of the tree so diversification rates represent an upper estimate for the net rate of differentiation.

3.5.3 Tree imbalance

Although there appear to be faster speciation rates in different lineages, the overall shape of the all versions of the tree are balanced. This is because the three distinct clades within the tree are balanced so even though there may be some imbalance within each clade the overall shape of the tree remains balanced. The Yule model has a constant per lineage probability of speciation which results in a relationship between parent clade size and daughter clade size. The average node age of the three different clades differ, with node ages from the 'Vanuatu' clade being the oldest on average and from the '*Z. lateralis'* clade being the youngest. This suggests that the three clades are of different ages which would support the theory of successive waves of *Zosterops* colonisation.

3.5.4 Stages of speciation: geography, allopatry and sympatry

Speciation rates have been shown to be much faster on the islands of the South Pacific than they are on the mainland, but speciation rates are also noticeably faster in the south west Pacific, than they are in the Indian Ocean, (0.99 taxa per million years versus 0.63 taxa per million years). Here I ask why the *Zosterops* have speciated so quickly and why are there different diversification rates in different geographic regions.

The first rate limiting step in species formation is the frequency of barriers or dispersal events (Mayr 1947; Phillimore & Price 2009). The advantage of an oceanic setting is that islands provide an opportunity for both colonisation and isolation. Here, it seems that the differences in speciation rates is not due to within clade characteristics but due to the number of opportunities for population divergence. In this case a greater number of islands in the south west Pacific seems to account for a greater number of species. Islands are closer together on average which potentially means more opportunity for a stepping stone pattern of dispersal and speciation. However, with only a single comparison between the south west Pacific and the Indian Ocean, it is not possible to indentify causes beyond the association between a high rate of speciation and a large number of islands.

The second rate limiting step in species formation is the divergence of traits in response to selection or drift (Mayr 1947; Phillimore & Price 2009). The emergence of taxonomically distinguishable species is likely to correlate with the time required for divergence in allopatry. However, the time that is required for allopatric species to develop does not seem to differ significantly between the two regions suggesting that ecological or sexual divergence happens at a constant rate and does not limit the rate of speciation. It should be noted that, because the species from the same region were in the same clades, many of the estimated ages passed through the same nodes and the analysis could be considered to contain pseudoreplication. Again, therefore, these results need to be interpreted cautiously until a larger phylogeny is available.

Randomisations of sympatric species pairs showed that, for the both the conservative tree and the reciprocally monophyletic tree, sympatric species were no more distantly related than expected by chance. This result is surprising because sympatric congeners are not expected to be able to coexist unless they occupy different niches and closely related species will ordinarily have similar niches (Darwin 1859). There are two possible explanations for this result. The first is that *Zosterops* species are not excluded by congenerics occupying a similar niche and so competition does not limit range expansion or, consequently, the rate of speciation. Moyle *et al.* (2009) suggested that rapid evolutionary change in dispersal ability is the driver of diversification and that this is more likely to be important than ecological speciation because there is little morphological or ecological variation in the Zosteropidae. Certainly there is little that could be described as spectacular morphological variation among the Zosteropidae, but it is not clear that that means that there is no ecological speciation going on. Indeed some islands have sympatric species that appear to have been in an ecologically stable state for thousands of years. To coexist in sympatry species must have niche differences and in some cases they are known to do so with, for example, *Z. murphyi* and *Z. kulambangrae* separating by altitude on Kulambangrae (Mayr & Diamond 2001). One possibility is that character displacement takes place, at least partly, after sympatry is achieved. Another possibility is that character displacement occurs in allopatry and this takes a substantial time to complete. This is supported by the significant age differences between sympatric pairs in the incipient species tree. This result is at least partly driven by the addition of multiple *Z. lateralis* at the tips of the tree. This unusual species has only recently colonised the region and so all its forms are extant and only recently diverged. It may be the most recent wave of a taxon cycle that occurs repeatedly across the region. If colonisation happens in waves then the age structure would also be layered with the set of species from the oldest wave being the oldest in the region and successive waves being younger. In general, sympatric species would consist of forms from different waves and this might mask any signal of sympatrics having to have diverged by a minimum amount.

3.5.5 Summary

Rabosky and Lovette (2008b) showed that a decline in diversification rates through time, as evidenced by lineage through time plots and identified in this study, is more likely to be the result of declining speciation rates rather than increasing extinction rates. This strongly suggests that as availability of islands can be evoked as a reason for rapid speciation in the Zosteropidae, so saturation of islands might be the reason for the subsequent slowdown. Interestingly there is a strong suggestion that a tree based on extant lineages (Chapter 2) is not the whole story. The scenario of multiple waves and extinction implies that there are a number of extinct species missing from this tree. Many clades appear to undergo rapid diversification in their history because speciation but not extinction rates have changed over the histories of those groups (Nee *et al.* 1994a). Interestingly, there is evidence of separate colonisation waves on the Indian Ocean islands again with sympatric species coming from different clades. For example, *Zosterops mouroniensis* from Grande Cormore is part of the ‘Ancient Indian Ocean’ white-eye clade and the sympatric *Zosterops maderaspatanus kirki* being part of the more recent ‘Maderaspatanus’ clade (clade names taken from Warren *et al.* 2005).

Although an overall slowdown in speciation rate is clearly detectable in the Zosteropidae of the south west Pacific, the rate of slowdown is not constant and potentially shows repeated periods of accelerated speciation. Taken together these results suggest that the fast speciation rates are associated with extensive island and niche availability in the south west Pacific and that variations in the diversification rate across the lineage through time plots are consistent with a model of a taxon cycle with repeated waves of colonisation.

Chapter 4

Morphological evolution in an insular radiation of passerine birds

4.1 Abstract

Studies of island systems have been instrumental in the formation of many of the theories of trait evolution. Molecular phylogenies for insular taxa now offer the potential for the phenotypic evolution of insular populations to be studied in a historical context. Here I combine morphological data and molecular phylogenetic trees to investigate the mode of evolution, character displacement among sympatric species and influence of biogeography on morphological evolution in south west Pacific white-eyes. This group is of particular interest because it has been shown to have undergone rapid recent phylogenetic divergence and has been invoked to support theories on ecological speciation. I find no evidence for either an early-burst of morphological evolution or for morphological evolution accompanying speciation events. Instead, across most traits there is no significant departure from a Brownian motion null model. Similarly, I find little general evidence for character displacement among sympatric species, although there is some evidence for particular traits in a small number of individual island cases. Finally, although I find no correlation between wing length and indices of dispersal, I do find a significant association between large body size and dwelling on small islands. This last finding is consistent with the 'Island Rule' in passerine birds and indicates a role for community ecology in morphological evolution in this group. However, taken together, my results do not support many of the predictions regarding ecological speciation. I suggest that this is because ongoing waves of colonisation and extinction mean that this avian radiation has not reached a stable equilibrium in terms of its morphological evolution, and the dynamic nature of the system means that at any one

moment it is unlikely to be at such an equilibrium. Under this scenario, rapid species turnover in island communities will tend to obscure underlying ecological mechanisms, such as character displacement and habitat filtering.

4.2 Introduction

What drives the exceptional morphological diversification of many island species? Islands typically support fewer species of animals and plants than an equivalent area of the mainland, yet insular clades are often thought to be unusually diverse in form (Grant 1968; MacArthur & Wilson 1967). Consequently, island taxa have been instrumental in the development of ideas about trait evolution including the roles of founder effects (Barton & Charlesworth 1984; Carson & Templeton 1984; Grant 2001; Lande 1980; Mayr 1954; Templeton 1980), character displacement (Grant & Grant 1994; 2006; Schluter 2000a) and adaptive radiation (Grant & Grant 2008b; Lovette *et al.* 2002) and trait-mediated competition in community assembly (e.g. Connor & Simberloff 1979; Diamond 1975). In reaching an understanding of the influences of these processes on trait evolution, morphological differences should be studied in the light of both their ecological setting and the evolutionary relationships among the taxa concerned (Harvey & Pagel 1991; Webb *et al.* 2002). The existence of closely related species on islands, in combination with the apparent ecological simplicity of such systems, means that evolutionary ecology can be more easily studied for island species than their mainland counterparts (Darwin 1859; Wallace 1891). Here, I use south west Pacific white-eyes, Zosteropidae, a classic system in the study of island evolution (Diamond 1970; Lack 1971; Mayr 1940), to test how evolutionary history, ecology and biogeography have influenced the tempo and mode of morphological diversification.

4.2.1 Trait evolution

Phenotypic differences among island populations may potentially arise due to neutral processes, or as a result of selection, or as a combination of the two. There are two neutral processes whereby island populations may diverge from each other: drift and founder effects. These are both mechanisms by which trait divergence occurs due to the stochastic process involved when successive generations are a subsample of preceding generations, or founding populations are a subsample of a source population (Lande 1980). Random genetic drift is expected to act slowly but, especially in small populations, could lead to trait divergence in allopatric populations (Dobzhansky 1951; Wright 1931). Founder effects models describe a the process whereby a founding population carries only a small fraction of the genes that are present in the parent population, thereby leading to unusually high frequencies for previously rare genes and unusual gene combinations (Huxley 1938; Kaneshiro 1989). Theoretically, therefore, founder effects could lead to rapid evolutionary change. In his original formulation of founder effects theory, Mayr (1954) proposed his ‘genetic revolution’ model to explain greater phenotypic differences among island populations than among taxa on a continent. There have since been other variants on this founder-induced model (Carson 1968; Templeton 1981) but empirical evidence in support of founder effects from naturally-founded, wild insular populations remains scarce and, if they occur at all, they appear to only play a minor role (Coyne & Orr 2004; Price 2008; Rice & Hostert 1993).

Selection also has the potential to cause rapid trait divergence, especially when it is directional in nature. This can be the result of natural selection where survival in a novel environment can select for phenotypic change and can result in repeated patterns in similar environments, for example the frequent evolution of large size and flightlessness in island birds (Losos & Ricklefs 2009a). It can also be the result of sexual selection either due to male competition (Liker & Barta 2009; Wilson 1992) or female choice (Anderson 1994; Hill 1994; Senar *et al.* 2005). Or it can be a combination of the two types of selection. For example, the divergence of song types can be driven by female choice (Nowicki *et al.* 2000) or by the requirements for sound to travel in a novel environment (Slabbekoorn & Peet 2003; Slabbekoorn & Smith 2002).

Adaptive radiation is one type of selection-based model where trait evolution is initially fast as new forms occupy vacant ecological niches but then slows down as niches become filled (Schluter 2000b). Darwin's finches (Geospizinae) are a classic example of the first phase of an adaptive radiation (Grant & Grant 2008a; Lack 1945; 1947). The first stage is ecological divergence, typically with associated morphological specialisations and often followed by the establishment of congeneric sympatrics (Grant & Grant 2008a). Usually the first phase is characterised by pre-mating rather than post-mating reproductive isolation (Grant 2001; Grant & Grant 1997). Subsequent phases that lead to complete isolation may be, at least partially, driven by morphological differences but full reproductive divergence may take a considerable time. A broad survey of speciation mechanisms in birds by Price and Bouvier (2002) found that partial incompatibility was reached, on average, after about 2.5 million years and other studies have shown that average hybridisation persistence, the period during which viable hybrids can be produced between diverging species, is of the order of 32 million years in birds (Grant & Grant 2008a; Gray 1958; Prager & Wilson 1975). In the short term therefore, character displacement is likely to be particularly important in maintaining reproductive barriers in sympatric congenerics (Rolando 1993).

4.2.2 Community structure, sympatric species and character displacement

While community composition and change come about partly via repeated colonisation and extinction, community structure is also likely to be governed by factors that determine the extent to which related species can co-exist (Lack 1971). In particular, competition for limited resources, such as food and breeding opportunities, is expected to strongly influence which species can and cannot co-occur. Darwin (1859) argued that competition should be most severe amongst closely related species. Thus, theory predicts that for a species to colonise an area that is occupied by a congener the colonising species should be ecologically divergent from the incumbent (Mees 1969). Reproductive isolation, particularly in birds, is generally thought to evolve in allopatry or perhaps parapatry (Coyne & Price 2000; Phillimore *et al.* 2008a). Consequently, congeners may be able to coexist due to morphological divergence that has previously arisen while in allopatry, or as a result of character displacement on secondary sympatry. Schluter (2000b) concluded that character displacement occurs frequently and plays an important role in the evolution of diversity. Stable sympatric pairs are expected to compete very little with each other in the present because past competition drove them to separate into different niches (Macarthur & Levins 1967). This is often referred to as the 'ghost of competition past' (Connell 1980; Schluter 2000a).

Sympatric species are expected to differ in traits associated with the ecological differences between them, which in the case of birds are typically thought to be size (Losos 1990) and bill shape (Grant 1966; Yamagishi & Eguchi 1996). Hutchinson (1959) deduced that competing species might differ in size by a constant ratio and concluded that a mean ratio of 1:3 was needed to co-exist at the same trophic level (Losos *et al.* 1989; Roth 1981; Simberloff 1983). There are many examples in birds of congeners in a single location differing in size and shape leading to separation in feeding behaviour (Ashmole 1968; Lack 1971; Newton 1967; Vaurie 1951). This has often been interpreted as the result of character displacement, although it is very difficult to prove (Lack 1971). Even when they occupy a single island, congenerics may diverge ecologically along a number of axes that may be behavioural or morphological. For example, the sympatric African species *Zosterops senegalensis* and *Zosterops mouroniensis* separate by altitude on Moheli (Benson 1960). In other cases, sympatric species might be found in the same habitat but differ either in which part of the habitat they occupy or the size or type of food that they take (Baldwin 1953; Betts 1955; Bowman 1961; Grant 1968). While it is possible to detect ecological differences between sympatric species, it remains a major challenge to determine if their origin and maintenance are due to the role of interspecific competition (Law & Watkinson 1989).

4.2.3 Biogeography: dispersal and endemism

In MacArthur and Wilson's (1963; 1967) theory of island biogeography, the arrival of new species are expected to balance extinctions of incumbents in a dynamic equilibrium. Under these conditions, isolated islands that have a low rate of immigration are also expected to have a low natural rate of extinction (Diamond 1984; Steadman 2006). This may afford more time for isolated insular faunas to diverge resulting in high levels of endemism on islands (Diamond 1980; Price 2008). Although biased towards species with strong dispersal ability there will be an element of stochasticity in the sample and order of species that arrive on isolated islands. Newly formed oceanic islands can provide highly novel environments for evolution with potentially extensive vacant niche space. Early colonists will therefore have an opportunity to adapt to new ecological niches, which either did not exist in their area of origin or were occupied by other species (Barton 1989; Cox & Ricklefs 1977; Lack 1969). Hence, the direction of evolution and adaptation is likely to depend not only on the physical characteristics of the island (e.g., area, elevation, location and prevailing weather conditions) but also the particular assemblage of species that find their way to the island and the order in which they arrive (Robinson & Dickerson 1987).

One of the paradoxes of island evolution in birds is that many endemic species that occur on very isolated islands are poor dispersers or even flightless (Diamond *et al.* 1976). Complete flightlessness is known from eleven bird families, most of which are islands dwelling species (McCall *et al.* 1998). In addition, many island forms that retain the power of flight have very limited distributions, commonly being endemic to single islands despite the close proximity of other islands (Mayr & Diamond 2001). It has been suggested that dispersive ability might be a disadvantage on islands (Roff 1997). Strong dispersers in many groups of birds have long wings relative to body size (Lockwood *et al.* 1998). Since island endemic birds often exhibit some decline in dispersal ability, I suggest that morphological diversification along axes of relative wing length will be influenced by the degree of geographic and temporal isolation of a given island from its neighbouring landmasses.

The ‘Island Rule’ predicts that, on islands, large-bodied forms evolve to become smaller whereas small-bodied forms evolve to become larger (Brown *et al.* 1993; Forster 1964; Heaney 1978; Lawlor 1982; Lomolino 1985; Lomolino 2005; van Valen 1973; Williamson 1981). The Island Rule remains controversial (Meiri *et al.* 2004), especially in birds (Blondel 2000), but a comprehensive comparative analysis found that birds did obey the island rule with the cut-off point between large- and small-bodied species being approximately 100g (Clegg & Owens 2002). I therefore test the expectation that *Zosterops* species, as small passerines of substantially less than 100g in mass, should evolve towards larger body size on small islands. A related prediction is that relative bill size should also increase in insular bird species (Grant 1965; Lack 1947), a trend that is thought to be a result of niche expansion in feeding ecology on islands (Blondel 2000; Clegg & Owens 2002). I therefore also investigate if this prediction holds true for the Zosteropidae of the south west Pacific.

4.2.4 Trait evolution in the Zosteropidae

The Zosteropidae of the south west Pacific are an ideal system for exploring ideas of trait evolution in an insular context. This group is known to be the result of an explosive radiation into an oceanic region of recently emerged islands (Moyle *et al.* 2009) and is thought to be among the earliest colonisers of remote islands and so are expected to have had access to novel niches during their radiation (Diamond *et al*. 1976; Lack 1971). They are therefore expected to show both early-burst trait evolution, because of their expansion into sparsely occupied areas, and evolution of traits at speciation events.

Island Zosteropidae are also unusual in the high frequency of sympatry they exhibit (Lack 1971). This phenomenon is very rare on the mainland and therefore island *Zosterops* are expected to exhibit character displacement whereby sympatric species differ more than average in morphological traits, allowing them to co-exist in sympatry (Lack 1971). Certainly island *Zosterops* display a wider range of forms than mainland *Zosterops* with both the largest and smallest members of the family being island forms, as are almost all the unusual morphological and colour variants (Lack 1971; Mees 1957; 1961; 1969).

4.3 Methods

4.3.1 Data selection and Phylogenetic trees

In order to minimise the risk of bias from obtaining data from different sources, all morphological data and species and subspecies definitions were taken from Mees (1957; 1961; 1969). I collated data on wing length (maximum chord), tarsus length, tail length and culmen length from 34 species, 67 subspecies and 71 total forms of *Zosterops* from the south west Pacific region. The sample sizes and measurements used for the two trees are shown in Appendix 4.1, with measurements being combined or used separately as necessary to match the taxa as defined in the two different trees outlined below. Data are combined across the sexes due to a combination of small sample size in some species, the unavailability of separate measurements for males and females for many taxa, and the known difficulty of accurately sexing *Zosterops* specimens (McKean 1965; Mees 1969).

I used two alternative phylogenetic trees based on the Four Gene Tree (Chapter 3): the ‘Reciprocally Monophyletic Tree’ (Figure 4.1) and the ‘Incipient Species Tree’ (Figure 4.2), both of which were previously described in Chapter 3. The ‘Reciprocally Monophyletic’ Tree consists of full species for which mitochondrial and microsatellite data is available (Chapter 3 and Clegg & Phillimore 2010; Moyle *et al*. 2009; Phillimore *et al*. 2008b). Where species were missing from the ‘Reciprocally Monophyletic’ Tree due to the unavailability of sequence data, they were inserted into the tree based on the taxonomic treatment of Mees (1957; 1961; 1969) and Mayr (1967) using PhyloWidget (Jordan & Peil 2008).

The Incipient Species Tree is an extension of the Four Gene Tree based on the evolutionary relations deduced by Mees (1957; 1961; 1969) and Mayr (1967). In the Incipient Species Tree the individual species were split up into subgroups. These groups were mainly based around subspecies but in cases where designations indicated by the phylogeny differed from traditional subspecies classifications the phylogenetic designations were generally followed. For instance, *Z. palpebrosus unica* was located outside of the south west Pacific clade as the sister group to *Z. citrinellus* and for this analysis, I treat this relationship as real. This subspecies along with *Z. p. melanura* have been grouped as the Indonesian “yellow-bellied” forms of *Z. palbebrosus* and considered distinct from other *Z. palpebrosus* subspecies (Mees 1957). Therefore I refer to the subspecies pair of *Z. p. unica* and *Z. p. melanura* as *Zosterops parvula*, a now disused specific name that has previously been applied to both subspecies. I include the combined measurements from these two species in the trait analysis based on the Reciprocally Monophyletic Tree and the measurements from each subspecies separately in the trait analysis based on the Incipient Species Tree. In one case, that of *Z. flavifrons perplexa* from Vanuatu, the traditional morphological classification was followed rather than the phylogeny. Genetic analyses by Phillimore *et al.* (2008b) suggest that *Z. flavifrons perplexa* is not a monophyletic taxon. Instead the population of this subspecies from Vanua Lava in the north of Vanuatu is more closely related to *Zosterops flavifrons brevicauda* from Espiritu Santo than the rest of the subspecies (see also Chapter 2). As the morphological data from Mees (1969) lumps measurements from different islands within subspecies, the genetic distinction of *Z. f. perplexa* was ignored. The clade of the Zosteropidae that includes all the species in the south west Pacific also includes a number of species from outside the region. For completeness these species are included in the analyses. Despite the assumptions involved in compiling the larger tree, it has value because it allows use of a far greater range of morphological data and finer grained analysis of morphological divergence.

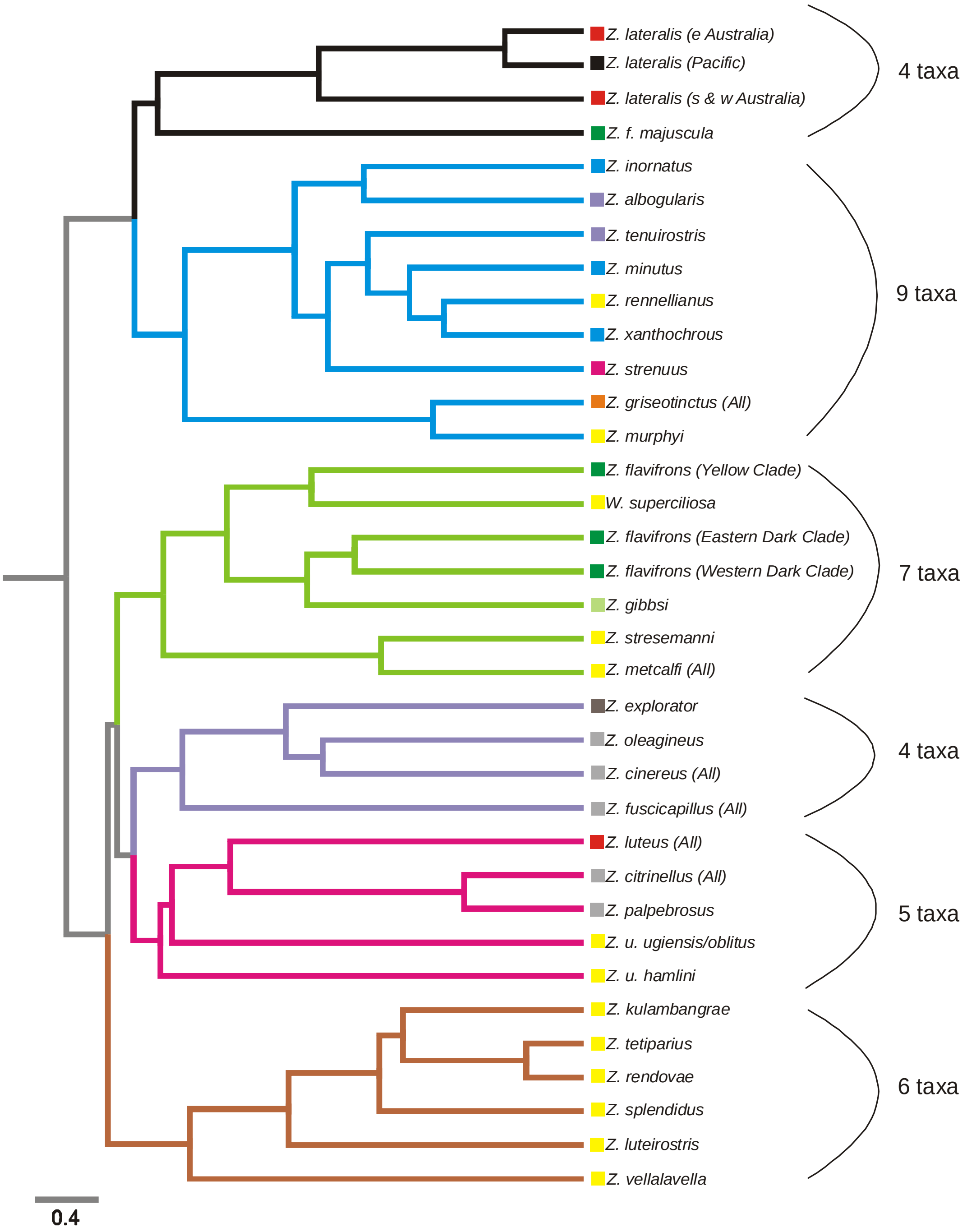


Figure 4.1. The Reciprocally Monophyletic Tree, including all those species for which mitochondrial data was available. Subspecies are not considered as separate entities but are deemed to be included within the species. The different clades considered in the analysis are indicated by the different coloured branches. The geographical locations of individual species are indicated by the coloured boxes at the end of each branch: Australia (Red), New Guinea (Orange), the Bismarks and the Solomons (Yellow), the Santa Cruz Islands (Light Green), Vanuatu (Dark Green), New Caledonia (Blue), Norfolk Island (Purple), Fiji (Brown), Lord Howe Island (Pink) and New Zealand (Dark Grey).

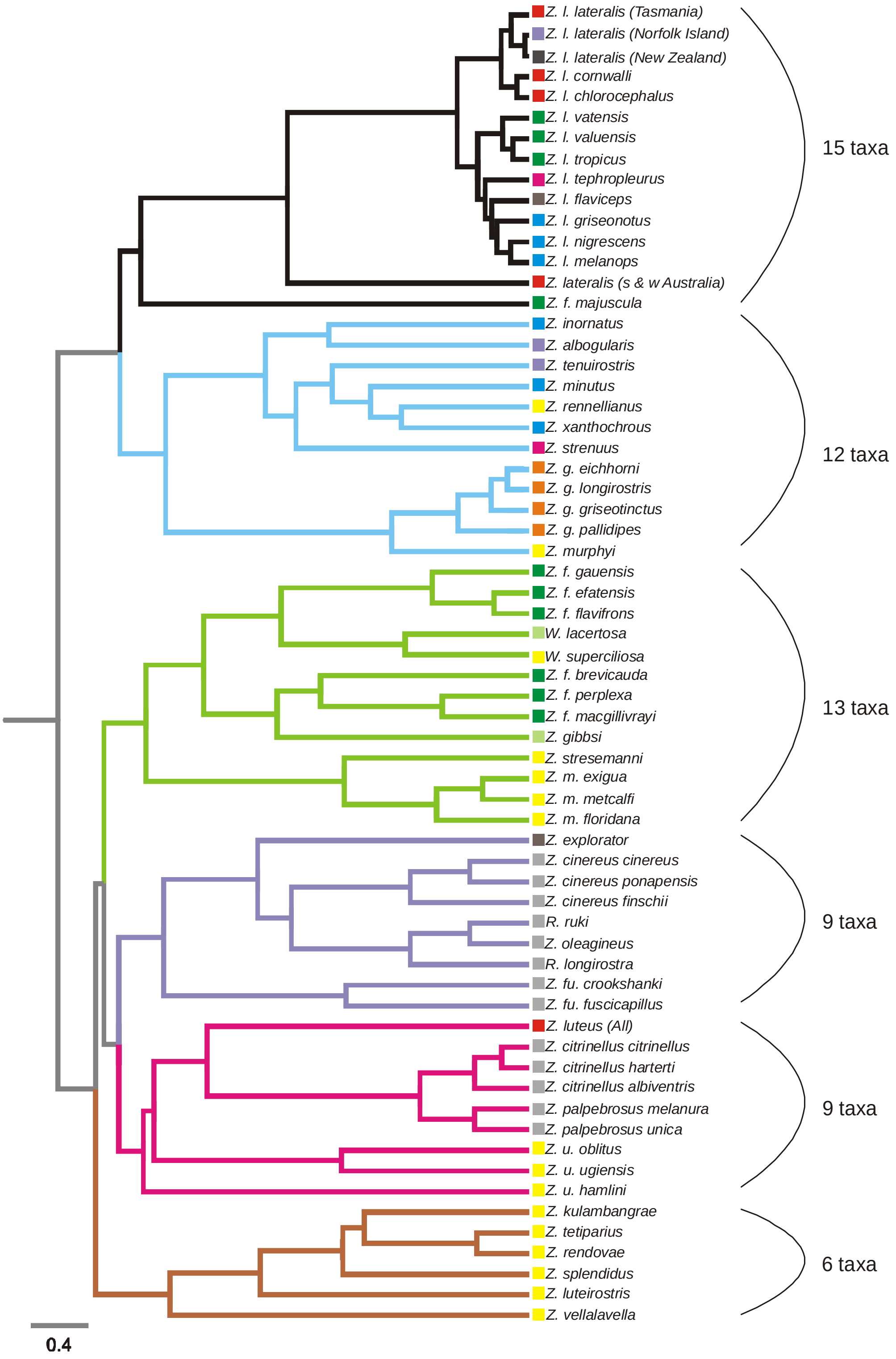


Figure 4.2. The Incipient Species Tree, including all subspecies plus species for which mitochondrial data was not available. The tree is based on mitochondrial data and deductions of the probable positions of those species or subspecies where mitochondrial data was not available or inconclusive using the relationships inferred by Mees (1957; 1961; 1969). The different clades considered in the analysis are indicated by the different coloured branches. The geographical locations of individual species are indicated by the coloured boxes at the end of each branch: Australia (Red), New Guinea (Orange), the Bismarks and the Solomons (Yellow), the Santa Cruz Islands (Light Green), Vanuatu (Dark Green), New Caledonia (Blue), Norfolk Island (Purple), Fiji (Brown), Lord Howe Island (Pink) and New Zealand (Dark Grey).

4.3.2 Principal Component Analysis

In order to reduce the dimensionality of the morphological data for some analyses, principal component analysis (PCA) based on trait covariances was performed on log-transformed wing length (maximum chord), tarsus length, tail length and entire culmen length. These analyses yielded principal component axes, trait loadings and the proportion of the variance each component.

4.3.3 Modelling trait evolution

I tested for departure from the neutral Brownian model using a range of alternative models. First, I tested whether trait diversification is concentrated early in the radiation of a species group: referred to as ‘early-burst’ trait evolution. I also tested whether trait diversification is concentrated at speciation events themselves, this later model is referred to as punctuated or speciational evolution (Pagel 1999). Finally, I tested whether trait variation may be non-random but also non-phylogenetic. For example, I tested whether there is a tendency for traits to evolve around a fixed optimum meaning they can be modelled by the Ornstein-Uhlenbeck model of stabilising selection (Butler & King 2004).

Brownian motion is the simplest model of trait evolution and describes the random walk of a trait through time, such that variance increases through time but the expected mean is always equal to the ancestral mean (Felsenstein 1985). This model corresponds to the expectation under random genetic drift or fluctuating selection. However, it is not an appropriate model where trait change is not proportional to time, such as persistent directional selection or where different lineages are under the same selection (Felsenstein 1985; Martins & Hansen 1996). I used Pagel’s λ as a simple test for departure from the Brownian model (Pagel 1997; 1999). It tests the degree to which trait evolution is independent of the phylogeny by altering the internal branch lengths. Internal branches are multiplied by the scaler λ (0 – 1) and the value of λ that makes the data most likely is optimised, with λ = 1 consistent with a Brownian model, λ = 0 suggests that trait values are independent of phylogeny and 0< λ < 1 indicating intermediate phylogenetic signal. Λ values that are significantly lower than one suggest non-Brownian trait evolution but do not provide information on the processes that may have caused departure from the null. I therefore used three additional models to test for alternative non-Brownian modes of trait evolution. I used the Ornstein-Uhlenbeck (OU) model to test for stabilizing selection. The OU model includes the parameters α, which measures the strength of selection (in the special case α being zero results in Brownian motion) and θ which is the optimum trait value. If the phenotype moves away from the optimum or the optimum changes then selection toward the optimum occurs (Butler & King 2004).

I tested for evidence of speciational trait change using Pagel's (1997) kappa. The kappa speciational model is similar to lambda but rather than using a simple scalar to transform internal branch lengths it raises all branch lengths to a power ranging from 0-1. Where kappa=0 trait change is inferred to occur only at speciation events; kappa=1 is equivalent to the Brownian motion model; and 0< kappa >1 suggests that trait change may be concentrated at speciation events but not limited to them. Finally, I tested for evidence of rapid early trait change followed by a slow down (akin to diversity dependence in adaptive radiations) using the Early-burst model (Harmon *et al.* 2008). The support for different statistical models of trait evolution was assessed using the Geiger package (Harmon *et al.* 2008). I used the fitContinuous function to test the fit of the data to the following models: Brownian Motion (BM), Lambda (λ), Ornstein-Uhlenbeck (OU), Kappa (κ), and Early-burst (EB). I used delta AICc scores with trait and phylogeny data to investigate which model of trait evolution receives most support.

4.3.4 Trait differences between sympatric congeners

In order to test whether the phenotypic diversification between sympatric species has been faster than expected under a constant Brownian motion I applied a simulation approach (Martins & Garland 1991). One difficulty that needs to be taken into account here is that phenotypic measurements cannot be considered as independent observations because the species involved are part of a structured phylogeny (Felsenstein 1985; Harvey & Pagel 1991; but see also Ricklefs & Starck 1996). Independent contrasts were therefore calculated as the difference in trait values between pairs of taxa at adjacent tips of the phylogeny, which can be considered independent under a Brownian model (Ricklefs & Starck 1996). These contrasts were then scaled by dividing each raw contrast value by its standard variation (Felsenstein 1985).

In analyses based on the Reciprocally Monophyletic Tree species were used as the tips of the phylogeny as described above. However, in analyses based on the Incipient Species Tree, I had to estimate the phylogenetic position of some subspecies that were missing from the phylogeny. This potentially introduced two sorts of error into the analysis. Firstly, the estimated branch lengths for these inserted taxa may be incorrect. It has been shown, however, that this type of error weakens the method but should not lead to spurious patterns (Grafen 1989; Martins & Garland 1991). The second type of error, which is potentially more serious, was that the assignment of pairs of sister taxa may not be accurate (Purvis & Garland 1993). The impact of this problem should be small for the key analyses because all of the sympatric taxa were fixed in the tree by sequence data so contrasts taken between them should be accurate. Additionally, most of the estimated taxa were subspecies whose relationships are thought to be relatively well known (Mees 1957; 1961; 1969). Nevertheless, given the known existence of cryptic *Zosterops* species (Phillimore *et al.* 2008b), the results from the Incipient Species Tree simulation should be considered with a degree of caution.

To calculate the degree of divergence among sympatric species, I obtained the observed absolute standardized contrasts for sympatric pairs and triplets on each island in turn by dropping all other tips from the phylogeny first. Each island was therefore represented only once by its mean standardized contrast. I then calculated the mean absolute standardized contrast across the entire tree. Dividing the mean contrast of sympatric taxa by the mean calculated across the entire tree gives an indication of whether sympatric species have diverged faster (ratio >1) or slower (ratio <1) than expected. To examine whether mean values across all islands departed from the null expectation I simulated random trait values at the tips under Brownian motion. For each simulated set of trait values I then calculated the statistics described above. This was repeated 10,000 times and observed values were compared with the values generated under Brownian motion using two-tailed tests. This test makes no assumption regarding the Brownian rate parameter and was conducted for both the Reciprocally Monophyletic Tree and the Incipient Species Tree for each trait individually and the first two principal components. Subsequently, I also repeated these calculations for each island in turn to test whether there any island-trait combinations showed significant departure from the simulated null expectation. In addition, I also repeated all analyses with *Z. lateralis* excluded. This was because *Z. lateralis* is known to have been a recent radiation across the islands of the South Pacific (Chapter 2) so if competition after first contact is important, these sympatric pairs may not yet demonstrate character displacement.

I also tested the prediction that a certain minimum difference in multivariate morphological space might be necessary for two species to coexist on a single island. To achieve this I measured the Euclidian distance in two-dimensional morphospace between the position of each species-pair according to the co-ordinates on PC1 and PC2 (see lines between sympatric species in Figure 4.4). The minimum distances across all islands were taken as the observed values. Expected values were generated as the mean minimum distance across 10000 trees simulated in a Brownian motion model. I then tested for a difference between this observed distribution and the simulated distribution. Again these analyses were subsequently repeated for both phylogenetic trees, for each individual island as well as across all islands, and with and without *Z. lateralis*. I also repeated all analyses using mean rather than minimum distance between sympatric pairs.

A step by step description of the simulations together with the R code used to perform them are included in Appendix 4.2.

4.3.5 Biogeographic analyses

I tested for a relationship between morphology and dispersal behaviour using phylogenetic generalised least squares. To quantify variation in dispersal behaviour I used three indices: the number of islands occupied by each species; the area of the largest island occupied by each species; and a maximum distance based on how far each taxa was likely to have dispersed in its current form. Island data was taken from the United Nations Environmental Programme's Island Directory Tables (UNEP). In some cases the maximum distance travelled is known, such as for *Z. l. lateralis* which self-colonised New Zealand from Tasmania in 1830 (Falla *et al.* 1966; North 1904). Where there is no such record it is considered to be the distance to the nearest archipelago for species that occupy more than one island. For endemic species the maximum distance travelled is taken to be zero since it is assumed the species evolved on the island concerned and has not travelled between islands in its current form. Finally the age of each species, as estimated from the Four Gene tree (Chapter 3), is included.

The trait measures considered were the first two axes from the principal component analyses, as well as average wing length, average entire culmen length and average tarsus length. Weight measurements were not available for most species but in a regression of specimens where both weight and tarsus length were known, the two were highly correlated (N = 301, adjusted R2 = 0.55, p-value = <0.001). All the measurements except the two PCA axes and species age were $\log_{10}$ transformed in the models. Wing length and entire culmen length are both modelled as a function of all these potential measures of dispersal ability. Tarsus is also included in both these models to account for overall body size. Finally, I also constructed models for the first two PCA axes based on the potential measures of dispersal ability.

Comparisons across species are potentially confounded by statistical non-independence of data due to shared evolutionary history (Felsenstein 1985; Harvey & Pagel 1991). To account for this I used phylogenetic general linear models implemented in the CAIC package for the statistical program R (Sourceforge). The lambda parameter described above was fitted simultaneously with the regression model to account for the appropriate degree of phylogenetic signal in the model residuals (Pagel 1999).

All statistical analyses were conducted in the R programming environment (R Development Core Team 2009).

4.4 Results

4.4.1 Principal Component Analysis

The PCA loadings for the South Pacific Clade of the Zosteropidae are shown in Table 4.1. In both datasets of *Zosterops* from the Reciprocally Monophyletic Tree and the Incipient Species Tree, the first principal component (PC1) is a general body size measure that explains 81% of the trait variance for each tree dataset. Principal component two (PC2), explaining 12 per cent of the data in the Reciprocally Monophyletic Tree (Table 2a) and 13 per cent of the data in the Incipient Species Tree (Table 2b), is a measure of relative bill length, contrasting bill length with tail and to a lesser extent wing and tarsus. Larger values of PC2 correspond to a relatively longer bill compared with other body traits. The third principal component (PC3) contrasted bill and tail length against wing and tarsus length and accounted for five per cent or less of the data. PC3 and subsequent components are not considered further. The PC values for each species are shown in Appendix 4.1.

Table 4.1. Loadings from principal component analyses for the South Pacific *Zosterops* based on four size measures per species: average maximum wing chord, average tarsus length, average tail length and average culmen length (from bill tip to skull). a) scores based on the dataset from the Reciprocally Monophyletic Tree and b) scores from the Incipient Species Tree.

	a) The species tree				**b) the subspecies tree**			
Loadings:	PC1	PC2	PC3	PC4	PC1	PC2	PC3	PC4
log (average wing length)	0.383	-0.177		0.902	0.355	-0.195	-0.135	0.904
log (average tarsus length)	0.4	-0.333	-0.792	-0.319	0.388	-0.198	-0.841	-0.32
log (average tail length)	0.404	-0.665	0.58	-0.241	0.319	-0.812	0.428	-0.236
log (average bill length)	0.728	0.645	0.164	-0.165	0.789	0.513	0.301	-0.154
Proportion of Variance	0.81	0.12	0.05	0.02	0.81	0.13	0.04	0.01

The relationships of different species in morpho-space as defined by PC1 and PC2 are shown in Figures 4.3 to 4.5. In Figure 4.3 the species are coloured by archipelago matching the colours used in Figure 4.1 and 4.2. Grouping by archipelago does not produce a clear clustering pattern of species in morpho-space (Figure 4.3), suggesting that the archipelago itself is not particularly important in the development of species traits. Grouping by clade produces noticeable clusters, with the possible exception of the blue New Caledonian clade, which appears to be more geographically widespread (Figure 4.4).

Figure 4.5 shows that, while sympatric species differ in morphology these differences are not always along the same axis. For example, *Z. explorator* and *Z. lateralis flaviceps* from Fiji (Figure 4.5b, brown braches) are differentiated by relative bill length but not overall size. In contrast the relative bill lengths of *Z. minutus* and *Z. inornatus* on Lifou (Figure 4.5b, purple branches) are very similar but they are differentiated strongly on the general size axis. The third species in this triplet, *Z. lateralis melanops,* is almost exactly mid-way between the two on the general size axis but is differentiated on axis two relating to beak length, having a particularly short thick bill in comparison to its sympatric congeners.

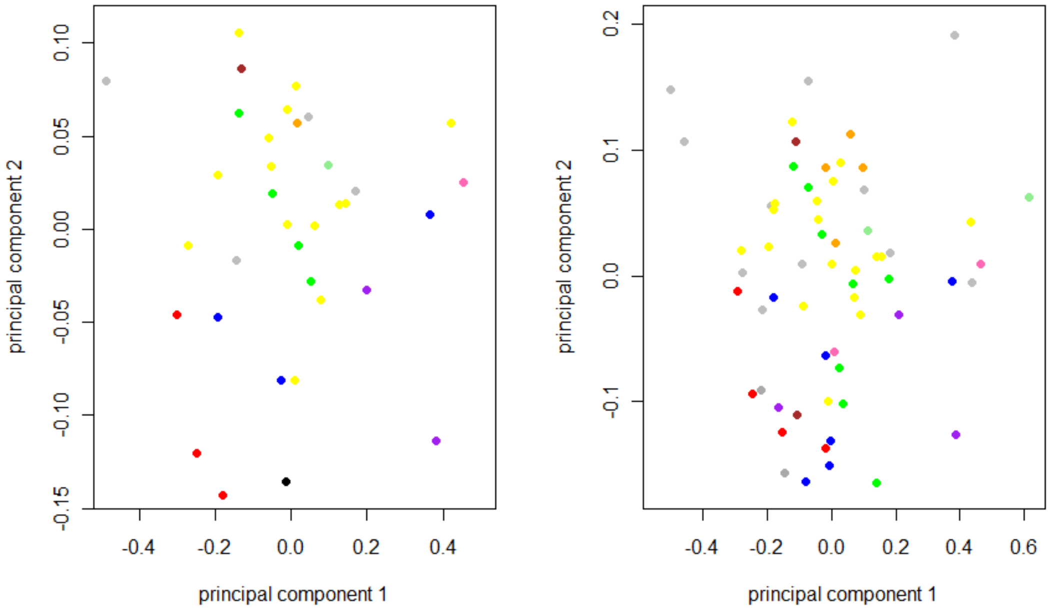


Figure 4.3. *Zosterops* taxa plotted in morphospace for datasets drawn from a) the Reciprocally Monophyletic Tree and b) the Incipient Species Tree. Colours represent taxa from the same archipelago or island matching those in Chapter 2: Figure 2.1. and in Figure 4.1 and 4.2. In both cases, principal component 1 is an index of overall body size while principal component 2 is an index of relative culmen length.

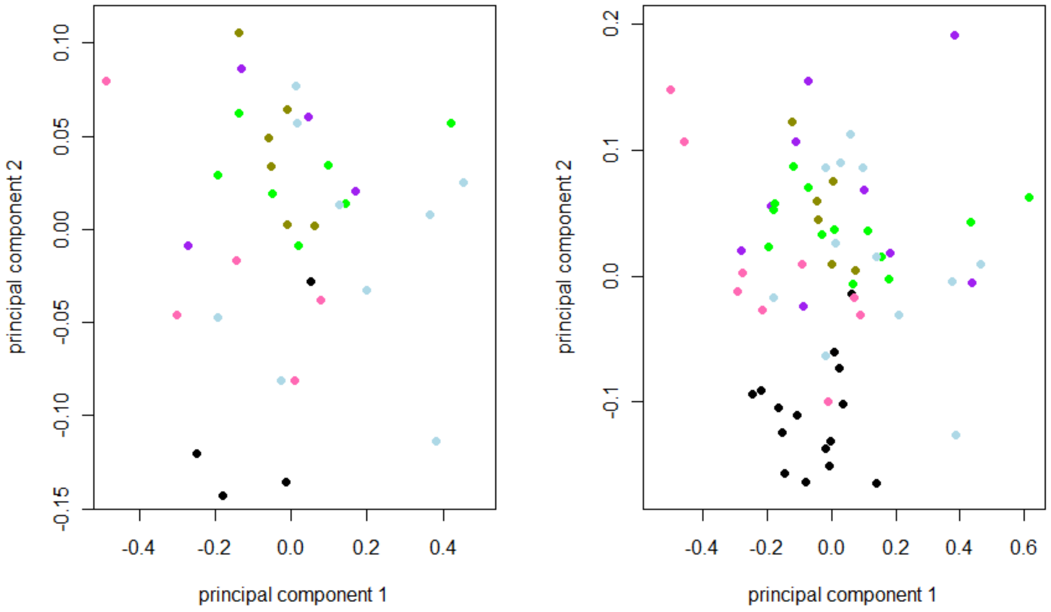


Figure 4.4. *Zosterops* taxa plotted in morphospace for datasets drawn from a) the Reciprocally Monophyletic Tree and b) the Incipient Species Tree. Colours represent taxa from the same clade, as shown in Figures 4.1 and 4.2. In both cases, principal component 1 is an index of overall body size while principal component 2 is an index of relative culmen length.

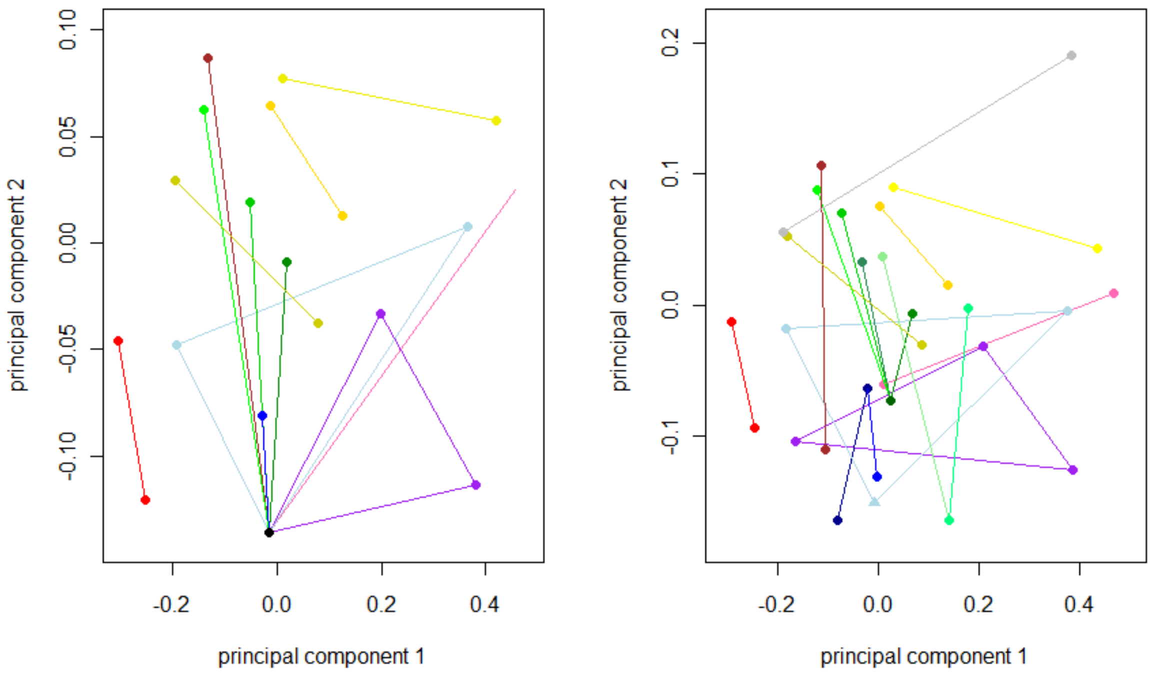


Figure 4.5. Sympatric *Zosterops* taxa plotted in morphospace for datasets drawn from a) the Reciprocally Monophyletic Tree and b) the Incipient Species Tree. Colours represent taxa from the same archipelago with different shades representing different islands. Lines join sympatric pairs or trios. In both cases, principal component 1 is an index of overall body size while principal component 2 is an index of relative culmen length.

4.4.2 Model testing

In all cases using the Reciprocally Monophyletic Tree, the Brownian motion model had the lowest ΔAICc score (Table 4.2), For the Incipient Species Tree, the Brownian model either has the lowest AICc score, or ΔAICc between the Brownian model and the best-fitting model was < 2, in all but two cases. The two exceptions are PC2, (relative bill length), and average tail length. The analysis suggests that these data are best explained by a lambda model (for relative bill length) and kappa model (for tail length) of trait evolution, however in neither case is the one model significantly different from the other. The parameter estimates are shown in Table 4.3. The Brownian model is the best fit for all the traits. It is noteworthy that in no case was the early-burst model preferred to constant rate Brownian motion.

Table 4.2. Comparison of models of morphometric evolution for PC1, PC2 and univariate body size measures based on Akaike Information Criteria (AICc) for a) the Reciprocally Monophyletic Tree, and b) the Incipient Species Tree. The lowest (AICc) score for all models tested is shown and with a Delta AICc of zero indicating the model that applies to. Model abbreviations: BM = Brownian motion; OU = Ornstein-Uhlenbeck; EB = Early Burst. PC1 is an index of overall body size while PC2 is an index of relative culmen length.

a) The species tree

Trait	Lowest AICc	BM ΔAICc	OU ΔAICc	Lambda ΔAICc	Kappa ΔAICc	EB ΔAICc
PC1	-9.80	0	0.16	1.62	1.85	2.41
PC2	-93.76	0	1.04	0.73	2.35	2.41
Wing	224.88	0	0.36	2.08	52.38	2.41
Tail	204.91	0	0.53	0.84	1.51	2.41
Tarsus	144.69	0	1.11	0.84	1.97	2.41
Bill length	160.72	0	1.80	2.41	2.32	2.41

b) The subspecies tree

Trait	Lowest AICc	BM ΔAICc	OU ΔAICc	Lambda ΔAICc	Kappa ΔAICc	EB ΔAICc
PC1	-49.65	0.42	1.28	0.67	0	2.63
PC2	-177.72	15.53	4.42	0	1.97	17.73
Wing	383.58	0.42	0.64	0.15	0	2.63
Tail	347.78	11.83	5.48	0.88	0	14.04
Tarsus	234.22	0	1.32	1.57	0.45	2.21
Bill length	267.24	0	1.45	2.20	2.16	2.21

Table 4.3. Parameter estimates for the first two principal components and the various body size measures for a) the Reciprocally Monophyletic Tree, and b) the Incipient Species Tree. Model abbreviations: BM = Brownian motion; OU = Ornstein-Uhlenbeck; EB = Early Burst. PC1 is an index of overall body size while PC2 is an index of relative culmen length.

a) The species tree

Trait	BM beta	OU alpha	OU theta	Lambda	Kappa	EB
PC1	0.02	0.28	0	0.73	0.62	0
PC2	0.00	0.23	0	0.70	0.86	0
Wing	12.85	0.45	0	0	0.90	0
Tail	7.26	0.28	0	0.61	0.54	0
Tarsus	1.30	0.25	0	0.72	0.70	0
Bill length	2.06	0.19	0	1.00	0.80	0

b) The subspecies tree

Trait	BM beta	OU alpha	OU theta	Lambda	Kappa	EB
PC1	0.02	0.17	0	0.97	0.68	0
PC2	0.00	0.59	0	0.81	0.38	0
Wing	17.71	0.22	0	0.97	0.68	0
Tail	12.10	0.42	0	0.91	0.37	0
Tarsus	1.71	0.13	0	0.98	0.73	0
Bill length	2.86	0.09	0	1.00	0.95	0

4.4.3 Trait differences between sympatric congeners

For islands with sympatric species, the observed contrasts between those species are shown in Tables 4.4 and Table 4.5 for the Reciprocally Monophyletic Tree and the Incipient Species Tree, respectively. In each Table, the observed contrasts are taken across each island both with sympatric species individually and across all species. In each case an observed value of greater than one indicates that trait diversification among sympatrics is faster than expected and an observed value of less than one indicates that it is slower than expected. The contrasts in the overall variance are also calculated across the whole set of islands. Across all islands sympatric species are not significantly more diverse that would be expected by chance based on the dataset from either tree. Indeed the only significant value in either table for the analysis including all the islands, as opposed to just individual islands, is on the Incipient Species Tree (Table 4.5) and indicates that sympatric species have diverged in tarsus length less rapidly than would be expected by chance, perhaps indicative of habitat filtering. This result appears to be a consequence of including individual island data for the different *Z. lateralis* subspecies as in some cases individual island subspecies of *Z. lateralis* appear to be more similar to their congeneric sympatrics than is the species as a whole. There are a few island-trait combinations where the observed contrasts are in the expected direction showing that sympatric species are different in overall body size (PC1), such as Lifou and Rennell. However in many cases the contrasts are <1, indicating similarity of morphologies, and in some cases these trends were significant, for example between *Z. explorator* and *Z. l. flaviceps* on Fiji. However, although these two species are very similar in terms of overall size, they are significantly more dissimilar with respect to PC2 than would be expected by chance.

Table 4.4. Observed differences across sympatric species on each island and for the islands taken as a whole according to the Reciprocally Monophyletic Tree. Part a) shows the results when all species are considered and part b) shows the results when *Z. lateralis* is excluded. In each case the observed differences between pairs or triplets on an island is shown. Values of less than one indicate that sympatric species are more similar than expected and values of more than one indicate that sympatrics are less similar than expected based on differences across the whole tree. Stars then indicate if this value is significantly more different than expected by chance based on a Brownian simulation model as follows: * P<0.05, ** P<0.01. PC1 is an index of overall body size while PC2 is an index of relative culmen length.

a) Including *Zosterops lateralis*

Island	PC1	PC2	Wing	Tarsus	Tail	Bill length
North West Vanuatu	0.43	2.46*	0.51	0.02*	1.53	0.04*
North East Vanuatu	0.13	1.92	0.25	0.14	1.04	0.24
South Vanuatu	0.12	1.58	0.03*	0.29	0.67	0.43
Fiji	0.41	2.76*	0.28	0.29	1.60	0.16
Rennell	1.44	0.25	1.62	1.43	1.29	1.53
Australia	0.44	1.20	0.78	0.07*	0.90	0.14
Lifou	1.39	1.45	1.74	0.99	1.16	1.36
Grande Terre	0.049*	0.73	0.39	0.04*	0.31	0.19
Norfolk Island	1.10	1.07	1.17	1.08	0.71	1.22
Lord Howe Island	1.78	2.14	1.02	1.01	0.99	2.97*
Bougainville	1.01	0.87	1.10	1.43	0.99	0.54
Kulambangra	0.49	0.64	0.42	0.33	0.73	0.40
All islands	0.73	1.42	0.78	0.59	0.99	0.77
Overall variance	0.35	0.60	0.31	0.31	0.14*	0.74

b) Excluding *Zosterops lateralis*

Island	PC1	PC2	Wing	Tarsus	Tail	Bill length
Rennell	1.44	0.25	1.62	1.43	1.29	1.53
Lifou	2.63*	0.92	3.06*	1.85	1.86	2.92*
Norfolk Island	0.87	1.34	1.70	1.08	1.31	0.35
Bougainville	1.01	0.88	1.10	1.43	0.99	0.54
Kulambangra	0.49	0.64	0.42	0.33	0.73	0.40
All islands	1.29	0.80	1.58	1.22	1.24	1.15
Overall variance	0.68	0.16	0.95	0.33	0.18	1.22

Table 4.5. Observed differences across sympatric species for each island and for the islands taken as a whole according to the Incipient Species Tree. Part a) shows the results when all species are considered and part b) shows the results when *Z. lateralis* is excluded. In each case the observed differences between pairs or triplets on an island is shown. Values of less than one indicate that sympatric species are more similar than expected and values of more than one indicate that sympatrics are less similar than expected based on differences across the whole tree. Stars then indicate if this value is significantly more different than expected by chance based on a Brownian simulation model as follows: * P<0.05, ** P<0.01. PC1 is an index of overall body size while PC2 is an index of relative culmen length.

a) Including *Zosterops lateralis*

Island	PC1	PC2	Wing	Tarsus	Tail	Bill length
Malekula	0.32	1.21	0.47	0.12	0.93	0.02*
Espiritu Santo	0.48	1.36	0.50	0.16	1.16	0.17
North East Vanuatu	0.19	0.90	0.22	0.01*	0.71	0.002*
Gaua	0.14	0.56	0.13	0.32	0.30	0.21
Southern Vanuatu	0.43	1.71	0.80	0.42	1.33	0.10
Tanna	0.12	1.38	0.31	0.04*	0.71	0.59
Fiji	0.02**	1.84	0.02*	0.05*	1.10	0.37
Rennell	1.33	0.39	1.52	1.36	1.12	1.32
Australia	0.15	0.69	0.22	0.18	0.54	0.04*
Lifou	1.29	1.15	1.64	0.95	1.07	1.15
Grande Terre	0.21	0.92	0.31	0.12	0.27	0.50
Norfolk Island	1.52	0.71	1.27	1.67	1.08	1.41
Lord Howe Island	1.61	0.64	1.32	0.95	1.03	2.26
Bougainville	0.92	0.75	1.05	1.31	0.87	0.46
Kulambangra	0.44	0.51	0.39	0.31	0.64	0.34
Ponape	2.64*	1.62	1.64	1.19	1.24	3.85
All islands	0.74	1.02	0.74	0.57*	0.88	0.80
Overall variance	0.55	0.21	0.33	0.32	0.10**	1.06*

b) Excluding *Zosterops lateralis*

Island	PC1	PC2	Wing	Tarsus	Tail	Bill length
Rennell	1.33	0.39	1.52	1.36	1.12	1.32
Lifou	2.45	0.15	2.86*	1.77	1.61	2.52*
Norfolk Island	0.78	1.08	1.59	1.03	1.13	0.30
Bougainville	0.92	0.75	1.05	1.31	0.87	0.46
Kulambangra	0.44	0.51	0.39	0.31	0.64	0.34
Ponape	2.64*	1.62	1.64	1.19	1.24	3.85**
All islands	1.43	0.75	1.51	1.16	1.10	1.47
Overall variance	0.83	0.28	0.66	0.23	0.11	2.09

Table 4.6. The observed minimum distance for Euclidian distances between sympatric pairs in the Reciprocally Monophyletic Tree, the median of the simulated distribution and the P-value indicating whether the observed distances are more different than would be expected by chance. Part a) shows the results when all species are considered and part b) shows the results when *Z. lateralis* is excluded.

a) Including *Zosterops lateralis*

Island	Median of distribution	Observed minimum	P-value
North West Vanuatu	0.25	0.23	0.93
North East Vanuatu	0.25	0.16	0.57
South Vanuatu	0.25	0.13	0.41
Fiji	0.25	0.25	0.99
Rennell	0.26	0.41	0.50
Australia	0.25	0.16	0.54
Lifou	0.11	0.20	0.33
Grande Terre	0.24	0.06	0.08
Norfolk Island	0.11	0.20	0.33
Lord Howe Island	0.23	0.50	0.25
Bougainville	0.25	0.28	0.88
Kulambangra	0.26	0.15	0.48
All islands	0.0527	0.06	0.93

b) Excluding *Zosterops lateralis*

Island	Median of distribution	Observed minimum	P-value
Rennell	0.25	0.41	0.43
Lifou	0.19	0.56	0.03
Norfolk Island	0.20	0.20	0.99
Bougainville	0.24	0.28	0.82
Kulambangra	0.24	0.15	0.51
All islands	0.086	0.147	0.34

The minimum Euclidian distances observed among sympatric species and corresponding null expectations from the simulations are shown in Tables 4.6 and 4.7, for the Reciprocally Monophyletic Tree and Incipient Species Tree, respectively. Neither tree shows significantly greater distance than would be expected by chance. This is also true when the mean Euclidian distance rather than the minimum is considered. P-values for the Reciprocally Monophyletic Tree using mean Euclidian distance are: a) with Z. lateralis = 0.74, b) without Z. lateralis = 0.23. P-values for the Incipient Species Tree using mean Euclidian distance are: a) with Z. lateralis = 0.29, b) without Z. lateralis = 0.38. The only significant result is for the difference between Z. minutus, the smallest Zosterops in the region and Z. inornatus, one of the largest, on Lifou (Table 4.7) and this only appears when Z. lateralis is taken out of the analysis.

Table 4.7. The observed minimum distance for Euclidian distances between sympatric pairs in the Incipient Species Tree is shown as is the simulated median of the distribution and whether the observed distances are more different than would be expected by chance. Part a) shows the results when all species are considered and part b) shows the results when *Z. lateralis* is excluded.

a) Including *Zosterops lateralis*

Island	Median of distribution	Observed minimum	P-value
Malekula	0.31	0.17	0.41
Espiritu Santo	0.30	0.22	0.67
North East Vanuatu	0.31	0.12	0.22
Gaua	0.32	0.08	0.09
Southern Vanuatu	0.30	0.24	0.70
Tanna	0.31	0.17	0.42
Fiji	0.31	0.22	0.63
Rennell	0.31	0.41	0.69
Australia	0.30	0.09	0.12
Lifou	0.15	0.22	0.53
Grande Terre	0.28	0.12	0.22
Norfolk Island	0.15	0.20	0.54
Lord Howe Island	0.28	0.46	0.40
Bougainville	0.31	0.28	0.90
Kulambangra	0.31	0.15	0.32
Ponape	0.23	0.59	0.08
All islands	0.0636	0.0788	0.70

b) Excluding *Zosterops lateralis*

Island	Median of distribution	Observed minimum	P-value
Rennell	0.32	0.41	0.69
Lifou	0.24	0.56	0.11
Norfolk Island	0.23	0.20	0.82
Bougainville	0.31	0.28	0.88
Kulambangra	0.31	0.15	0.33
Ponape	0.23	0.59	0.07
All islands	0.0981	0.147	0.50

4.4.4 Biogeographic model testing

Wing length was highly significantly correlated to tarsus size (Table 4.8) and this was also true of entire culmen length (Appendix 4.3). However neither trait showed any significant correlation with measures of dispersal ability. Table 4.9 and Table 4.10 show two different measures of body size modelled as a function of the measures of dispersal ability. In both these models there is a significant effect of island size, with larger birds being found on smaller islands. These models explained 18-35% of the data in different versions of the model of the effect of body size.

Table 4.8. Models estimates for wing length modelled as a function of various factors indicating dispersal ability for a) Reciprocally Monophyletic Tree and b) Incipient Species Tree.

	a) The species tree				**b) the subspecies tree**			
Term	Estimate	Std Err	T-value	P-value	Estimate	Std Err	T-value	P-value
(Intercept)	0.852	0.128	6.682	2.50E-07	0.883	0.100	8.796	3.33E-12
log10 (tarsus average)	0.761	0.096	7.949	9.12E-09	0.724	0.077	9.378	3.74E-13
log10 (number of islands)	-0.016	0.011	-1.404	0.17	0.008	0.004	1.858	0.07
log10 (largest island area)	-0.002	0.003	-0.613	0.54	-0.001	0.001	-1.512	0.14
log10 (maximum distance)	-0.003	0.004	-0.721	0.48	-0.004	0.002	-1.743	0.09
Species age	-0.004	0.006	-0.670	0.51	-0.001	0.005	-0.197	0.84
Lambda statistic	1.00				1.00			
Adjusted R^2	0.74				0.71			
F statistic	20.37				31.55			
P model	1.08E-08				3.00E-15			

Table 4.9. Models estimates for principal component one, an index of general body size for a) Reciprocally Monophyletic Tree and b) Incipient Species Tree.

	a) The species tree				**b) the subspecies tree**			
Term	Estimate	Std Err	T-value	P-value	Estimate	Std Err	T-value	P-value
(Intercept)	0.290	0.106	2.740	0.010	0.055	0.096	0.570	0.571
log10 (number of islands)	0.023	0.095	0.244	0.809	0.131	0.031	4.182	9.80E-05
log10 (largest island area)	-0.084	0.021	-3.951	0.0004	-0.030	0.006	-5.259	2.19E-06
log10 (maximum distance)	-0.039	0.036	-1.101	0.279	-0.048	0.016	-2.960	0.004
Species age	0.016	0.043	0.371	0.713	0.034	0.041	0.848	0.400
Lambda statistic	0.28				1.00			
Adjusted R^2	0.35				0.32			
F statistic	5.61				8.20			
P model	0.002				2.61E-05			

Table 4.10. Models estimates for principal component two, an index of relative bill length for a) the Reciprocally Monophyletic Tree and b) the Incipient Species Tree.

	a) The species tree				**b) the subspecies tree**			
Term	Estimate	Std Err	T-value	P-value	Estimate	Std Err	T-value	P-value
(Intercept)	0.054	0.041	1.326	0.195	0.006	0.032	0.200	0.843
log10 (number of islands)	-0.020	0.034	-0.576	0.569	-0.048	0.023	-2.076	0.042
log10 (largest island area)	-0.015	0.008	-1.994	0.055	0.000	0.004	-0.037	0.971
log10 (maximum distance)	0.010	0.013	0.817	0.420	0.021	0.010	2.039	0.046
Species age	-0.002	0.016	-0.145	0.886	0.006	0.014	0.394	0.695
Lambda statistic	0.43				0.83			
Adjusted R^2	0.04				0.02			
F statistic	1.35				1.24			
P model	0.28				0.30			

4.5 Discussion

My analyses showed that the two main axes of phenotypic variation among island *Zosterops* were overall body size followed by relative bill length. I found no evidence for an early-burst of morphological divergence with respect to either of these axes and little support for morphological evolution being specifically associated with speciation events since the Brownian motion null model was not rejected in most cases. Whilst I found that sympatric species do differ phenotypically, sympatric species were typically not more phenotypically different than expected by chance alone. In fact, for many islands the *Zosterops* inhabiting that island were more similar than expected by chance, although there were a handful of island-trait combinations that did show some evidence for character displacement. There was also some evidence for biogeographic effects since, while the predicted correlation between dispersal ability and wing length did not emerge, there was evidence for increasing body size on smaller islands, which agrees with the ‘small island effect’ of Mees (1969). This final result is consistent with the island rule for passerine birds and indicates a potential role for and effect of community ecology in morphological evolution in this group.

4.5.1 Modes of trait evolution

Although the *Zosterops* are known to have speciated rapidly, particularly early in their evolutionary history (Chapter 3 and Moyle *et al.* 2009), I found no evidence for a similar early-burst in terms of morphological diversification. This is perhaps surprising, given that they are known to have recently colonised and expanded to a series of islands and archipelagos where novel ecological opportunities might be expected to occur. Analysis of modes of evolution using the Incipient Species Tree suggest that certain traits might have been subject to speciational evolution, specifically relative bill and tail length. The latter result is unexpected and difficult to explain because tail length is not thought to be of very great adaptive significance in the Zosteropidae (Mees 1969). However, the fact that this occurs only in the Incipient Species Tree may indicate that it reflects competitive displacement of *Z. lateralis* subspecies that have recently arrived on islands with similar sized sympatrics. The bill length result may also reflect competitive displacement as on many of the islands the *Z. lateralis* population appears to have a relatively shorter and thicker bill than their sympatric congeners (RAB pers. obs.). It is possible that this represents the beginnings of character displacement and trait divergence. Overall, however, these results do not suggest that speciation leads to an increased rate of morphological evolution (Harmon & Gibson 2006).

4.5.2 Character displacement and lineage sorting

Differences in bill length between sympatric island birds are frequently greater than equivalent differences on the mainland, which suggests that the requirements for co-existence are more stringent on islands (Grant 1968). Additionally, since species of the same genus tend to be phenotypically similar, competition between them is expected to be more severe (Bagenal 1951; Lack 1965; Williams 1964). The resource partitioning model predicts that adjacent species need to be separated by a critical minimum space to survive and if they are too close one will go extinct (Schoener 1986). It has been shown that size changes resulting from niche shifts driven by character displacements can happen quickly in birds. For example, two co-existing *Myzomela* honeyeaters on the Long Islands are known to have been in sympatry for less than 300 years but are significantly more different in bill length from each other than birds in the allopatric source populations (Diamond *et al.* 1989). Other known examples of rapid bill size changes in birds are found in Laysan finches, *Telespyza cantans*, introduced to novel habitats (Conant 1988) and Darwin's finches responding to drought conditions on Daphne Major (Grant & Grant 1989).

Sympatric species may therefore be ecologically distinct before they come into contact or they may be reproductively isolated and diverge subsequently in morphological traits as a result of character displacement. Often it is likely to be a combination of the two forces that are at work, an initial difference reinforced by character displacement (Grant & Grant 2006). However, the signal of these processes may potentially be masked by non-genetic environmental factors related to particular times or islands (Webb *et al.* 2002). Sympatric species may be constrained in the degree to which they can diverge by environmental factors. For example, the largest seed size available may place an upper limit on the size to which a seed eating bird can usefully grow. Selection will not favour the evolution of a larger beak which results in a reduction of the range of successfully strategies, or limits the morphological space that a species can occupy (Cornwell *et al.* 2006; Keddy 1992). This will obviously also limit the degree to which two sympatric congenerics can exhibit character displacement. It should be noted however that sexual selection can be a confounding factor as mate choice can drive selection in a direction that is non-adaptive from a niche point of view (Buchanan & Evans 2000; Rowe *et al.* 2001; Zahavi 1975).

Nevertheless it is surprising that I found little evidence to suggest that the survival of congenerics in sympatry depends on them being any more different from each other than is typical among *Zosterops* species. Across all the islands there was no significant tendency for sympatric species to have diverged more rapidly from each other than expected under a Brownian model. Perhaps more surprisingly, in many traits sympatric species appeared to have diverged less rapidly than expected by chance. For example the two Fiji forms, *Z.*

explorator and *Z. lateralis flaviceps* were almost identical on the general body size axis (PC1, Figure 4.5). On the relative bill size axis, however, the two species were very different and the trend was in the expected direction. In fact, in most cases sympatric species are noticeably different from each other in at least one of these two components. This suggests that there might be character displacement between sympatric species but that the important traits are different on each island, making it difficult to detect except on a case by case basis. This suggestion is, perhaps, made more plausible by the fact that two exceptions to the rule of differing in the expected direction on at least one axis are species pairs that segregate by altitude on their respective islands (Mayr & Diamond 2001). These are the Solomons islands pairs *Z. murphyi* and *Z. kulambangrae* from Kulambangra and *Z. ugiensis* and *Z. metcalfi* from Bougainville. The other exception is *Z. xanthochrous* and *Z. l. griseotinctus* on Grande Terre, New Caledonia. In this case, although the former species is more common in the mountains and the latter on the coasts (RAB pers. obs.), their ranges show extensive overlap and the ecological differences between them are, as yet, unclear.

This potential instance of competition, inferred from an overlap in size and habitat, suggests another possible explanation, which is that the inclusion of *Z. lateralis* is a confounding factor. Without *Z. lateralis* included, the other sympatrics were still not significantly more different but the differences were in the expected direction in most traits except relative bill length. These pairs and triplets that become pairs without *Z. lateralis* are older and therefore have had more time in sympatry. The body size axis appears to be important in certain older sympatrics, such as *Z. minutus* and *Z. inornatus* on Lifou, which are significantly more different than expected by chance with respect to overall body size. The older pair of sympatric species from Norfolk Island, *Z. albogularis* and *Z. tenuirostris*, are more similar than expected with respect to overall body size but show a trend towards being more different than expected with respect to bill length. The latter trend is not statistically significant but Grant (1972a) determined that the important difference in the bill between these species is not in length but in depth and width. Thus, he concluded that in sympatric double-invasions, species pairs of insular birds differ in at least one bill dimension by 15% or more. In the same study, Grant also noted an apparent example of character displacement evolving, or at least re-enforcing in sympatry. Specimens of *Z. l. lateralis* collected in 1926 had narrower bills than those collected in 1912 and 1913, although sample size were admittedly small for the later date. This change does not appear in the other two species making differences in measurement accuracy or the effects of fluctuating selection unlikely as explanations. It seems at least possible that this is evidence of divergence due to selection since the later specimens are more different from *Z. tenuirostruis* than the earlier specimens.

I found no evidence to support the theory that congenerics can only coexist in sympatry if sufficient time has passed to allow them to be already ecologically completely separate from each other (Lack 1971). Were this the case the sympatric species should be less close phylogenetic relatives than expected by chance and this is not the case (Chapter 3). Sympatric species are found in different parts of *Zosterops* morphospace but they are not always at the extremes and indeed they do not appear to be obviously more separate than any two random species. It appears, therefore, that the range of niches occupied by sympatric species is a subset of the overall range of the family. This suggests that almost any two random species coming into sympatry would be far enough apart to survive, at least in the short term. Following establishment in sympatry competition would either lead to character displacement or the eventual exclusion of one species.

One possible interpretation of my results is that character displacement is important in sympatric Zosteropidae but that the form of character displacement is not consistent. In some cases there is a size difference, such as between *Z. minutus* and *Z. inornatus* on Lifou, or between *Z. cinera ponapensis* and *Rukia ruki* on Ponape. In other cases, however, there is little difference in size but there are important differences in bill length or other morphological characteristics that are less easy to measure, such as tongue morphology or wing formula (Mees 1957). However because differences are dictated by the particular circumstances on each island overall there are no strong trends in the overall data. Linked to this is the possibility that, as recent colonists, the *Z. lateralis* species group has, in many cases not yet, achieved a stable sympatric state and that these pairing represent not the ghost of competition past but of active competition in the present.

4.5.3 Biogeography

A combination of theory and observation suggests that species with longer wings would be better dispersers and therefore that more widespread species should have longer wings (Mees 1969). However, I found no evidence that this is the case based on the data analysed here. It seems logical to conclude, therefore, that *Zosterops* species are not limited by dispersal ability to be endemics or confined to small groups of islands. Differences in dispersal ability are likely to be a result of behavioural rather than physical limitations (Diamond 1981).

I did find a significant effect of island size on overall body size, with a significant tendency for large-bodied taxa being found on smaller islands, as predicted by the Island Rule (Clegg & Owens 2002; Lomolino 2000; van Valen 1973; Welch 2009). The classic scenario is that the first *Zosterops* species to arrive gets larger, particularly in bill morphology as bigger beaked birds can handle a wider range of food (Lack 1971). Under this scenario species on smaller islands with few competitor species should evolve to become larger. Later arriving, more normally sized, conspecifics may get have a tendency to evolve larger size too but are constrained by character displacement competition with the resident species. Of the two islands populated by three species, the molecular clock indicates that the largest birds on both Lifou and Norfolk island are the oldest. However the latest arrival is the smallest species in one case (Norfolk Island) but the middle species in the other case (Lifou), where the subspecies present (*Z. l. melanops*) is larger than the subspecies on nearby islands with only two *Zosterops* species. This may indicate that even within the general framework of selection for increased the specific circumstances of individual islands are of huge importance.

4.5.4 Conclusions

Taken together these results diverge in important ways from the usual interpretation of *Zosterops* colonisation of the islands which is a rapid west to east colonisation of the islands with associated rapid trait evolution. Typically, the first colonisers on each island are expected to increase in size with later arrivals fitting in at lower sizes on a character displacement basis. However in many cases, in particular *Z. lateralis griseonatus* and *Z. xanthrochrous* on the main island of New Caledonia and *Z. flavifrons* and *Z. lateralis* in Vanuatu, the later arriving species is the larger species. It has been predicted that there is a large element of stochasticity in evolutionary processes and that chance will result in very different outcomes even when conditions are similar (Lenormand & Rousset 2009; Losos *et al.* 1998; Travisano *et al.* 1995). However it has been shown in *Anolis* lizards that adaptive radiation in similar environments often leads to convergent evolution (Losos *et al.* 1998). Here I show that the effect of phylogeny is more important than selection for trait evolution. It may be significant that species from the New Caledonian clade are more often sympatric with each other than other clades. Clade specific factors can be very important different taxa respond in different ways so by extension taxa from the same clade respond in the same way (Harvey & Pagel 1991).

In some cases failure to find agreement with long-standing ecological predictions may be due to a lack of data. For example (Grant 1972a), showed that the crucial bill differences between *Z. albogularis* and *Z. tenuirostris* are in bill width and depth rather than bill length so they are not, as at first appeared an exception to the rule that sympatric species bills must differ by at least 15% (Grant 1968; Lack 1944). My data set only includes one bill measure and it would certainly be a useful next step to repeat the analysis with depth and width measures included. Another factor to consider is that it is not always obvious which trait characteristics reflect resource use. For example Carothers (1982) found that tongue morphology was important in the foraging rates of three Hawaiian honeycreepers (Fringillidae: Drepanidinae). Competition may also not be only, or even mainly, between congeneric sympatrics and we have not considered competition with other bird families or more distantly related taxa. For example, Schluter (1986) demonstrated character displacement between Darwin's finches and carpenter bees (*Xylocopa darwini*). However it still remains true that if the classic scenario were true I would expect to find evidence of overall trends in bill and body size with the data that we have and I do not.

I suggest that, in general, my results are more consistent with an extreme non-equilibrium scenario of insular colonisation and evolution. Under this model the islands of the south west Pacific are a dynamic system in a permanent state of flux. The classic forces of character displacement and habitat filtering are operating but at any one moment the effects are obscured by new invasions and turnover. The special cases provide information about the forces that are acting but don't give much predictive power because only the most extreme differences in size difference show a significant effect in the models. For example, Figure 4.6 shows the huge difference in size between *Z. minutus* and *Z. inornatus* and my analyses show that it is this is the sort of morphological size difference that is needed to show significance in the model. Even so, when *Z. l. melanops* is included in the model the significance is obscured although the size difference must have evolved before *Z. l. melanops* arrived on Lifou. It is highly probable that much more subtle differences between species than these can create important differences in the use of niche space.

Grant (1968) notes that individual islands vary hugely in physical conditions and so broad conclusions cannot be drawn from single island studies. For example, endemic subspecies on Rennell Island show a marked tendency towards reduction in size (Murphy 1938). The classic pattern of segregation by size among sympatric *Zosterops* may be true in some cases but not across all islands being correct only in carefully selected cameos. Older pairs show evidence of character displacement whereas younger pairs, including *Z. lateralis* subspecies, do not. This suggests that ecological differences might be developing in sympatry rather than having to be in place before sympatry occurs. That sympatric pairs are not significantly older than would be expected on average is supporting evidence for this (Chapter 3).

Figure 4.6. The size differences between the three *Zosterops* species found on the island of Lifou. *Z. minutus*, on the left, has an average weight of 9.3 grams (N=51), *Z. lateralis melanops*, in the middle, has an average weight of 14 grams (N=30) and *Z. inornatus*, on the right has an average weight of 21.4 grams (N=14) (RAB unpublished data) (Photograph: S. Clegg).

Neither the expected early-burst nor speciational modes of trait evolution are supported by my results. One possible explanation for this is that colonisation of these islands is not a simple west-to-east stepping stone colonisation as expected by long-standing predictions. Instead, it proceeds in a series of waves, some large ones emanating from the continental source and other smaller ones happening between, or even within archipelagos. The forms of *Zosterops* emerging on each island depends heavily on chance events of habitat and species composition as well as colonisation and extinction events (Grant 2001; Price 2008). Classic processes may be in operation but on any given island at any one moment the *Zosterops* species present may be at any stage of the speciation and trait evolution process. The overall picture therefore is a product or snapshot of the time and the pattern only a few thousand years in the past or into the future may be very different.

Chapter 5

General Discussion

In the General Introduction (Chapter 1) I addressed three principal themes of speciation. Here I reassess those themes in the light of the analyses presented in this thesis and draw together the findings that are relevant to each of these main themes. The Zosteropidae of the south west Pacific is a remarkable system for the study of diversification in the wild and the combination of repeated bouts of dispersal and colonisation with a diversity of island settings has resulted in an enormous amount of speciation in a very short time. It is therefore hoped that the insights gleaned from studying this unusual group will prove to be applicable to broader scale questions in evolutionary biology.

5.1 Themes of evolution

5.1.1 Modes of Speciation

The lineage through time plots presented in Chapter 3 indicate that speciation happened fast and early in the Zosteropidae of the south west Pacific. The white-eyes were already known to represent an unusually rapid radiation and Moyle *et al*. (2009) estimated a diversification rate of approximately 2.24 taxa per million years using a geologically calibrated tree. My tree was calibrated on a molecular clock and although I estimated a slower overall rate of 0.80 (CI 0.69 – 0.91) taxa per million years this is still fast compared to most bird groups (Price 2008). The fast rate of speciation in the *Zosterops* of the south west Pacific appears to be concentrated early in the radiation with a significant slowdown in speciation rate over time (Chapter 3). The observed pattern of phylogenetic diversification matches predictions of an evolutionary radiation spreading into archipelagos composed largely of recently emerged islands (Newton 2003; Whittaker & Fernández-Palacios 2007). Under this scenario, there are initially there are many available niches but stochastic variations among islands leads to some islands becoming ecologically ‘full’ more rapidly than others. As niches fill and ecological opportunities close, the speciation rate gradually slows down (Hallam 1977; Harvey & Rambaut 2000; Nee *et al.* 1992; Simpson 1953).

Although my analyses suggested that, phylogenetically speaking, the *Zosterops* diversification happened fast and early, I did not find evidence for fast and early - or “early-burst” - evolution with respect to morphology (Chapter 4). Nor did I find evidence for speciational evolution with respect to morphology or “punctuated trait early evolution”, where trait evolution is concentrated around speciation events (Chapter 4). The early-burst model predicts that the rate of trait evolution should reflect the rate of speciation because it is the availability of opportunities for novel ecological evolution that causes rapid, early speciation (Gavrilets & Vose 2005; Schluter 2000a). In the south Pacific Zosteropidae, speciation is linked with the colonisation of new islands which is in turn expected to be linked to morphological change. Indeed it is thought that rapid speciation is most likely when either natural or sexual selection is strong and that in the absence of selection divergence is a slow process (Coyne & Orr 2004; Gavrilets 2004). There is little positive evidence for strong sexual selection in the Zosteropidae as there is little sexual dimorphism, with males being only slightly larger and more colourful in some species and very little evidence for sexual selection through extra-pair paternity (Frentiu *et al.* 2008; Mees 1957; 1961; 1969; Robertson *et al.* 2001). In fact, the Capricorn silvereye *Z. lateralis chlorocephalus* is one of relatively few passerines species that has been found to be genetically monogamous even when using hyper-variable genetic markers (Robertson *et al.* 2001). Thus, although it is impossible to rule out a role for sexual selection, especially as there is currently rather little known about the evolution of song in this group (Diamond 1998; Kikkawa 1963), it is likely that ecological speciation via divergent natural selection is a more powerful mechanism for diversification in this family (Clegg *et al.* 2002b). A consequence of this is that speciation events are expected to coincide with phenotypic changes, especially with trait changes related to shifts in ecological niche space.

Given the expectation that ecologically relevant traits, such as body size and relative bill length, should be closely associated with the process of speciation, it is therefore surprising that I was unable to reject a Brownian null model of trait evolution which implies that changes in morphological traits may have been random with respect to speciation (Chapter 4). However a comparison of the number of ecological niches, as represented by the number of islands, appears to be correlated with the number of species in a given region (Chapter 3). The lineage through time plots suggest three bouts of increased speciation rates that could be explained by three main invasions waves of *Zosterops* to the region: an initial colonisation wave across the region, a second represented by the increase in speciation rates in the middle of the phylogeny, and a third ‘incipient’ speciation wave dominated by *Z. lateralis* subspecies (Chapter 3). These rounds of colonisation, along with sympatry and extinction, hint that taxon cycles - sequential expansions and contractions in the range of species (Ricklefs & Bermingham 2002; Wilson 1961) - may be partly responsible for the distribution of *Zosterops* species of vastly different ages in the region. This scenario differs from the suggestions of Mees (1969) who grouped all *Z. lateralis* plus several endemic *Zosterops* species into a species complex. However, the phylogeny (Chapter 2) shows that the *Z. lateralis* radiation contains only the *Z. lateralis* subspecies and not all the species grouped by Mees (1969) into the larger species complex.

5.1.2 The Origin and Consequences of Sympatry

The phylogenetic hypothesis for the *Zosterops* of the south west Pacific that I presented in Chapter 2 provided no support for sympatric speciation as a cause of sympatric congeners, supporting the consensus that this mode of speciation is very rare in birds (Coyne & Orr 2004; Coyne & Price 2000; Newton 2003; Phillimore *et al.* 2008a; Price 2008). The co-occurrence of congenerics on small islands therefore must be the result of multiple invasions. Island speciation is typically expected to lead to a decline in dispersal ability (Diamond 1981). Speciation and particularly the development of endemism on nearby islands implies a reluctance or inability to cross water bodies so that gene flow is reduced to zero (Diamond *et al.* 1976). In the south west Pacific there are many examples of endemic species separated by very narrow stretches of water, such as the Solomons species *Z. vellalavella* and *Z. splendidus,* which are separated by only 8km (Mayr 1967; Mayr & Diamond 2001). Therefore poorly dispersing endemic species are unlikely candidates for the range expansions required to produce conspecific sympatrics. I suggest that the colonisation events resulting in sympatric species in general represent large scale events involving the rapid spread and subsequent speciation of a vagile species emanating from a continental population source.

I also found that sympatric pairs of *Zosterops* show no tendency to be more distantly related to each other than expected by chance (Chapter 3) Similarly, in general I found that sympatric species are no more dissimilar to one another with respect to their morphology than expected by chance, although the morphological tests did reveal a handful of island-trait combinations where there was significant divergence (Chapter 4). The factor that produces differing *Zosterops* forms therefore would not seem to be the time available for divergence but the availability of novel niche opportunities. Significantly most of the Zosteropidae that are unusual in size and/or colour are island forms, such as the large, brown *Woodfordia* species of Rennell and the Santa Cruz Islands (Mees 1969) and the very small pygmy white-eye, *Oculocincta squamifrons* of Borneo (Lack 1971). The key then for *Zosterops* to come into sympatry is for the endemic on an island to have diverged sufficiently for a later arriving more ‘typical’ form to be able to occupy a different niche. The available evidence suggests that it does not take long for quite dramatic morphological change to happen in the Zosteropidae. For example *Z. l. chlorocephalus* from the southern Great Barrier Reef Islands, has increased in size by between 2.8 to 7 standard deviation units, depending on which trait is considered, compared to the nearby mainland subspecies

(Frentiu *et al.* 2007; Kikkawa & Wilson 1983; Mees 1969). Clegg *et al.* (2008) showed that this shift is likely to have occurred in less than 500 generations following colonisation and that the phenotype has since hovered around an optimum size. It is therefore not surprising to find that sympatric Zosteropidae are not more distantly related than you would expect by chance (Chapter 3). More perplexing is the lack of evidence that there needs to be some minimum phenotypic distance between *Zosterops* species for sympatry to occur (Chapter 4). Hence, rather than shedding light on factors that allow sympatry of *Zosterops* species, phylogenetic information has introduced further complexities than were apparent prior to the use of phylogenetic methods (Stern & Grant 1996).

There are at least three possible scenarios that may explain the failure to find significant phylogenetic or phenotypic divergence between sympatric congeners (Chapter 4). The first possibility is that *Zosterops* species simply do not have to be phenotypically, or even ecologically, very different in order to co-exist. This is what would be predicted by Hubbell's unified neutral theory of biodiversity and biogeography which considers that differences between species are neutral as regards their competitive abilities (Hubbell 2001; Hubbell & Borda-de-Agua 2004). However this does not seem very probable for the Zosteropidae because many of the older sympatric species do show marked differences in traits and ecology. For instance, on several of the other islands where there is more than one *Zosterops* species, various authors have suggested ecological niche differentiation on the basis of major ecological factors, including altitude, habitat use and foraging behaviour (Lack 1971; Mayr & Diamond 2001). A good example of this occurs on Lifou where *Z. inornatus* averages more than three times the weight of *Z. minutus* (Chapter 4) and appears to feed higher in the canopy than the smaller species (RAB pers. obs.).

A second possibility is that the character displacement, while real, is very difficult to detect, and that even in this speciose region there is simply not enough statistical power to be able to reliably detect such subtle patterns of variation. In support of this is the fact that, although the phenotypic differences between sympatric species are not significantly greater than expected by chance, in individual cases they are often in the expected direction (Chapter 4). Part of the problem in detecting significance in this overall trend may be that the exact form of character displacement shown by any particular set of sympatric species is idiosyncratic and, rather than following general rules, depends on the particular circumstances of each individual case. In some cases differences in overall size may be important, for example between *Z. rennellianus* and *W. superciliosa* on Rennell (Mayr & Diamond 2001), but in other cases it might be bill dimensions for example between *Z. albogularis* and *Z. tenuirostris* on Norfolk Island (Grant 1972a). It is noticeable that most of the sympatric species are very different from one another in either body size or relative bill length, but rarely different in both aspects (Chapter 3). This has also been noticed in sympatric *Zosterops* in other parts of the world (Gill 1971; Grant 1968) and, although I attempted to test for multidimensional divergence by calculating Euclidian distances, the unpredictability of individual island effects is exemplified in the case of Lifou. Lifou is a small, low lying island that, in comparison with many other islands of the region, has an almost entirely homogenous forest habitat and yet it supports three very distinct *Zosterops* species. This suggests that, while ecological differences may exist among sympatric *Zosterops* they are very hard to check except on a case by case basis, such that it is extremely challenging to derive generalities.

A third explanation is that the overall effect of character displacement may be masked by recurrent invasion of new forms and, in particular, the recent invasion of *Z. lateralis*. When viewing island populations of this species cohabiting an island with an earlier colonist, we may be viewing competition in progress rather than “the ghost of competition past” and coexistence (Connell 1980). On Grande Terre of New Caledonia, for example, *Z. xanthochrous* and *Z. l. griseonatus* are often observed feeding in the same way on the same foods (RAB pers. obs.). This competition may result in character displacement and eventual sympatry or in one species going extinct. Many of the islands with stable sympatric pairs or with single species may be a result of previous iterations of this process. In support of this when *Z. lateralis* was excluded from the morphological tests the remaining species showed evidence in the direction of character displacement. I will return to this idea of recurrent invasions and the effect it has on detecting general ecological patterns later in this General Discussion.

5.1.3 Biogeographical Effects on divergence

The phylogenetic hypotheses I present here indicate that the *Zosterops* of the south west Pacific are not a monophyletic group and so cannot represent a single colonisation wave from the mainland (Chapter 2). Instead the Zosteropidae of the south west Pacific consists of three distinct clades which I have termed the Vanuatu Clade, the New Caledonia clade and the *Zosterops lateralis* clade (Chapter 2) and the origins of all three clades appear to be Asian rather than Australian. Neither do endemic taxa seem to have arisen from currently widespread species. Nor does a pattern of colonisation from west to east hold true for the family as a whole. However in the three different clades there is a strong suggestion that easterly species tend to be younger (Chapter 2). A stepping stone colonisation model predicts that species on more remote islands, easterly in this case, should be younger as it takes longer to reach those islands. This again supports recurrent waves of colonisation across the region.

Phylogeography does appear to be important in the speciation of the Zosteropidae. The sheer number of available islands in the south west Pacific, as compared to other regions, appears to be the reason that speciation in the region is particularly fast and the recent nature of many of them is the reason for signatures of early-burst of speciation and a subsequent slow down (Chapter 3). However this is hard to test beyond a simple comparison of island and species numbers.

My analyses of the link between morphology and biogeography produced mixed results (Chapter 4). I did not find any evidence of reduced wing length relative to body size in less widely dispersed taxa which supports the conclusion of Diamond (1981) that loss of dispersal in the Zosteropidae is due to psychological rather than physiological changes. However I was only able to look at relative wing length and it would be valuable to repeat the analysis with some measure of wing shape as this is also likely to be important in determining dispersal ability (Mees 1969). I did, however, find that the island rule did holds for the Zosteropidae, i.e. that there was a tendency for them to evolve large body size on small islands (Chapter 3). Clegg and Owens (2002) suggested that in small birds this trend is an adaptation to high population densities and intense intraspecific competition on islands(Blondel *et al.* 1988; MacArthur *et al.* 1972; Wright 1980). This seems to support the theory that the first *Zosterops* to arrive on an island diverges from the norm, typically in the direction of increased size, which allows a more typical *Zosterops* to invade subsequently (Gill 1971; Lack 1971).

5.2 Speciation scenario for insular *Zosterops*

In my analysis of the phylogenetic relationships in Chapter 2 I discussed three possible scenarios of diversification in the *Zosterops* of the south west Pacific. I rejected the simple model of a single wave of west to east colonisation (Scenario i) as being unable to explain the observed pattern once phylogenetic relationships were taken into consideration. However it proved harder to determine which of the other two scenarios, the mosaic of colonisation Scenario ii) and waves of colonisation (Scenario iii) was more likely to be correct. Based on the evidence from the analyses presented in the subsequent Chapters, I consider that the scenario of waves of colonisation seems to be more probable and here I draw together the relevant evidence.

There are five lines of evidence to support a scenario of large scale colonisation waves as the predominant dispersal pattern throughout the region. First, within each of the three distinct clades in the phylogeny there is some signal of west to east migration suggesting that they may represent three different colonisation waves (Chapter 2). Second, there are examples of old isolated species on remote islands, for example *Z. f. majuscula* on Aneityum. These are more convincingly explained as remnants of ancient colonisation waves rather than as single species dispersals over huge distances due to the improbability of a sedentary island endemic making a single large dispersal jump (Chapter 2). Third, the existence of sympatric *Zosterops* despite the lack of evidence for sympatric speciation (Chapter 2) suggests multiple colonisation events. Again this is more parsimoniously explained by colonisations of widely dispersed vagile species than by range expansions by island endemics that must, almost by definition, be poor dispersers. Fourth, there is a suggestion of repeated increases in speciation rates followed by slowdown through time and this may indicate repeated colonisation waves (Chapter 3). Fifth, a species that is probably still in the process of spreading across the region, *Z. lateralis*, possibly represents the latest phase of a taxon cycle (Chapters 3 and 4). It is reasonable to conclude that a phenomenon that is occurring in the present might have also occurred in the past. Individually none of these strands of evidence could be considered convincing but taken together they suggest that repeated waves of colonisation is the most likely scenario.

5.3 Future Research

My work suggests strongly the existence of recurrent waves of colonisation of Pacific islands by white-eyes but several questions remain unanswered. If periodic waves of colonisation from mainland sources are responsible for the current species complex, what is the root cause of these expansions? What determines which species are involved and when expansions occur? Answers to these questions must be sought among the mainland source populations. One possible hypothesis is that these dispersal events are linked to climatic changes. Another is that they are essentially stochastic events linked to chance dispersal, particularly in partially migratory taxa such as *Z. l. lateralis* (Higgins *et al.* 2006).

I have not demonstrated significant character displacement among the *Zosterops* of the south west Pacific, yet evidence from some islands suggests that sympatrics may tend to be more different from each other than random pairs, at least for some traits. Here I have used the morphological data available to examine trait differences in the Zosteropidae. It is possible that additional traits that I did not include will prove to be important. For example bill shape as well as bill length is thought to be important in the Zosteropidae (Grant 1972a; Robinson-Wolrath & Owens 2003; Scott *et al.* 2003). It would certainly be valuable to repeat the analyses in Chapter 3 including measures of bill width and bill depth. Another step towards the elucidation of this question would be to establish what the ecological differences in sympatric pairs actually are, especially in terms of feeding niche. The best way to do this convincingly would be a detailed feeding study of multiple sympatric pairs.

Although I have assumed that sexual selection is not an important mechanism in *Zosterops* this has not been thoroughly tested. In some bird species sexual dimorphism is cryptic from a human point of view for example the ultraviolet colour of the throat in male bluethroats, *Luscinia svecica* (Andersson & Amundsen 1997). Moreover lack of sexual dimorphism does not necessarily mean there is no sexual selection, for example females could be choosing large males and high genetic covariance between the sexes could pull the females in the same direction. Further study is warranted to investigate possible sexual selection in the Zosteropidae. Perhaps most crucially for a passerine bird species, however I have not considered evolution of vocal communication in this group and, in particular the character displacement with respect to song (Irwin 2000; Irwin *et al.* 2001; Payne *et al.* 2000; ten Cate 2000). Typically in morphologically uniform bird groups, vocalisations, especially song, are important in conspecific recognition. A comparison of song in the Zosteropidae would be an important next step. Here the prediction would be that if song is important in character displacement then song divergence will be greater among species that show a sympatric geographic than those which are allopatric (Noor 1999). The alternative hypothesis is that it is the acoustic environment that is important and differences in song structure among closely-related species are associated with interspecific variation in habitat use

5.4 Conclusions

One of the reasons for selecting *Zosterops* as the study group for this work is that cameo examples from this group have frequently been invoked to support classical theories regarding dispersal, ecological niche differentiation, founder events and sympatric speciation (e.g. Emerson 2008; Grant 1972b; Lack 1947; Lack 1971; Mayr 1941; Mayr 1954). In general, however, my larger scale comparative analyses of *Zosterops* have tended not to support these theories. For instance, only in a handful of cases do the classic predictions of niche divergence with body size (Lack 1971; Mees 1957; 1961; 1969) appear to be true. Similarly, I find no evidence to support sympatric speciation, stepping stone models of biogeographic dispersal or speciational trait evolution. Instead, it appears that a major driver of speciation in the region is recurrent waves of colonisation emanating from the population sources. It is these waves that produce the patterns of sympatry on multiple islands. Nor does it seem at all clear that these pairs, when they come into sympatry, are always occupying different niches. The surviving species on certain islands may have outcompeted earlier congeneric inhabitants of the islands or have themselves outcompeted later arriving competitors. In species pairs involving the most recent colonist, *Z. lateralis*, this competition may still be going on. This suggests that the make up of the Zosteropidae of the south west Pacific may not stable but in a constant state of flux. I believe that the processes of ecological speciation and character displacement are likely to be important in defining the characteristics of each individual species or the differences between sympatric pairs, but the signal of these mechanisms is swamped by the dynamic equilibrium of past and present colonisation.

There is a natural tendency to look for the trace of competition past to explain current patterns of species diversity. However speciation is a constant process and competition in the present may often be just as important. The field of historical biogeography should perhaps be the field of historical and current biogeography. Overall, the Zosteropidae of the south west Pacific reflect a general truth: that speciation is a constant process and that the potential for change always underlies apparent stability. The unusual situation of this particular family in these particular islands makes the effects of this process more obvious.

Appendices

Appendix 2.1

Appendix Table 2.1.A. Individual *Zosterops* and *Woodfordia* samples sequenced as part of this study, showing geographic origin, sample number, collector and the genes for which sequence was obtained: “y” indicates that the gene has been sequenced for that individual and “n” indicates that it has not. The table is divided into four parts: i) *Z. lateralis* from Vanuatu, ii) other *Z.* lateralis, iii) *Z. flavifrons,* and iv) other *Zosterops* and *Woodfordia* species. Sequences used from GenBank are listed separately in Table 2.1.B.

Part i) *Zosterops lateralis* samples from Vanuatu

Taxon			**Collection details**			**Sequencing details**			
Genus	**species**	**subspecies**	**island**	**Sample number**	**Collection**	**CB1**	**ND3**	**ATPase**	**TGFB2**
Zosterops	lateralis	tropica	Ambae	AMB55	SMC	y	y	y	y
Zosterops	lateralis	tropica	Ambae	AMB56	SMC	y	y	y	y
Zosterops	lateralis	tropica	Ambae	AMB57	SMC	y	y	y	y
Zosterops	lateralis	tropica	gaua	255	ABP	y	n	y	y
Zosterops	lateralis	tropica	gaua	261	ABP	y	y	n	y
Zosterops	lateralis	tropica	gaua	267	ABP	y	y	n	y
Zosterops	lateralis	tropica	gaua	296	ABP	n	y	n	n
Zosterops	lateralis	tropica	Pentecost	PEN03	SMC	y	y	y	y
Zosterops	lateralis	tropica	Pentecost	PEN08	SMC	y	y	y	y
Zosterops	lateralis	tropica	Pentecost	PEN16	SMC	y	y	y	y
Zosterops	lateralis	tropica	Pentecost	PEN18	SMC	y	y	y	y
Zosterops	lateralis	tropica	Pentecost	PEN33	SMC	y	y	y	y
Zosterops	lateralis	tropica	santo	222	ABP	y	y	y	y
Zosterops	lateralis	tropica	santo	233	ABP	y	y	n	y
Zosterops	lateralis	tropica	santo	ABP245	ABP	y	y	n	y
Zosterops	lateralis	tropica	santo	345	ABP	y	y	n	y
Zosterops	lateralis	tropica	santo	353	ABP	y	y	n	y
Zosterops	lateralis	tropica	santo	SAN2	SMC	y	y	y	y
Zosterops	lateralis	tropica	santo	SAN7	SMC	y	y	y	y
Zosterops	lateralis	tropica	santo	SAN9	SMC	y	y	y	y
Zosterops	lateralis	tropica	vanua lava	317	ABP	y	y	n	y
Zosterops	lateralis	tropica	vanua lava	319	ABP	y	y	y	y
Zosterops	lateralis	tropica	vanua lava	322	ABP	y	y	n	y
Zosterops	lateralis	tropica	vanua lava	VAN46	SMC	y	y	y	y
Zosterops	lateralis	vatensis	Ambrym	ABY07	SMC	y	y	y	y
Zosterops	lateralis	vatensis	Ambrym	ABY25	SMC	y	y	y	y
Zosterops	lateralis	vatensis	Ambrym	ABY26	SMC	y	y	y	y
Zosterops	lateralis	vatensis	Ambrym	ABY36	SMC	y	y	y	y
Zosterops	lateralis	vatensis	Ambrym	ABY39	SMC	y	y	y	y
Zosterops	lateralis	vatensis	efate	EF44	SMC	y	y	y	y
Zosterops	lateralis	vatensis	efate	153	ABP	y	y	y	y
Zosterops	lateralis	vatensis	efate	155	ABP	y	y	n	y
Zosterops	lateralis	vatensis	efate	164	ABP	y	y	n	y
Zosterops	lateralis	vatensis	efate	174	ABP	y	y	y	y
Zosterops	lateralis	vatensis	epi	412	ABP	y	y	n	y
Zosterops	lateralis	vatensis	epi	415	ABP	y	y	y	y
Zosterops	lateralis	vatensis	epi	418	ABP	y	y	n	y
Zosterops	lateralis	vatensis	epi	423	ABP	y	y	n	y
Zosterops	lateralis	vatensis	erromango	371	ABP	y	y	n	y
Zosterops	lateralis	vatensis	erromango	373	ABP	y	y	y	y
Zosterops	lateralis	vatensis	erromango	380	ABP	y	y	n	y
Zosterops	lateralis	vatensis	erromango	389	ABP	y	y	n	y
Zosterops	lateralis	vatensis	malekula	176	ABP	y	y	n	y
Zosterops	lateralis	vatensis	malekula	ABP178	Rich	y	y	n	y
Zosterops	lateralis	vatensis	malekula	183	ABP	y	y	n	y
Zosterops	lateralis	vatensis	malekula	199	ABP	y	y	n	y
Zosterops	lateralis	vatensis	malekula	215	ABP	y	y	y	y
Zosterops	lateralis	vatensis	tanna	77	ABP	n	n	n	y
Zosterops	lateralis	vatensis	tanna	ABP082	ABP	y	y	y	y
Zosterops	lateralis	vatensis	tanna	85	ABP	y	y	n	y
Zosterops	lateralis	vatensis	tanna	90	ABP	y	y	n	y
Zosterops	lateralis	vatensis	tanna	109	ABP	y	y	y	y

Part ii) Remaining *Zosterops lateralis* samples

Taxon			**Collection details**			**Sequencing details**			
Genus	**species**	**subspecies**	**island**	**Sample number**	**Collection**	**CB1**	**ND3**	**ATPase**	**TGFB2**
Zosterops	lateralis	chlorocephalus	Heron	H1404	SMC	y	n	n	y
Zosterops	lateralis	chlorocephalus	Heron	H1568	SMC	y	y	n	n
Zosterops	lateralis	chlorocephalus	Heron	H1613	SMC	y	y	n	n
Zosterops	lateralis	chlorocephalus	Heron	9010	SMC	y	y	n	n
Zosterops	lateralis	chlorocephalus	Heron	9601	SMC	y	y	n	n
Zosterops	lateralis	cornwalli	Queensland	B74(Z1)	SMC	y	y	y	y
Zosterops	lateralis	cornwalli	Queensland	B83(Z2)	SMC	y	y	n	y
Zosterops	lateralis	cornwalli	Queensland	B71	SMC	y	y	n	n
Zosterops	lateralis	cornwalli	Queensland	B79	SMC	y	y	n	n
Zosterops	lateralis	cornwalli	Queensland	B82	SMC	y	y	n	n
Zosterops	lateralis	flaviceps	Fiji	1988.9.1.781	Tring	y	y	n	n
Zosterops	lateralis	flaviceps	Fiji	1998.9.30.186	Tring	y	y	n	n
Zosterops	lateralis	flaviceps	Fiji	1998.9.30.187	Tring	y	n	n	n
Zosterops	lateralis	flaviceps	Fiji	1998.9.30.188	Tring	y	n	n	n
Zosterops	lateralis	gouldi	Australia	1965.43.992	Tring	y	y	n	n
Zosterops	lateralis	gouldi	Australia	1965.43.993	Tring	y	y	n	n
Zosterops	lateralis	gouldi	Australia	1966.21.269	Tring	y	y	n	n
Zosterops	lateralis	gouldi	Australia	1966.21.270	Tring	y	y	n	n
Zosterops	lateralis	griseonatus	Northern GT	N018	Rich	y	y	n	y
Zosterops	lateralis	griseonatus	Northern GT	N024	Rich	y	y	y	y
Zosterops	lateralis	griseonatus	Northern GT	N037	Rich	y	y	n	y
Zosterops	lateralis	griseonatus	Northern GT	N091	Rich	y	y	y	y
Zosterops	lateralis	griseonatus	Northern GT	N109	Rich	y	y	n	y
Zosterops	lateralis	griseonatus	Southern GT	S014	Rich	y	y	y	y
Zosterops	lateralis	griseonatus	Southern GT	S015	Rich	y	y	n	y
Zosterops	lateralis	griseonatus	Southern GT	S020	Rich	y	y	n	y
Zosterops	lateralis	griseonatus	Southern GT	S030	Rich	y	y	y	y
Zosterops	lateralis	griseonatus	Southern GT	S035	Rich	y	y	y	y
Zosterops	lateralis	halmaturina	Australia	1965.43.990	Tring	y	y	n	n
Zosterops	lateralis	halmaturina	Australia	1965.43.990	Tring	y	y	n	n
Zosterops	lateralis	lateralis	new zealand	C132	SMC	y	y	y	y
Zosterops	lateralis	lateralis	new zealand	D3	SMC	y	y	n	y
Zosterops	lateralis	lateralis	norfolk	N103	SMC	y	y	y	n
Zosterops	lateralis	lateralis	norfolk	N120	SMC	y	y	n	y
Zosterops	lateralis	lateralis	Tasmania	TAS01	SMC	y	y	n	n
Zosterops	lateralis	lateralis	Tasmania	TAS15	SMC	y	y	n	n
Zosterops	lateralis	lateralis	Tasmania	TAS06	SMC	y	y	n	n
Zosterops	lateralis	lateralis	Tasmania	TAS04	SMC	y	y	n	n
Zosterops	lateralis	melanops	Lifou	L002	Rich	y	y	n	y
Zosterops	lateralis	melanops	Lifou	L031	Rich	y	y	n	y
Zosterops	lateralis	melanops	Lifou	L088	Rich	y	y	n	y
Zosterops	lateralis	melanops	Lifou	L102	Rich	y	y	n	y
Zosterops	lateralis	melanops	Lifou	L122	Rich	y	y	y	y
Zosterops	lateralis	nigrescens	Mare	M001	Rich	y	y	y	y
Zosterops	lateralis	nigrescens	Mare	M027	Rich	y	y	y	y
Zosterops	lateralis	nigrescens	Mare	M044	Rich	y	y	y	y
Zosterops	lateralis	nigrescens	Mare	M071	Rich	y	y	y	y
Zosterops	lateralis	nigrescens	Mare	M089	Rich	y	y	y	y
Zosterops	lateralis	ramsayi	Australia	1964.60.999	Tring	y	y	n	n
Zosterops	lateralis	ramsayi	Australia	1964.60.1001	Tring	y	y	n	n
Zosterops	lateralis	ramsayi	Australia	1964.60.1012	Tring	y	y	n	n
Zosterops	lateralis	ramsayi	Australia	1964.60.1014	Tring	y	y	n	n

Part iii) *Zosterops flavifrons* samples

Taxon			**Collection details**			**Sequencing details**			
Genus	**species**	**subspecies**	**island**	**Sample number**	**Collection**	**CB1**	**ND3**	**ATPase**	**TGFB2**
Zosterops	flavifrons	brevicauda	Santo	SAN6	SMC	y	y	y	y
Zosterops	flavifrons	brevicauda	santo	227	ABP	AM946044	y	n	y
Zosterops	flavifrons	brevicauda	santo	229	ABP	AM946045	y	n	y
Zosterops	flavifrons	brevicauda	santo	D	J. Kirchman	AM946068	y	y	y
Zosterops	flavifrons	brevicauda	santo	K	J. Kirchman	AM946069	y	y	y
Zosterops	flavifrons	efatensis	efate	18	ABP	AM946040	y	n	y
Zosterops	flavifrons	efatensis	efate	25	ABP	AM946046	y	y	y
Zosterops	flavifrons	efatensis	efate	40	ABP	AM946059	y	n	y
Zosterops	flavifrons	efatensis	efate	59	ABP	AM946064	y	n	y
Zosterops	flavifrons	efatensis	efate	EF50	SMC	y	y	y	y
Zosterops	flavifrons	efatensis	erromango	378	ABP	AM946055	y	n	y
Zosterops	flavifrons	efatensis	erromango	385	ABP	AM946056	y	n	y
Zosterops	flavifrons	efatensis	erromango	392	ABP	AM946057	y	n	y
Zosterops	flavifrons	efatensis	erromango	405	ABP	AM946058	y	y	y
Zosterops	flavifrons	flavifrons	tanna	73	ABP	AM946065	y	n	y
Zosterops	flavifrons	flavifrons	tanna	ABP075	ABP	y	y	n	y
Zosterops	flavifrons	flavifrons	tanna	84	ABP	AM946066	y	n	y
Zosterops	flavifrons	flavifrons	tanna	94	ABP	AM946067	y	n	y
Zosterops	flavifrons	flavifrons	tanna	110	ABP	AM946034	y	y	y
Zosterops	flavifrons	gauensis	gaua	ABP251	ABP	n	y	n	n
Zosterops	flavifrons	gauensis	gaua	269	ABP	AM946047	y	y	y
Zosterops	flavifrons	gauensis	gaua	271	ABP	AM946048	y	n	y
Zosterops	flavifrons	gauensis	gaua	285	ABP	AM946049	y	n	y
Zosterops	flavifrons	gauensis	gaua	294	ABP	AM946050	y	y	y
Zosterops	flavifrons	macgilivrayi	malekula	ABP181	ABP	y	y	y	y
Zosterops	flavifrons	macgilivrayi	malekula	185	ABP	AM946039	y	n	y
Zosterops	flavifrons	macgilivrayi	malekula	193	ABP	AM946041	y	n	y
Zosterops	flavifrons	macgilivrayi	malekula	201	ABP	AM946042	y	y	y
Zosterops	flavifrons	macgilivrayi	malekula	211	ABP	AM946043	y	y	y
Zosterops	flavifrons	majuscula	aneityum	124	ABP	AM946035	y	n	y
Zosterops	flavifrons	majuscula	aneityum	130	ABP	AM946036	y	n	y
Zosterops	flavifrons	majuscula	aneityum	132	ABP	AM946037	y	y	y
Zosterops	flavifrons	majuscula	aneityum	139	ABP	AM946038	y	n	y
Zosterops	flavifrons	majuscula	aneityum	ABP131	ABP	y	y	y	y
Zosterops	flavifrons	perplexa	Ambae	AMB3	SMC	AM946081	y	y	y
Zosterops	flavifrons	perplexa	Ambae	AMB4	SMC	AM946082	y	y	y
Zosterops	flavifrons	perplexa	Ambae	AMB5	SMC	AM946083	y	n	y
Zosterops	flavifrons	perplexa	Ambae	AMB7	SMC	AM946084	y	y	y
Zosterops	flavifrons	perplexa	Ambae	AMB8	SMC	AM946085	y	n	y
Zosterops	flavifrons	perplexa	Ambrym	ABY09	SMC	AM946086	y	y	y
Zosterops	flavifrons	perplexa	Ambrym	ABY10	SMC	AM946087	n	y	y
Zosterops	flavifrons	perplexa	Ambrym	ABY11	SMC	AM946088	y	n	y
Zosterops	flavifrons	perplexa	Ambrym	ABY12	SMC	AM946089	y	y	y
Zosterops	flavifrons	perplexa	Ambrym	ABY13	SMC	AM946090	y	y	y
Zosterops	flavifrons	perplexa	epi	420	ABP	AM946060	y	n	y
Zosterops	flavifrons	perplexa	epi	421	ABP	AM946061	y	n	y
Zosterops	flavifrons	perplexa	epi	426	ABP	AM946062	y	n	y
Zosterops	flavifrons	perplexa	epi	427	ABP	AM946063	y	y	y
Zosterops	flavifrons	perplexa	Maewo	MW02	SMC	AM946071	y	y	y
Zosterops	flavifrons	perplexa	Maewo	MW03	SMC	AM946072	y	n	y
Zosterops	flavifrons	perplexa	Maewo	MW04	SMC	AM946073	y	n	y
Zosterops	flavifrons	perplexa	Maewo	MW06	SMC	AM946074	y	y	y
Zosterops	flavifrons	perplexa	Maewo	MW07	SMC	AM946075	y	y	y
Zosterops	flavifrons	perplexa	Pentecost	PEN17	SMC	AM946076	y	n	y
Zosterops	flavifrons	perplexa	Pentecost	PEN37	SMC	AM946077	y	n	y
Zosterops	flavifrons	perplexa	Pentecost	PEN54	SMC	AM946078	y	y	y
Zosterops	flavifrons	perplexa	Pentecost	PEN69	SMC	AM946079	y	y	y
Zosterops	flavifrons	perplexa	Pentecost	PEN70	SMC	AM946080	y	n	y
Zosterops	flavifrons	perplexa	vanua lava	311	ABP	AM946051	y	n	y
Zosterops	flavifrons	perplexa	vanua lava	320	ABP	AM946052	y	n	y
Zosterops	flavifrons	perplexa	vanua lava	329	ABP	AM946053	y	y	y
Zosterops	flavifrons	perplexa	vanua lava	338	ABP	AM946054	y	n	y

Part iv) Remaining *Zosterops* and *Woodfordia* samples

	Taxon			**Collection details**			**Sequencing details**		
Genus	**species**	**subspecies**	**island**	**Sample number**	**Collection**	**CB1**	**ND3**	**ATPase**	**TGFB2**
Woodfordia	superciliosa		Rennell	1954.51.61	Tring	y	y	n	n
Woodfordia	superciliosa		Rennell	1954.51.65	Tring	y	y	n	n
Zosterops	albogularis		Norfolk	1939.12.9.2306	Tring	y	y	n	n
Zosterops	albogularis		Norfolk	1939.12.9.2307	Tring	y	y	n	n
Zosterops	albogularis		Norfolk	1939.12.9.2310	Tring	y	y	n	n
Zosterops	albogularis		Norfolk	1939.12.9.2311	Tring	y	y	n	n
Zosterops	explorator		Fiji	1898.9.30.206	Tring	n	n	n	n
Zosterops	explorator		Fiji	1898.9.30.207	Tring	y	y	n	n
Zosterops	explorator		Fiji	1903.12.30.94	Tring	n	n	n	n
Zosterops	explorator		Fiji	1966.8.9	Tring	y	y	n	n
Zosterops	gibbsi		Vanikolo	Z.gi1	Tring	y	y	n	n
Zosterops	inornatus		Lifou	L070	Rich	y	y	y	y
Zosterops	inornatus		Lifou	L094	Rich	y	y	y	y
Zosterops	inornatus		Lifou	L097	Rich	y	y	n	y
Zosterops	inornatus		Lifou	L106	Rich	y	y	y	y
Zosterops	inornatus		Lifou	L128	Rich	y	y	y	y
Zosterops	luteus	balstoni	Australia	1966.21.271	Tring	y	y	n	n
Zosterops	luteus	balstoni	Australia	1966.21.274	Tring	y	y	n	n
Zosterops	luteus	balstoni	Australia	1969.4.695	Tring	y	y	n	n
Zosterops	luteus	balstoni	Australia	1969.4.695	Tring	y	y	n	n
Zosterops	luteus	luteus	Australia	1964.60.1041	Tring	y	y	n	n
Zosterops	luteus	luteus	Australia	1964.60.1044	Tring	y	y	n	n
Zosterops	luteus	luteus	Australia	1964.60.1045	Tring	y	y	n	n
Zosterops	luteus	luteus	Australia	1964.60.1046	Tring	y	y	n	n
Zosterops	minutus		Lifou	L001	Rich	y	y	y	y
Zosterops	minutus		Lifou	L004	Rich	y	y	y	y
Zosterops	minutus		Lifou	L009	Rich	y	y	y	y
Zosterops	minutus		Lifou	L074	Rich	y	y	y	y
Zosterops	minutus		Lifou	L087	Rich	y	y	y	n
Zosterops	rennelianus		Rennell	Z.rn1	C. Smith	y	y	y	n
Zosterops	strenuus		Lord Howe	1919.7.15.160)	Tring	y	y	n	n
Zosterops	strenuus		Lord Howe	1919.7.15.161	Tring	y	y	n	n
Zosterops	strenuus		Lord Howe	1919.7.15.162	Tring	y	y	n	n
Zosterops	strenuus		Lord Howe	1919.7.15.164	Tring	y	y	n	n
Zosterops	tenuirostris		norfolk	N125	SMC	y	y	y	y
Zosterops	tenuirostris		norfolk	N141	SMC	y	y	n	y
Zosterops	tephropleurus		lord howe	LH106	SMC	y	y	y	y
Zosterops	tephropleurus		lord howe	LH140	SMC	y	y	n	y
Zosterops	xanthochrous		Mare	M002	Rich	y	y	y	y
Zosterops	xanthochrous		Mare	M013	Rich	y	y	y	y
Zosterops	xanthochrous		Mare	M034	Rich	y	y	y	y
Zosterops	xanthochrous		Mare	M057	Rich	y	y	y	y
Zosterops	xanthochrous		Mare	M074	Rich	y	y	y	y
Zosterops	xanthochrous		Northern GT	N030	Rich	y	y	y	y
Zosterops	xanthochrous		Northern GT	N038	Rich	y	y	y	y
Zosterops	xanthochrous		Northern GT	N087	Rich	y	y	y	y
Zosterops	xanthochrous		Northern GT	N111	Rich	y	y	y	y
Zosterops	xanthochrous		Northern GT	N127	Rich	y	y	y	y
Zosterops	xanthochrous		Southern GT	S002	Rich	y	y	y	y
Zosterops	xanthochrous		Southern GT	S003	Rich	y	y	y	y
Zosterops	xanthochrous		Southern GT	S005	Rich	y	y	y	y
Zosterops	xanthochrous		Southern GT	S016	Rich	y	y	n	n
Zosterops	xanthochrous		Southern GT	S039	Rich	y	y	y	y

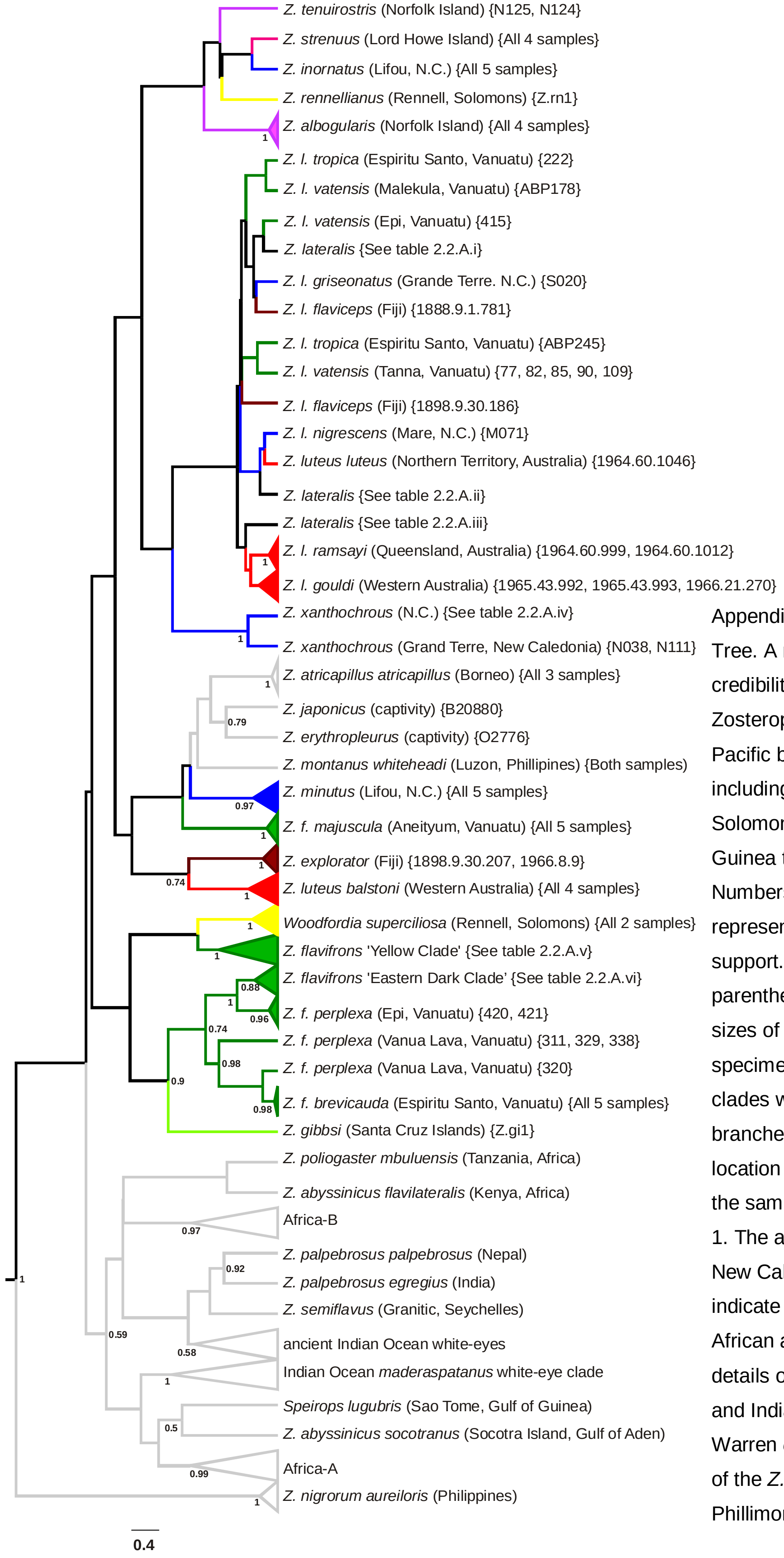
Appendix Table 2.1.B. The GenBank numbers of sequences used in this study, showing taxonomy, geographical location and voucher code. Sequences were taken for four mitochondrial regions ATPase 6 and 8 (ATP), *cytochrome b* (CB1), ND2 and ND3 gene fragments.

Taxon			**Collection details**		**GenBank Accession Numbers**			
Genus	**Species**	**subspecies**	**Location**	**Voucher Code**	**ATP**	**CB1**	**ND2**	**ND3**
Chlorocharis	emiliae		not given	LSUMNS B51361			FJ460796	FJ460864
Speirops	lugubris		Sao Tome & Principe	MM2	DQ328434	DQ328403		DQ328503
Speirops	brunneus		not given	AMNH 706105			FJ460821	FJ460889
Speirops	melanocephalus		not given	AMNH 461540			FJ460822	FJ460890
Woodfordia	superciliosa		not given	UWBM 58818		FJ460934		FJ460865
Zosterops	abyssinicus		not given	LSUMNS B20825				FJ460867
Zosterops	abyssinicus	flavilateralis	Kenya	RB3		DQ328339		DQ328439
Zosterops	abyssinicus	flavilateralis	Tanzania	ZMUC O7570		DQ328341		DQ328441
Zosterops	abyssinicus	socotranus	Yemen: Socotra	BW293		DQ328400		DQ328500
Zosterops	abyssinicus	socotranus	Yemen: Socotra	BW292	DQ328432	DQ328401		DQ328501
Zosterops	atricapillus	atricapillus	Malaysia	LSUMZ B36444		DQ328398		DQ328498
Zosterops	atricapillus	atricapillus	Malaysia	LSUMNS B36444				FJ460870
Zosterops	atricapillus	atricapillus	Malaysia	LSUMZ B36434	DQ328431	DQ328399		DQ328499
Zosterops	atrifrons		not given	AMNH DOT12620			FJ460809	FJ460877
Zosterops	borbonicus	borbonicus	Reunion	BWM54	DQ328430	DQ328395		DQ328495
Zosterops	borbonicus	borbonicus	Reunion	BWM47		DQ328396		DQ328496
Zosterops	borbonicus	borbonicus	Reunion	BWM46		DQ328397		DQ328497
Zosterops	borbonicus	mauritianus	Mauritius	BWM25		DQ328364		DQ328464
Zosterops	borbonicus	mauritianus	Mauritius	BWM24	DQ328417	DQ328365		DQ328465
Zosterops	borbonicus	mauritianus	Mauritius	BWM17		DQ328366		DQ328466
Zosterops	chloris		not given	AMNH DOT12558			FJ460798	FJ460866
Zosterops	cinerea		not given	AMNH 332201			FJ460823	FJ460891
Zosterops	citrinellus		not given	WAM 23542			FJ460815	FJ460883
Zosterops	erythropleurus		from captivity	ZMUC O2776	DQ328427	DQ328391		DQ328491
Zosterops	erythropleurus		China	ZMUC O2653	DQ328428	DQ328392		DQ328492
Zosterops	erythropleurus		not given	LSUMNS B20626			FJ460800	FJ460868
Zosterops	flavifrons		not given	LSUMNS B45805			FJ460805	FJ460873
Zosterops	flavifrons	brevicauda	Santo	flavsantoD		AM946068		AM946118
Zosterops	flavifrons	brevicauda	Santo	flavsantoK		AM946069		AM946119
Zosterops	flavifrons	brevicauda	Santo	flavsanto227		AM946044		AM946116
Zosterops	flavifrons	brevicauda	Santo	flavsanto229		AM946045		AM946117
Zosterops	flavifrons	efatensis	Efate	flavefate18		AM946040		AM946096
Zosterops	flavifrons	efatensis	Efate	flavefate25		AM946046		AM946097
Zosterops	flavifrons	efatensis	Efate	flavefate40		AM946059		AM946098
Zosterops	flavifrons	efatensis	Efate	flavefate59		AM946064		AM946099
Zosterops	flavifrons	efatensis	Erromango	flaverro378		AM946055		AM946104
Zosterops	flavifrons	efatensis	Erromango	flaverro385		AM946056		AM946105
Zosterops	flavifrons	efatensis	Erromango	flaverro392		AM946057		AM946106
Zosterops	flavifrons	efatensis	Erromango	flaverro405		AM946058		AM946107
Zosterops	flavifrons	flavifrons	Tanna	flavtanna73		AM946065		AM946121
Zosterops	flavifrons	flavifrons	Tanna	flavtanna84		AM946066		AM946122
Zosterops	flavifrons	flavifrons	Tanna	flavtanna94		AM946067		AM946123
Zosterops	flavifrons	flavifrons	Tanna	flavtanna110		AM946034		AM946120
Zosterops	flavifrons	gauensis	Gaua	flavgaua269		AM946047		AM946108
Zosterops	flavifrons	gauensis	Gaua	flavgaua271		AM946048		AM946109
Zosterops	flavifrons	gauensis	Gaua	flavgaua285		AM946049		AM946110
Zosterops	flavifrons	gauensis	Gaua	flavgaua294		AM946050		AM946111
Zosterops	flavifrons	macgillivrayi	Male Kula	flavmalekula185		AM946039		AM946112
Zosterops	flavifrons	macgillivrayi	Male Kula	flavmalekula193		AM946041		AM946113
Zosterops	flavifrons	macgillivrayi	Male Kula	flavmalekula201		AM946042		AM946114
Zosterops	flavifrons	macgillivrayi	Male Kula	flavmalekula211		AM946043		AM946115
Zosterops	flavifrons	majuscula	Aneityum	flavaneityum124		AM946035		AM946092
Zosterops	flavifrons	majuscula	Aneityum	flavaneityum130		AM946036		AM946093
Zosterops	flavifrons	majuscula	Aneityum	flavaneityum132		AM946037		AM946094
Zosterops	flavifrons	majuscula	Aneityum	flavaneityum139		AM946038		AM946095

Taxon			Collection details		GenBank Accession Numbers			
Genus	**Species**	**subspecies**	**Location**	**Voucher Code**	**ATP**	**CB1**	**ND2**	**ND3**
Zosterops	flavifrons	perplexa	Vanua Lava	flavvanua329		AM946053		AM946126
Zosterops	flavifrons	perplexa	Ambae	flavamba3		AM946081		AM946130
Zosterops	flavifrons	perplexa	Ambae	flavamba4		AM946082		AM946131
Zosterops	flavifrons	perplexa	Ambae	flavamba5		AM946083		AM946132
Zosterops	flavifrons	perplexa	Ambae	flavamba7		AM946084		AM946133
Zosterops	flavifrons	perplexa	Ambae	flavamba8		AM946085		AM946134
Zosterops	flavifrons	perplexa	Ambrym	flavambr9		AM946086		AM946135
Zosterops	flavifrons	perplexa	Ambrym	flavambr10		AM946087		AM946136
Zosterops	flavifrons	perplexa	Ambrym	flavambr11		AM946088		AM946137
Zosterops	flavifrons	perplexa	Ambrym	flavambr12		AM946089		AM946138
Zosterops	flavifrons	perplexa	Ambrym	flavambr13		AM946090		AM946139
Zosterops	flavifrons	perplexa	Epi	flavepi420		AM946060		AM946100
Zosterops	flavifrons	perplexa	Epi	flavepi421		AM946061		AM946101
Zosterops	flavifrons	perplexa	Epi	flavepi426		AM946062		AM946102
Zosterops	flavifrons	perplexa	Epi	flavepi427		AM946063		AM946103
Zosterops	flavifrons	perplexa	Maewo	flavmaewo02		AM946071		AM946140
Zosterops	flavifrons	perplexa	Maewo	flavmaewo03		AM946072		AM946141
Zosterops	flavifrons	perplexa	Maewo	flavmaewo04		AM946073		AM946142
Zosterops	flavifrons	perplexa	Maewo	flavmaewo06		AM946074		AM946143
Zosterops	flavifrons	perplexa	Maewo	flavmaewo07		AM946075		AM946144
Zosterops	flavifrons	perplexa	Pentecost	flavpen17		AM946076		AM946145
Zosterops	flavifrons	perplexa	Pentecost	flavpen37		AM946077		AM946146
Zosterops	flavifrons	perplexa	Pentecost	flavpen54		AM946078		AM946147
Zosterops	flavifrons	perplexa	Pentecost	flavpen69		AM946079		AM946148
Zosterops	flavifrons	perplexa	Pentecost	flavpen70		AM946080		
Zosterops	flavifrons	perplexa	Vanua Lava	flavvanua311		AM946051		AM946124
Zosterops	flavifrons	perplexa	Vanua Lava	flavvanua320		AM946052		AM946125
Zosterops	flavifrons	perplexa	Vanua Lava	flavvanua338		AM946054		AM946127
Zosterops	fuscicapilla		not given	NMNH 2003062			FJ460829	FJ460896
Zosterops	griseotinctus		not given	NMNH 2003067			FJ460820	FJ460888
Zosterops	inornatus		not given	AMNH 337461			FJ460827	FJ460894
Zosterops	japonicus		from captivity	LSUMZ B20880	DQ328426	DQ328390		DQ328490
Zosterops	japonicus		not given	AMNH DOT10981			FJ460801	FJ460869
Zosterops	kikuyuensis		Kenya	ZMUC O8425	DQ328408	DQ328340		DQ328440
Zosterops	kikuyuensis		Kenya	ZMUC O8447		DQ328344		DQ328444
Zosterops	kikuyuensis		Kenya	RB2	DQ328409	DQ328347		DQ328447
Zosterops	kulambangrae		not given	UWBM 76278			FJ460831	FJ460898
Zosterops	lateralis		not given	LSUMNS B45835			FJ460804	FJ460872
Zosterops	lateralis		not given	KUNHM 6094			FJ460814	FJ460882
Zosterops	lateralis	familiaris	Australia	SCB77	DQ328425	DQ328388		DQ328488
Zosterops	lateralis	familiaris	Australia	SCB76		DQ328389		DQ328489
Zosterops	luteirostris		not given	AMNH DOT113			FJ460834	FJ460901
Zosterops	luteus		not given	KUNHM 8904			FJ460812	FJ460880
Zosterops	maderaspatanus		not given	FMNH 345980			FJ460813	FJ460881
Zosterops	maderaspatanus	aldabrensis	Seychelles	BW303		DQ328386		DQ328486
Zosterops	maderaspatanus	aldabrensis	Seychelles	BW301	DQ328424	DQ328387		DQ328487
Zosterops	maderaspatanus	anjuanensis	Comoros	BW255		DQ328380		DQ328480
Zosterops	maderaspatanus	anjuanensis	Comoros	BW253	DQ328423	DQ328381		DQ328481
Zosterops	maderaspatanus	anjuanensis	Comoros	BW252		DQ328382		DQ328482
Zosterops	maderaspatanus	comorensis	Comoros	BW169		DQ328377		DQ328477
Zosterops	maderaspatanus	comorensis	Comoros	BW127	DQ328422	DQ328378		DQ328478
Zosterops	maderaspatanus	comorensis	Comoros	BW121		DQ328379		DQ328479
Zosterops	maderaspatanus	kirki	Comoros	BW231		DQ328374		DQ328474
Zosterops	maderaspatanus	kirki	Comoros	BW147		DQ328375		DQ328475
Zosterops	maderaspatanus	kirki	Comoros	BW146	DQ328421	DQ328376		DQ328476
Zosterops	maderaspatanus	maderaspatanus	Madagascar	FMNH 393447	DQ328419	DQ328372		DQ328472
Zosterops	maderaspatanus	maderaspatanus	Madagascar	FMNH 393446	DQ328420	DQ328373		DQ328473
Zosterops	maderaspatanus	maderaspatanus	Madagascar	BW446		DQ328383		DQ328483
Zosterops	maderaspatanus	maderaspatanus	Madagascar	BW429		DQ328384		DQ328484
Zosterops	maderaspatanus	mayottensis	Mayotte	BW68		DQ328369		DQ328469
Zosterops	maderaspatanus	mayottensis	Mayotte	BW67	DQ328418	DQ328370		DQ328470
Zosterops	maderaspatanus	mayottensis	Mayotte	BW64		DQ328371		DQ328471
Zosterops	maderaspatanus	voeltzkowi	France: Europa	ML30		DQ328367		DQ328467
Zosterops	maderaspatanus	voeltzkowi	France: Europa	ML26		DQ328368		DQ328468

Taxon			Collection details		GenBank Accession Numbers			
Genus	**Species**	**subspecies**	**Location**	**Voucher Code**	**ATP**	**CB1**	**ND2**	**ND3**
Zosterops	metcalfii		not given	UWBM 63177			FJ460817	FJ460885
Zosterops	modestus		Seychelles	BW345		DQ328362		DQ328462
Zosterops	modestus		Seychelles	BW344	DQ328416	DQ328363		DQ328463
Zosterops	montanus		not given	AMNH DOT12552			FJ460810	FJ460878
Zosterops	montanus	whiteheadi	Philippines	ZMUC O2662	DQ328414	DQ328360		DQ328460
Zosterops	montanus	whiteheadi	Philippines	ZMUC O2655	DQ328415	DQ328361		DQ328461
Zosterops	mouroniensis		Comoros	BW141		DQ328357		DQ328457
Zosterops	mouroniensis		Comoros	BW140	DQ328413	DQ328358		DQ328458
Zosterops	mouroniensis		Comoros	BW137		DQ328359		DQ328459
Zosterops	murphyi		not given	AMNH DOT193			FJ460833	FJ460900
Zosterops	nigrorum		not given	FMNH 432997			FJ460808	FJ460876
Zosterops	nigrorum	aureiloris	Philippines	ZMUC O3732		DQ328355		DQ328455
Zosterops	nigrorum	aureiloris	Philippines	ZMUC O2663	DQ328412	DQ328356		DQ328456
Zosterops	oleagineus		not given	LSUMNS B48626			FJ460825	FJ460892
Zosterops	olivaceus	chloronothos	Mauritius	BWM29		DQ328393		DQ328493
Zosterops	olivaceus	chloronothos	Mauritius	BWM28	DQ328429	DQ328394		DQ328494
Zosterops	olivaceus	olivaceus	Reunion	BWM55		DQ328353		DQ328453
Zosterops	olivaceus	olivaceus	Reunion	BWM49	DQ328411	DQ328354		DQ328454
Zosterops	pallidus	capensis	South Africa	RB1		DQ328351		DQ328451
Zosterops	pallidus	capensis	South Africa	RB4		DQ328352		DQ328452
Zosterops	palpebrosus	egregius	India	BMNH 1964.26.1		DQ328350		DQ328450
Zosterops	palpebrosus		not given	AMNH DOT5746			FJ460806	FJ460874
Zosterops	palpebrosus		not given	WAM 23218			FJ460807	FJ460875
Zosterops	palpebrosus	palpebrosus	Nepal	RF2		DQ328348		DQ328448
Zosterops	palpebrosus	palpebrosus	Nepal	RF1	DQ328410	DQ328349		DQ328449
Zosterops	poliogaster	kulalensis	Kenya	ZMUC O8629	DQ328433	DQ328402		DQ328502
Zosterops	poliogaster	mbuluensis	Tanzania	ZMUC O4191		DQ328346		DQ328446
Zosterops	poliogaster	silvanus	Kenya	ZMUC O8580	DQ328406	DQ328337		DQ328437
Zosterops	poliogaster	winifredae	Tanzania	ZMUC O5899		DQ328336		DQ328436
Zosterops	rendovae		not given	UWBM 76356			FJ460830	FJ460897
Zosterops	rendovae		not given	UWBM 76258			FJ460832	FJ460899
Zosterops	rennellianus		not given	UWBM 69808			FJ460818	FJ460886
Zosterops	rennellianus		Rennell	Z_rennellianus		AM946070		AM946129
Zosterops	semiflavus		Seychelles	BMNH 1927.12.18.398		DQ328345		DQ328445
Zosterops	senegalensis		not given	LSUMNS B39250			FJ460803	FJ460871
Zosterops	senegalensis	senegalensis	Ghana	LSUMZ B39250		DQ328343		DQ328443
Zosterops	senegalensis	stierlingi	Tanzania	ZMUC O8255	DQ328407	DQ328338		DQ328438
Zosterops	splendidus		not given	AMNH DOT171			FJ460835	FJ460902
Zosterops	stresemanni		not given	UWBM 66034			FJ460819	FJ460887
Zosterops	ugiensis		not given	KUNHM 12803			FJ460836	FJ460903
Zosterops	ugiensis		not given	AMNH 222105			FJ460826	FJ460893
Zosterops	vellalavella		not given	AMNH DOT166			FJ460828	FJ460895
Zosterops	virens		not given	FMNH 390165			FJ460811	FJ460879
Zosterops	wallacei		not given	WAM 22903				FJ460884
Zosterops	ugiensis		not given	KUNHM 12803			FJ460836	FJ460903
Zosterops	ugiensis		not given	AMNH 222105			FJ460826	FJ460893
Zosterops	vellalavella		not given	AMNH DOT166			FJ460828	FJ460895
Zosterops	virens		not given	FMNH 390165			FJ460811	FJ460879
Zosterops	wallacei		not given	WAM 22903				FJ460884

Appendix 2.2



Appendix Fig 2.2.A. The cyt b Tree. A maximum clade credibility tree of the Zosteropidae of the south west Pacific based on 308 bp of cyt b, including species from The Solomon Islands and New Guinea taken from GenBank. Numbers adjacent to nodes represent Bayesian branching support. Numbers in curly parentheses indicate sample sizes of more than one specimen. Monophyletic island clades were collapsed. Coloured branches indicate the geographic location of different taxa using the same colour code as Figure 1. The abbreviation N.C. refers to New Caledonia. Grey branches indicate extant species from the African and Asian Clades. For details of the collapsed African and Indian Ocean clades see Warren *et al.* (2006). For details of the *Z. flavifrons* groups see Phillimore *et al.* (2008b)

Table 2.2.A Voucher numbers of specimens included in tips representing more than one individual in Appendix Figure 2.2.A.

2.2.A.i

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	lateralis	chlorocephalus	Heron Island	LH106, LH140
Zosterops	lateralis	griseonatus	Grande Terre	N018, N024, N037, N091, N109, S014, S015
Zosterops	lateralis	tropica	Ambae	AMB55, AMB56, AMB57
Zosterops	lateralis	tropica	Espiritu Santo	SAN2, SAN7, SAN9, 233, 345, 353
Zosterops	lateralis	tropica	Pentecost	PEN03, PEN08, PEN 16, PEN 33
Zosterops	lateralis	tropica	Vanua Lava	317, 319, 322, VAN46
Zosterops	lateralis	vatensis	Ambrym	ABY07, ABY25, ABY26, ABY36, ABY39
Zosterops	lateralis	vatensis	Efate	EF44, 153, 155, 164, 174
Zosterops	lateralis	vatensis	Epi	412, 418, 423
Zosterops	lateralis	vatensis	Erromango	371, 373, 380, 389
Zosterops	lateralis	vatensis	Malekula	176, 183, 199, 215

2.2.A.ii

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	luteus	luteus	Australia	1964.60.1041, 1964.60.1044, 1964.60.1045
Zosterops	lateralis	melanops	Lifou	L002, L031, L088, L102, L122
Zosterops	lateralis	nigrescens	Mare	M001, M027, M044, M089

2.2.A.iii

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	lateralis	cornwalli	Australia	B74, B79, B82, B83
Zosterops	lateralis	flaviceps	Fiji	1898.9.30.187
Zosterops	lateralis	gouldi	Australia	1966.21.270
Zosterops	lateralis	lateralis	New Zealand	C132, D3
Zosterops	lateralis	lateralis	Norfolk Island	N103, N120
Zosterops	lateralis	lateralis	Tasmania	TAS01, TAS04, TAS06, TAS15
Zosterops	lateralis	ramsayi	Australia	1964.60.1001,1964.60.1014

2.2.A.iv

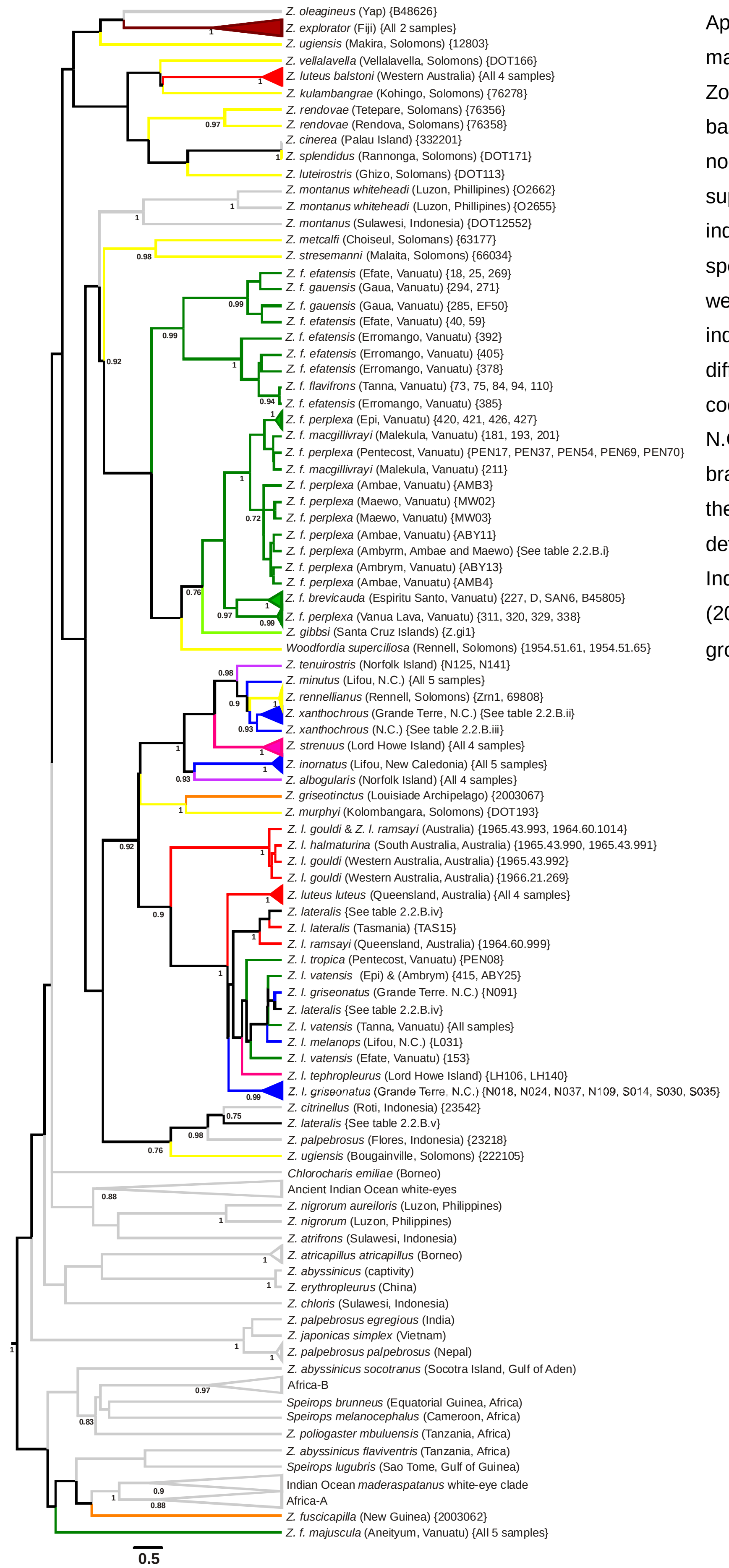
Genus	Species	Subspecies	Location	Sample numbers
Zosterops	xanthochrous		Grande Terre	N030, N087, N127, S002, S005, S016, S039
Zosterops	xanthochrous		Mare	M002, M013, M034, M057, M074

2.2.A.v

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	flavifrons	efatensis	Efate	18, 25, 40, 59
Zosterops	flavifrons	efatensis	Erromango	378, 385, 392, 405
Zosterops	flavifrons	flavifrons	Tanna	73, 75, 84, 94, 110
Zosterops	flavifrons	gauensis	Gaua	251, 269, 271, 285, 294

2.2.A.vi

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	flavifrons	macgilivrayi	Malekula	181, 185, 193, 201, 211
Zosterops	flavifrons	perplexa	Ambae	AMB3, AMB4, AMB5, AMB7
Zosterops	flavifrons	perplexa	Ambrym	ABY09, ABY10, ABY11, ABY12, ABY13
Zosterops	flavifrons	perplexa	Maewo	MW02, MW03, MW04, MW06, MW07



Appendix Fig 2.2.B The ND3 Tree. A maximum clade credibility tree of the Zosteropidae of the south west Pacific based on 393 bp. Numbers adjacent to nodes represent Bayesian branching support. Numbers in curly parentheses indicate sample sizes of more than one specimen. Monophyletic island clades were collapsed. Coloured branches indicate the geographic location of different taxa using the same colour code as Figure 1. The abbreviation N.C. refers to New Caledonia. Grey branches indicate extant species from the African and Asian Clades. For details of the collapsed African and Indian Ocean clades see Warren *et al.* (2006). For details of the *Z. flavifrons* groups see Phillimore *et al.* (2008b).

Table 2.2.B Voucher numbers of specimens included in tips representing more than one individual in Appendix Figure 2.2.B.

2.2.B.i

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	flavifrons	perplexa	Ambae	AMB5, AMB7, AMB8
Zosterops	flavifrons	perplexa	Ambrym	ABY09, ABY10, ABY12
Zosterops	flavifrons	perplexa	Maewo	MW02, MW04, MW06, MW07

2.2.B.ii

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	xanthochrous		Grande Terre	N038, N087, N111, N127, S002, S016, S039

2.2.B.iii

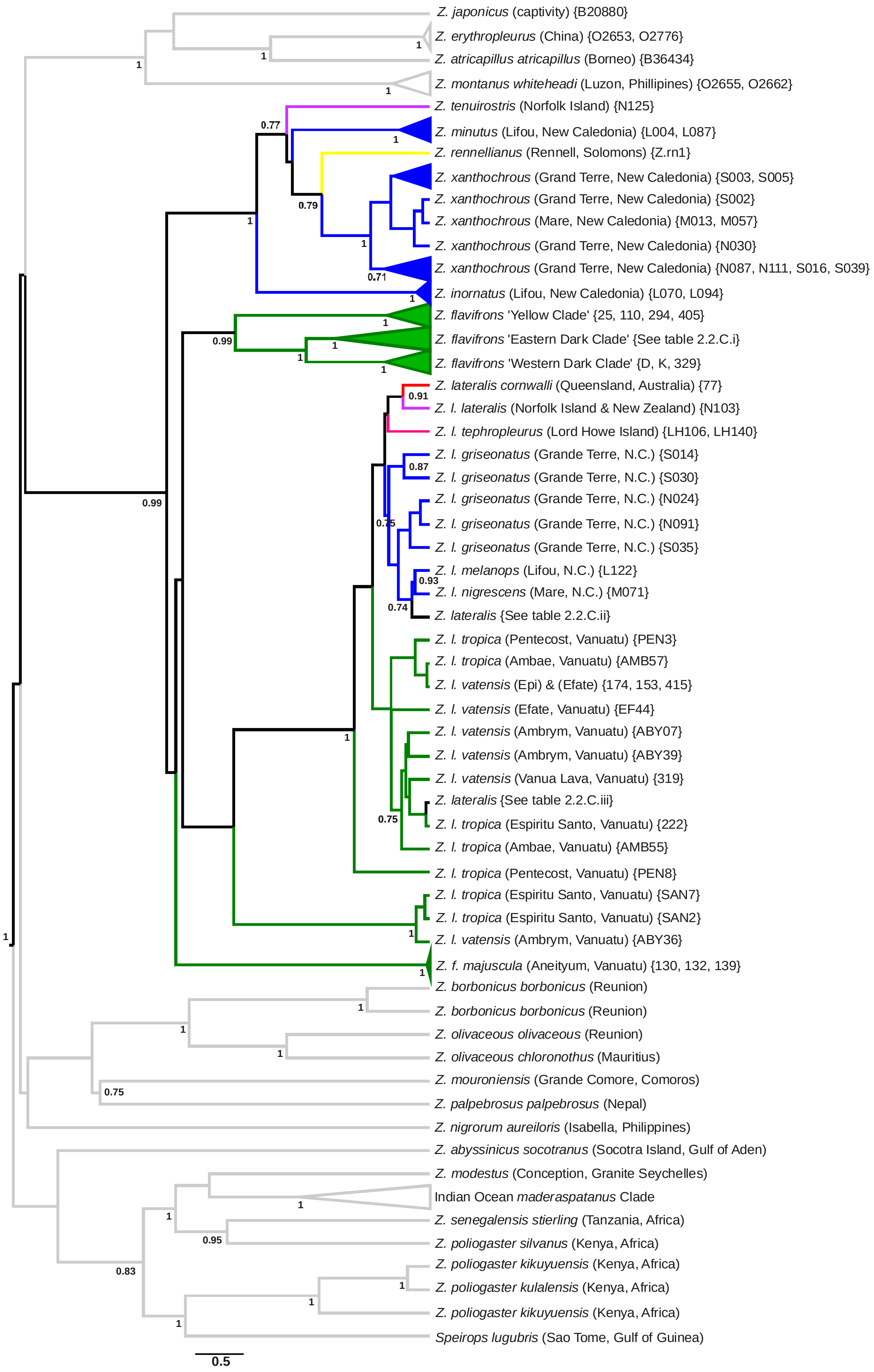
Genus	Species	Subspecies	Location	Sample numbers
Zosterops	xanthochrous		Grande Terre	N030, S003, S005
Zosterops	xanthochrous		Mare	M002, M0013, M034, M057, M074

2.2.B.iv

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	lateralis	chlorocephalus	Heron Island	9010, 9601, H1613, H1568
Zosterops	lateralis	cornwalli	Australia	B71, B79
Zosterops	lateralis	lateralis	New Zealand	C132, D3
Zosterops	lateralis	lateralis	Norfolk Island	N103, N120
Zosterops	lateralis	lateralis	Tasmania	TAS01, TAS04, TAS15
Zosterops	lateralis	gouldi	Australia	1966.21.270
Zosterops	lateralis	ramsayi	Australia	1964.60.1001

2.2.B.v

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	lateralis	flaviceps	Fiji	1888.9.1.781, 1898.9.30.186
Zosterops	lateralis	melanops	Lifou	L002, L088, L102, L122
Zosterops	lateralis	nigrescens	Mare	M001, M027, M044, M071, M089
Zosterops	lateralis	tropica	Ambae	AMB55, AMB56, AMB57
Zosterops	lateralis	tropica	Espiritu Santo	222, 233, 353, SAN9
Zosterops	lateralis	tropica	Gaua	261, 267
Zosterops	lateralis	tropica	Pentecost	PEN03, PEN16, PEN18, PEN33
Zosterops	lateralis	tropica	Vanua Lava	317, 319, VAN46
Zosterops	lateralis	vatensis	Ambrym	ABY07, AB26, ABY39
Zosterops	lateralis	vatensis	Efate	155, 174, EF44
Zosterops	lateralis	vatensis	Epi	412, 418, 423
Zosterops	lateralis	vatensis	Erromango	371, 373, 380
Zosterops	lateralis	vatensis	Malekula	176, 178, 183, 199, 215


Z. japonicus (captivity) {B20880}
Z. erythropleurus (China) {O2653, O2776}
Z. atricapillus atricapillus (Borneo) {B36434}
Z. montanus whiteheadi (Luzon, Phillipines) {O2655, O2662}
Z. tenuirostris (Norfolk Island) {N125}
Z. minutus (Lifou, New Caledonia) {L004, L087}
Z. rennellianus (Rennell, Solomons) {Z.rn1}
Z. xanthochrous (Grand Terre, New Caledonia) {S003, S005}
Z. xanthochrous (Grand Terre, New Caledonia) {S002}
Z. xanthochrous (Mare, New Caledonia) {M013, M057}
Z. xanthochrous (Grand Terre, New Caledonia) {N030}
Z. xanthochrous (Grand Terre, New Caledonia) {N087, N111, S016, S039}
Z. inornatus (Lifou, New Caledonia) {L070, L094}
Z. flavifrons 'Yellow Clade' {25, 110, 294, 405}
Z. flavifrons 'Eastern Dark Clade' {See table 2.2.C.i}
Z. flavifrons 'Western Dark Clade' {D, K, 329}
Z. lateralis cornwalli (Queensland, Australia) {77}
Z. l. lateralis (Norfolk Island & New Zealand) {N103}
Z. l. tephropleurus (Lord Howe Island) {LH106, LH140}
Z. l. griseonatus (Grande Terre, N.C.) {S014}
Z. l. griseonatus (Grande Terre, N.C.) {S030}
Z. l. griseonatus (Grande Terre, N.C.) {N024}
Z. l. griseonatus (Grande Terre, N.C.) {N091}
Z. l. griseonatus (Grande Terre, N.C.) {S035}
Z. l. melanops (Lifou, N.C.) {L122}
Z. l. nigrescens (Mare, N.C.) {M071}
Z. lateralis {See table 2.2.C.ii}
Z. l. tropica (Pentecost, Vanuatu) {PEN3}
Z. l. tropica (Ambae, Vanuatu) {AMB57}
Z. l. vatensis (Epi) & (Efate) {174, 153, 415}
Z. l. vatensis (Efate, Vanuatu) {EF44}
Z. l. vatensis (Ambrym, Vanuatu) {ABY07}
Z. l. vatensis (Ambrym, Vanuatu) {ABY39}
Z. l. vatensis (Vanua Lava, Vanuatu) {319}
Z. lateralis {See table 2.2.C.iii}
Z. l. tropica (Espiritu Santo, Vanuatu) {222}
Z. l. tropica (Ambae, Vanuatu) {AMB55}
Z. l. tropica (Pentecost, Vanuatu) {PEN8}
Z. l. tropica (Espiritu Santo, Vanuatu) {SAN7}
Z. l. tropica (Espiritu Santo, Vanuatu) {SAN2}
Z. l. vatensis (Ambrym, Vanuatu) {ABY36}
Z. f. majuscula (Aneityum, Vanuatu) {130, 132, 139}
Z. borbonicus borbonicus (Reunion)
Z. borbonicus borbonicus (Reunion)
Z. olivaceous olivaceous (Reunion)
Z. olivaceous chloronothus (Mauritius)
Z. mouroniensis (Grande Comore, Comoros)
Z. palpebrosus palpebrosus (Nepal)
Z. nigrorum aureiloris (Isabella, Philippines)
Z. abyssinicus socotranus (Socotra Island, Gulf of Aden)
Z. modestus (Conception, Granite Seychelles)
Indian Ocean maderaspatanus Clade
Z. senegalensis stierling (Tanzania, Africa)
Z. poliogaster silvanus (Kenya, Africa)
Z. poliogaster kikuyuensis (Kenya, Africa)
Z. poliogaster kulalensis (Kenya, Africa)
Z. poliogaster kikuyuensis (Kenya, Africa)
Speirops lugubris (Sao Tome, Gulf of Guinea)
1
1
1
1
0.77
1
0.79
1
1
0.71
1
1
0.99
1
1
1
0.91
0.87
0.99
0.75
0.93
0.74
1
0.75
1
1
1
1
1
1
0.75
1
1
0.95
0.83
1
1
1
0.5

Appendix Fig 2.2.C. The ATPase Tree. A maximum clade credibility tree of the Zosteropidae of the south west Pacific based on 393 bp of ND3, 308 bp of cyt *b* and 958 bp of ATPase combined in a partitioned analysis. Numbers adjacent to nodes represent Bayesian branching support. Numbers in curly parentheses indicate sample sizes of more than one specimen. Monophyletic island clades were collapsed. Coloured branches indicate the geographic location of different taxa using the same colour code as Figure 1. The abbreviation N.C. refers to New Caledonia. Grey branches indicate extant species from the African and Asian Clades. For details of the collapsed African and Indian Ocean clades see Warren *et al.*(2006). For details of the *Zosterops flavifrons* groups see Phillimore *et al.* (2008b).

Table 2.2.C Voucher numbers of specimens included in tips representing more than one individual in Appendix Figure 2.2.C.

2.2.C.i

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	flavifrons	macgilivrayi	Malekula	181, 201, 211
Zosterops	flavifrons	perplexa	Ambae	AMB3, AMB4, AMB5, AMB7
Zosterops	flavifrons	perplexa	Ambrym	ABY09, ABY10, ABY12, ABY13
Zosterops	flavifrons	perplexa	Epi	427
Zosterops	flavifrons	perplexa	Maewo	MW02, MW03, MW06, MW07
Zosterops	flavifrons	perplexa	Pentecost	PEN54, PEN69

2.2.C.ii

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	lateralis	nigrescens	Mare	M001, M044, M89
Zosterops	lateralis	griseonatus	Grande Terre	N018, N109
Zosterops	lateralis	vatensis	Tanna	082, 109

2.2.C.iii

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	lateralis	tropica	Espiritu Santo	SAN9
Zosterops	lateralis	tropica	Gaua	255
Zosterops	lateralis	tropica	Pentecost	PEN16, PEN18, PEN33
Zosterops	lateralis	tropica	Vanua Lava	VAN46
Zosterops	lateralis	vatensis	Ambrym	ABY25, ABY26
Zosterops	lateralis	vatensis	Erromango	373
Zosterops	lateralis	vatensis	Malekula	215

Figure 2.2.D. The Two Gene Tree. A maximum clade credibility tree of the Zosteropidae of the south west Pacific based on 393 bp of ND3 and 308 bp of cyt *b* in a partitioned analysis. Numbers adjacent to nodes represent Bayesian branching support. Numbers in curled parentheses indicate sample sizes of more than one specimen. Monophyletic island clades were collapsed. Coloured Branches indicate the geographic location of different taxa using the same colour code as Figure 2.1. Grey branches indicate species from African and Asian clades. For details of the collapsed African and Indian Ocean clades see Warren *et al.* (2006). For details of *the Z. flavifrons* groups see Phillimore *et al.* (2008b).

Table 2.2.D Voucher numbers of specimens included in tips representing more than one individual in Appendix Figure 2.2.D.

2.2.D.i

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	flavifrons	macgilivrayi	Malekula	185, 193, 201, 211
Zosterops	flavifrons	perplexa	Ambae	AMB3, AMB4, AMB5, AMB7
Zosterops	flavifrons	perplexa	Ambrym	ABY09, ABY10, ABY12, ABY13
Zosterops	flavifrons	perplexa	Epi	420, 421, 427
Zosterops	flavifrons	perplexa	Maewo	MW03, MW06, MW07
Zosterops	flavifrons	perplexa	Pentecost	PEN17, PEN69, PEN70

2.2.D.ii

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	flavifrons	brevicauda	Espirtu Santo	227, 229, SAN6, D
Zosterops	flavifrons	perplexa	Vanua Lava	311, 320, 329

2.2.D.iii

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	flavifrons	efatensis	Efate	18, 25, 40
Zosterops	flavifrons	efatensis	Erromango	378, 385, 392, 405
Zosterops	flavifrons	flavifrons	Tanna	73, 110
Zosterops	flavifrons	gauensis	Gaua	269, 271, 285, 294

2.2.D.iv

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	lateralis	gouldi	Australia	1965.43.992, 1966.21.269, 1965.43.993
Zosterops	lateralis	halmaturina	Australia	1965.43.990, 1965.43.991
Zosterops	lateralis	ramsayi	Australia	1964.60.1014

2.2.D.v

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	luteus	luteus	Queensland	1964.60.1041, 1964.60.1044, 1964.60.1045, 1964.60.1046

2.2.D.vi

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	lateralis	nigrescens	Mare	M001, M027, M044, M071, M089
Zosterops	lateralis	melanops	Lifou	L002, L031, L088, L102, L122

2.2.D.vii

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	lateralis	tropica	Ambae	AMB55, AMB56, AMB57
Zosterops	lateralis	tropica	Espiritu Santo	233, SAN9
Zosterops	lateralis	tropica	Gaua	251, 261, 267
Zosterops	lateralis	tropica	Pentecost	PEN03, PEN16, PEN18, PEN33
Zosterops	lateralis	tropica	Vanua Lava	317, 319, VAN46
Zosterops	lateralis	vatensis	Ambrym	ABY07, ABY26, ABY39
Zosterops	lateralis	vatensis	Efate	155, 174, EF44
Zosterops	lateralis	vatensis	Epi	412, 418, 423
Zosterops	lateralis	vatensis	Erromango	371, 373, 380
Zosterops	lateralis	vatensis	Malekula	176, 183, 199, 215

2.2.D.viii

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	lateralis	chlorocephalus	Heron Island	H1568, H1613, 9010, 9601
Zosterops	lateralis	cornwalli	Queensland	B71, 77

2.2.D.ix

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	lateralis	cornwalli	Queensland	B79, C132
Zosterops	lateralis	gouldi	Australia	1966.21.270
Zosterops	lateralis	lateralis	New Zealand	D3, C132
Zosterops	lateralis	lateralis	Norfolk Island	N103, N120
Zosterops	lateralis	lateralis	Tasmania	TAS01, TAS04, TAS06
Zosterops	lateralis	ramsayi	Queensland	1964.60.1001

Figure 2.2.E. The Three Gene Tree. A maximum clade credibility tree of the Zosteropidae of the south west Pacific based on 393 bp of ND3, 308 bp of cyt *b* and 958 bp of ATPase combined in a partitioned analysis. Numbers adjacent to nodes represent Bayesian branching support. Numbers in curled parentheses indicate sample sizes of more than one specimen. Monophyletic island clades were collapsed. Coloured branches indicate the geographic location of different taxa using the same colour code as Figure 2.1. Grey branches indicate extant species from the African and Asian clades. For details of the collapsed African and Indian Ocean clades see Warren *et al.* (2006). For details of the *Z. flavifrons* groups see Phillimore *et al.* (2008b).

Table 2.2.E Voucher numbers of specimens included in tips representing more than one individual in Appendix Figure 2.2.E.

2.2.E.i

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	flavifrons	brevicauda	Espirtu Santo	D
Zosterops	flavifrons	perplexa	Vanua Lava	329

2.2.E.ii

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	flavifrons	macgilivrayi	Malekula	181, 201, 211
Zosterops	flavifrons	perplexa	Ambae	AMB3, AMB4, AMB5, AMB7
Zosterops	flavifrons	perplexa	Ambrym	ABY09, ABY10, ABY12, ABY13
Zosterops	flavifrons	perplexa	Epi	427
Zosterops	flavifrons	perplexa	Maewo	MW03, MW06, MW07
Zosterops	flavifrons	perplexa	Pentecost	PEN69

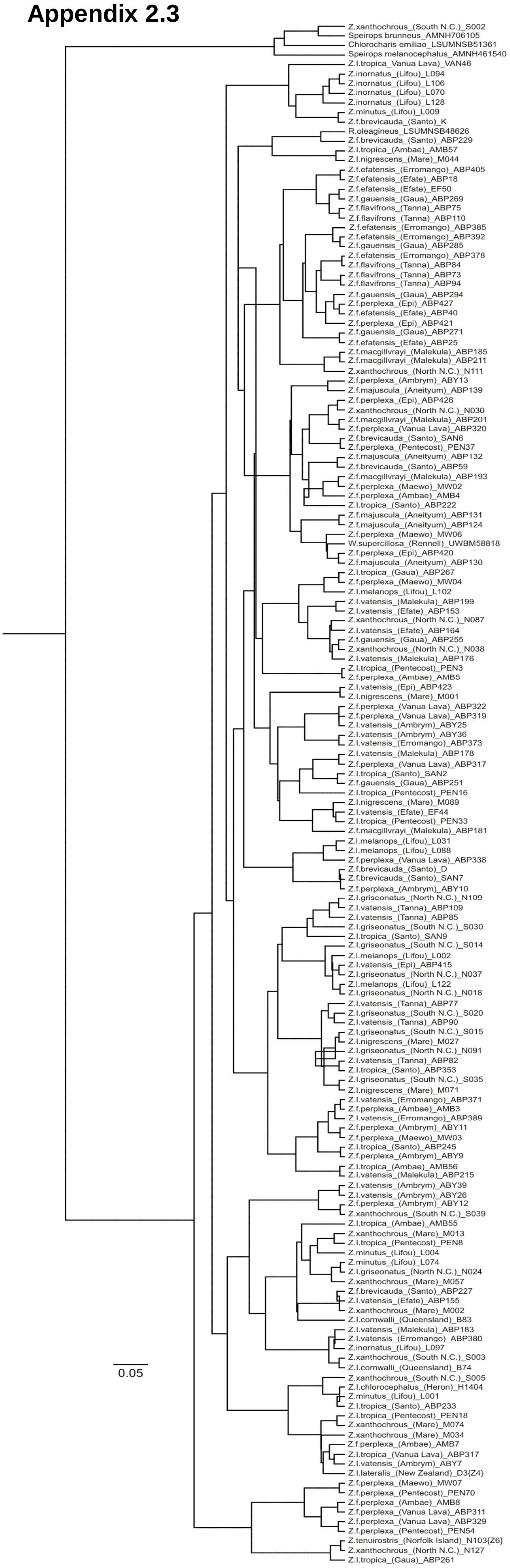
2.2.E.iii

Genus	Species	Subspecies	Location	Sample numbers
Zosterops	flavifrons	efatensis	Efate	25
Zosterops	flavifrons	efatensis	Erromango	405
Zosterops	flavifrons	flavifrons	Tanna	110
Zosterops	flavifrons	gauensis	Gaua	294

2.2.E.iv

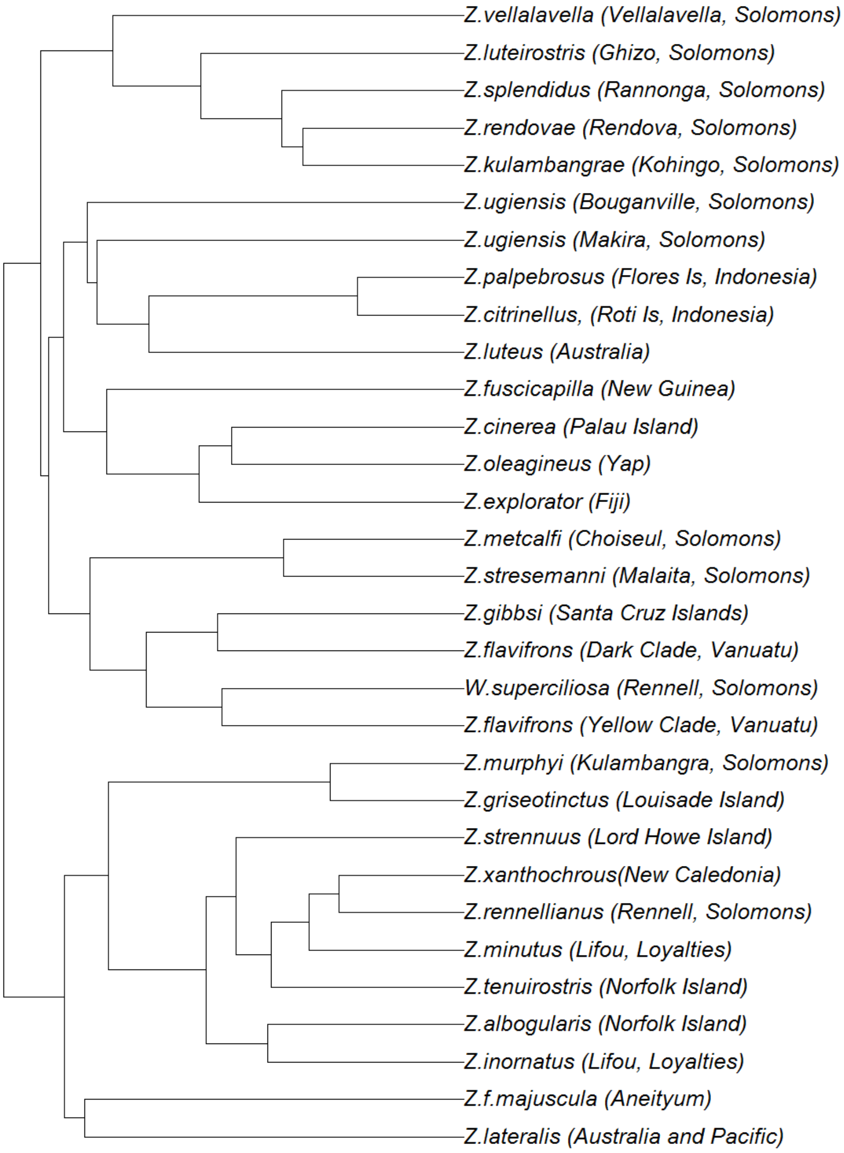
Genus	Species	Subspecies	Location	Sample numbers
Zosterops	lateralis	tropica	Espiritu Santo	SAN9
Zosterops	lateralis	tropica	Pentecost	PEN16, PEN18, PEN33
Zosterops	lateralis	tropica	Vanua Lava	VAN46
Zosterops	lateralis	vatensis	Ambrym	ABY26
Zosterops	lateralis	vatensis	Erromango	373
Zosterops	lateralis	vatensis	Malekula	215

Appendix 2.3

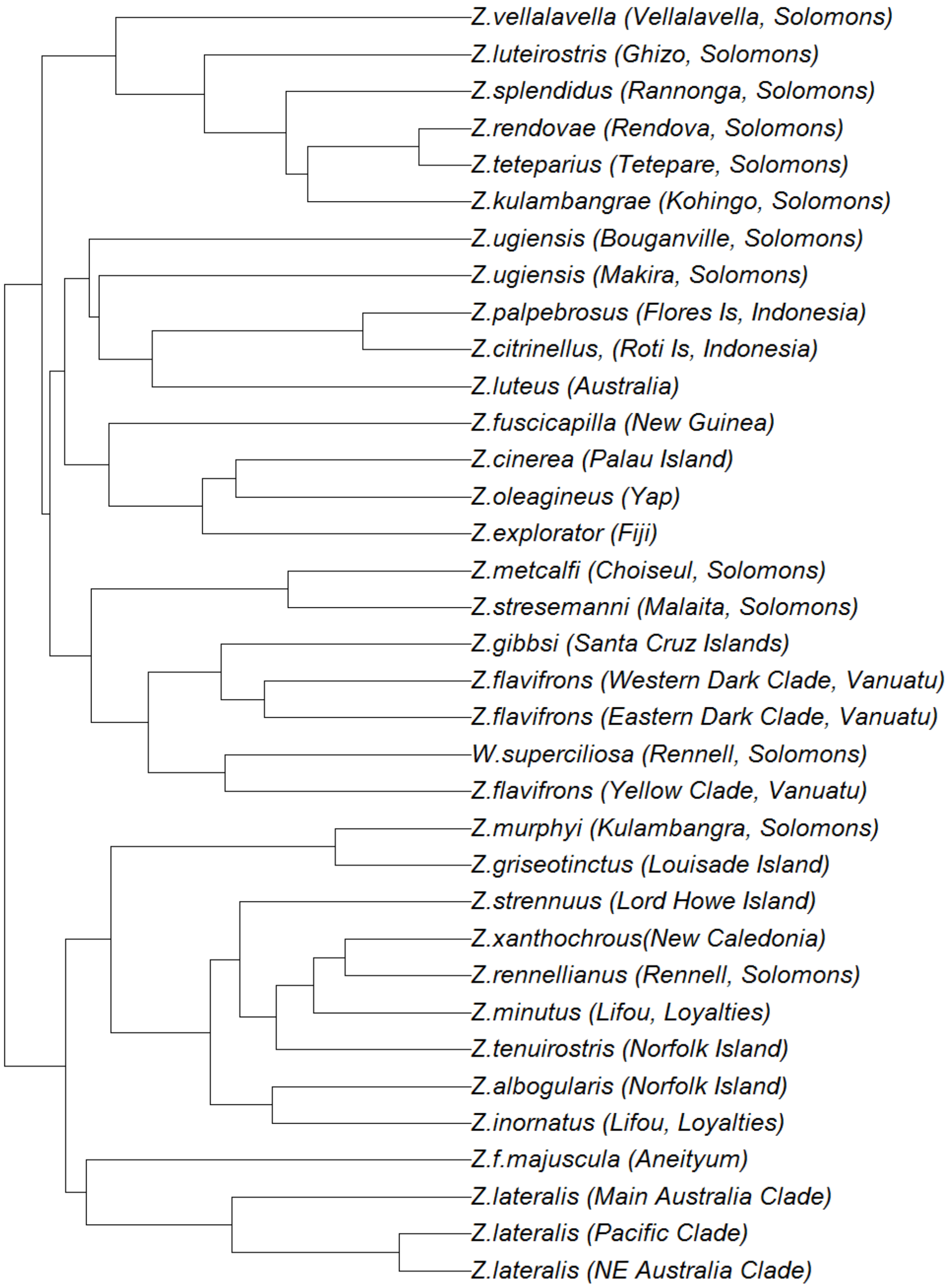


Appendix Figure 2.3. The TGFB2 Tree. A maximum clade credibility tree of the Zosteropidae of the south west Pacific based on 582 base pairs of the TGFB2 nuclear gener. There is not enough variation in the gene to resolve any relationships and thus this dataset cannot be used to test species hypothese. Bayesian posterior support was poor for all nodes (<0.2 in all cases). Tip labels show the taxonomic name of the sample followed, in brackets, by the location of collection if known and finally by the number of the sample. Abbreviations used in the tip labels are as follows: *flavifrons* (f), *lateralis* (l), New Caledonia (N.C.), Rukia (R), *Woodfordia* (W), *Zosterops* (Z).

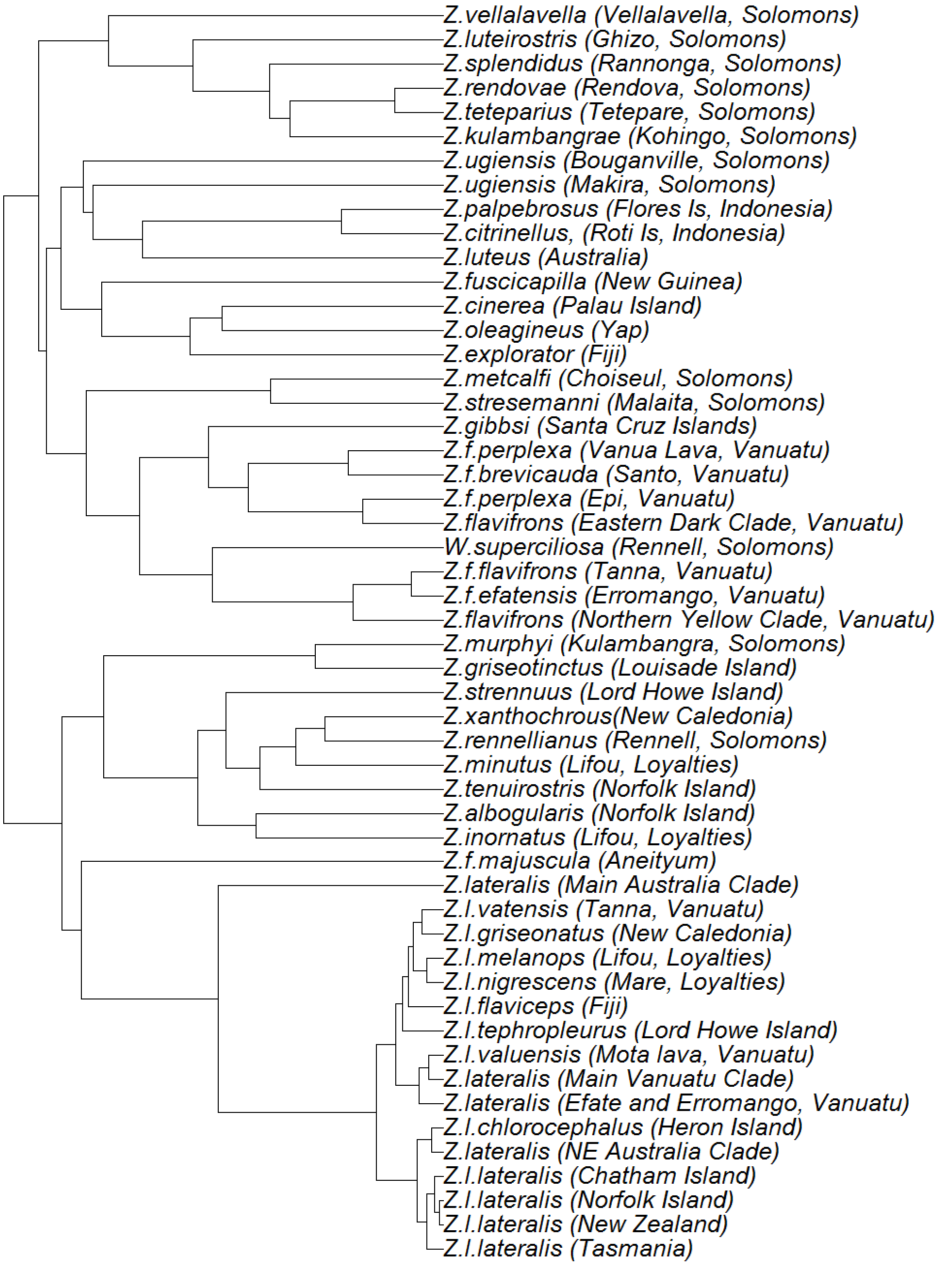
Appendix 3.1



Appendix Figure 3.1.A Conservative Species Tree. This is a conservative tree based on taxa that are accepted to be true, reproductively isolated species. There are 31 tips in this tree.



Appendix Figure 3.1.B Reciprocally Monophyletic Tree. This tree is made up of *Zosterops* forms that represent monophyletic tips in the tree. It includes some forms referred to as subspecies that are highly likely to be true species but which, because they are not yet in sympatry with congeners cannot be shown to be so through reproductive isolation. There are 35 tips in this tree.



Appendix Figure 3.1.C Incipient Species Tree. This tree includes not only currently recognised species but also potential incipient species. Incipient species were deduced from the molecular information where available or elsewhere from the treatments of Mayr (1967) and Mees (1957; 1961; 1969). There are 66 tips in this tree.

Appendix 3.2

Appendix Table 3.2.A *Zosterops* species from African and Pacific clades judged to be allospecies, their corresponding sister group, estimated and the age of divergence. Divergence times are taken from the Partitioned Two Gene Tree.

Superspecies	**Island**	**Region**	**Species**	**Sister**	**Divergence Time (mya)**
maderaspatanus	Seychelles	Africa	*Z. modestus*	rest of clade	1.45
	Grand Cormore	Africa	*Z. m. kirki*	*Z. m. cormorensis*	1.45
	Cormoros	Africa	*Z. m. cormorensis*	*Z. m. kirki*	1.45
	Madagasgar	Africa	*Z. maderaspatanus maderaspatanus/voeltzkowi*	*Z. m. Anjuanensis*	1.45
	Anjouan	Africa	*Z. m. anjuanensis*	*Z. m. maderaspatanus/voeltzkowi*	1.45
	Aldabra	Africa	*Z. m. aldabrensis*	*Z. m. mayottensis*	1.45
	Mayotte	Africa	*Z. m. mayottensis*	*Z. m. aldabrensis*	1.45
Africa-A	Africa	Africa	*Z. poliogaster silvanus*	rest of clade	1.8
	Africa	Africa	*Z. poliogaster winifredae*	*Z. pallidus/senegalensis*	1.8
	Africa	Africa	*Z. pallidus capensis*	*Z. s. stierlingi*	1.8
	Africa	Africa	*Z. s. stierlingi*	*Z. pallidus capensis*	1.8
Africa-B extended	Africa	Africa	*Z. poliogaster mbuluensis*	Africa-B	3.03
		Africa	*Z. poliogaster kikuyuensis* (Mount Kenya)	rest of Africa-B	3.03
		Africa	*Z. senegalensis senegalensis*	*Z. poliogaster*	3.03
		Africa	*Z. poliogaster kikuyuensis* (Aberdares)	*Z. poliogaster kulalensis*	3.03
		Africa	*Z. poliogaster kulalensis*	*Z. poliogaster kikuyuensis* (Aberdares)	3.03
olivaceus	Mauritius	Africa	*Z. chloronothus*	*Z. olivaceus*	1.08
	Reunion	Africa	*Z. olivaceus*	*Z. chloronothus*	1.08
borbonicus	Mauritius	Africa	*Z. mauritianus*	*Z. borbonicus*	1.06
	Reunion	Africa	*Z. borbonicus*	*Z. mauritianus*	1.06
Flavifrons	Vanuatu+	Pacific	Yellow Clade	Green Clade	3.02
Flavifrons Yellow Clade	Vanuatu+	Pacific	*W. superciliosa*	Yellow Clade	2.44
		Pacific	main yellow clade	Tanna/Erromango	2.44
		Pacific	Tanna	Erromango	2.44
		Pacific	Erromango	Tanna	2.44
Flavifrons Dark	Vanuatu+	Pacific	*Z. gibbsi*	Dark Clade	1.95
Dark Clade	Vanuatu	Pacific	Western Dark	Eastern Dark	1.61
		Pacific	*Z. f. brevicauda* (Santo)	*Z. f. perplexa* (Vanua Lava)	1.61
		Pacific	*Z. f. perplexa* (Vanua Lava)	*Z. f. brevicauda* (Santo)	1.61
		Pacific	*Z. f. perplexa* (Epi)	rest of eastern Dark Clade	1.61
		Pacific	rest of eastern Dark Clade	*Z. f. perplexa* (Epi)	1.61
lateralis	Australasia	Pacific	Australia group 1	rest of clade	1.89
	Australasia	Pacific	Australia group 2	Pacific lateralis	1.89
	New Caledonia	Pacific	*Z. l. griseonatus*	rest of pacific clade	1.89
	Loyalty Islands	Pacific	*Z. l. nigrescens-melanops*	*Z. l. vatensis/tephropleurus*	1.89
	Vanuatu	Pacific	*Z. vatensis*	*Z. l. tephropleurus*	1.89
	Vanuatu	Pacific	*Z. l. tropica*	*Z. l. flaviceps*	1.89
	Lord Howe Island	Pacific	*Z. l. tephropleurus*	*Z. l. vatensis*	1.89
	Fiji	Pacific	*Z. l. flaviceps*	*Z. l. tropica*	1.89

Appendix Table 3.2.B Sympatric pairs of species from African and Pacific clades and the estimated age of their most recent common ancestor. This age of most common ancestor is used as a proxy for the time taken for range expansion. Ages are taken from the Four Gene Tree for Pacific clades and from the Partitioned Three Gene Tree for African clades.

Island	**Region**	**Species1**	**Species2**	**Age (myr)**
Kenya	Africa	*Z. abyssinicus*	*Z. poliogaster*	3.27
Reunion	Africa	*Z. olivaceous*	*Z. mauritianus*	3.35
Mauritius	Africa	*Z. chloronothus*	*Z. borbonicus*	3.35
Grande Cormore	Africa	*Z. mouroniensis*	*Z. kirki*	3.67
South Africa	Africa	*Z. pallidus*	*Z. senegalensis*	4.21
Ethiopia	Africa	*Z. abyssinicus*	*Z. senegalensis*	4.21
Lifou	Pacific	*Z. inornatus*	*Z. minutus*	1.76
Norfolk Island	Pacific	*Z. albogularis*	*Z. tenuirostris*	1.76
Lifou	Pacific	*Z. inornatus*	*Z. l. melanops*	2.58
New Caledonia	Pacific	*Z. xanthochrous*	*Z. lateralis*	2.58
Norfolk Island	Pacific	*Z. albogularis*	*Z. l. lateralis*	2.58
Lord Howe Island	Pacific	*Z. strennus*	*Z. l. tephropleurus*	2.58
Epi	Pacific	*Z. f. perplexa*	*Z. l. vatensis*	3.53
Ambae	Pacific	*Z. f. perplaxa/macgillivrayi*	*Z. l. vatensis*	3.53
Vanua Lava	Pacific	*Z. f. perplexa*	*Z. l. tropica*	3.53
Espiritu Santo	Pacific	*Z. f. brevicauda*	*Z. l. tropica*	3.53
Tanna	Pacific	*Z. f. flavifrons*	*Z. l. vatensis*	3.53
Erromango	Pacific	*Z. f. efatensis*	*Z. lateralis*	3.53
Gaua	Pacific	*Z. f. efatensis/gauaensis*	*Z. l. topica/vatensis*	3.53
Rennell	Pacific	*W. superciliosa*	*Z. rennellianus*	3.53
Fiji	Pacific	*Z. explorator*	*Z. l. flaviceps*	3.95
Australia	Pacific	*Z. luteus*	*Z. l. ramsayi*	3.95
Bougainville	Pacific	*Z. rendovae*	*Z. metcalfi*	3.95
Kulambangra	Pacific	*Z. kulambangrae*	*Z. murphyi*	3.95

Appendix 4.1

Appendix Table 4.1.A Morphological data for the species in the Reciprocally Monophyletic Tree gathered from Mees (1957; 1961; 1969) and used in the trait analyses. PC scores from the principal component analysis (see Chapter 4) are also included.

	Wing length		**Tail length**		**Tarsus length**		**Bill length**		**PC scores**			
Species	**No. records**	**Mean (mm)**	**No. records**	**Mean (mm)**	**No. records**	**Mean (mm)**	**No. records**	**Mean (mm)**	**PC1**	**PC2**	**PC3**	**PC4**
Z. lateralis .eastern	153	61.66	149	43.39	121	17.14	146	12.98	-0.18	-0.14	0.02	0.04
Z. lateralis .pacific	244	63.28	244	46.22	236	19.28	228	14.50	-0.01	-0.14	-0.02	0.00
Z. lateralis .south & west	142	57.26	145	41.68	140	16.82	137	12.68	-0.25	-0.12	0.02	-0.01
Z. f.majuscula	12	61.29	12	44.08	11	20.07	12	16.40	0.05	-0.03	-0.02	-0.06
Z. inornatus	31	73.13	30	49.17	31	21.72	30	20.73	0.36	0.01	0.03	-0.01
Z. albogularis	19	77.21	18	53.20	19	23.07	20	18.83	0.38	-0.11	-0.04	0.04
Z. tenuirostris	12	66.92	12	47.08	11	20.95	12	18.00	0.20	-0.03	-0.01	-0.03
Z. minutus	29	54.58	29	40.47	29	18.07	29	13.84	-0.19	-0.05	-0.02	-0.08
Z. rennellianus	3	64.00	3	38.83	3	19.92	3	16.42	0.01	0.08	-0.05	0.01
Z. xanthochrous	8	60.31	8	44.44	8	19.19	8	15.06	-0.03	-0.08	-0.01	-0.05
Z. strenuus	74	71.02	73	52.03	74	21.76	74	23.23	0.46	0.03	0.08	-0.08
Z. griseotinctus .all	44	62.91	44	40.04	43	19.59	44	16.55	0.02	0.06	-0.03	-0.02
Z. murphyi	5	66.30	5	44.30	5	19.40	5	17.80	0.13	0.01	0.04	-0.01
Z. f. yellow clade	41	63.03	41	42.06	39	20.05	37	15.85	0.02	-0.01	-0.05	-0.02
W. superciliosa	22	77.18	22	46.91	22	23.69	20	21.24	0.42	0.06	-0.05	0.03
Z. flavifrons .eastern.dark	51	61.22	51	39.70	47	19.66	46	15.27	-0.05	0.02	-0.06	-0.02
Z. flavifrons .western.dark	9	59.11	9	36.67	8	19.22	7	14.64	-0.14	0.06	-0.08	-0.01
Z. gibbsi	3	67.67	3	42.67	3	19.00	2	17.50	0.10	0.03	0.04	0.03
Z. stresemanni	9	68.72	9	43.56	9	20.42	9	17.44	0.14	0.01	-0.02	0.02
Z. metcalfi .all	30	59.05	30	37.85	30	16.81	29	14.39	-0.19	0.03	0.04	0.01
Z. explorator	17	61.00	16	36.22	17	18.51	16	15.00	-0.13	0.09	-0.04	0.02
Z. oleagineus	3	70.67	3	43.83	3	20.33	3	17.83	0.17	0.02	0.00	0.04
Z. cinereus .all	24	65.38	23	39.28	24	21.09	21	16.26	0.04	0.06	-0.10	0.02
Z. fuscicapillus .all	19	58.82	19	37.38	17	16.41	17	13.19	-0.27	-0.01	0.03	0.03
Z. luteus .all	76	55.36	75	37.78	73	17.32	70	12.53	-0.30	-0.05	-0.04	-0.02
Z. citrinellus .all	73	59.36	73	39.65	70	18.25	71	14.24	-0.14	-0.02	-0.02	-0.01
Z. parvula	57	52.44	13	31.76	12	15.04	13	12.04	-0.49	0.08	0.02	0.01
Z. u. ugiensis & oblitus	26	67.12	26	44.92	25	18.26	18	15.33	0.01	-0.08	0.04	0.05
Z. u. hamlini	2	67.50	2	43.75	2	20.38	2	16.00	0.08	-0.04	-0.05	0.03
Z. kulambangrae	7	62.93	7	39.71	7	18.54	7	16.54	-0.01	0.06	0.02	0.00
Z. tetiparius	5	63.90	5	42.40	5	17.55	5	16.30	-0.01	0.00	0.08	0.01
Z. rendovae	6	65.75	6	43.67	6	18.29	6	17.04	0.06	0.00	0.07	0.01
Z. splendidus	6	61.25	6	40.75	6	17.33	6	16.21	-0.05	0.03	0.08	-0.02
Z. luteirostris	7	60.64	7	36.36	7	17.18	7	15.57	-0.14	0.11	0.04	0.01
Z. vellalavella	9	63.22	9	39.61	9	17.50	9	16.00	-0.06	0.05	0.06	0.02

Appendix Table 4.1.B Island data for islands inhabited by species in the Reciprocally Monophyletic Tree. The data comes from the UN system-wide Earthwatch website (http://islands.unep.ch/Tiarea.htm). Species age is the branch length calibrated for time in millions of years taken from the Four Gene Tree. Dist. = the maximum dispersal distance, based on how far each taxa was likely to have dispersed in its current form. UN index = UN Isolation index: sum of the square roots of the distances to the nearest island of at least equivalent size, the nearest island group and the nearest continent. If one of these three measures is invalid the next highest distance is used.

Species	**Island(s)**	**No. islands**	**Species Age (myr)**	**Area (km2)**	**Dist.**	**UN index**	**Distance to nearest (km)**		
							Island	**Group**	**Continent**
Z. lateralis .eastern	eastern Australia	6	0.54	7686850	0	0	72	150	0
Z. lateralis .pacific	Pacific Islands	54	0.54	145836	1600	86	50	1800	1600
Z. lateralis .south & west	south and west Australia	1	1.83	7686850	0	0	72	150	0
Z. f.majuscula	Aneityum	1	2.94	159.2	0	55	63	200	1100
Z. inornatus	Lifou	1	1.52	1146.2	0	48	100	75	850
Z. albogularis	Norfolk Island	1	1.52	36.8	0	101	1400	670	1400
Z. tenuirostris	Norfolk Island	1	1.49	36.8	0	101	1400	670	1400
Z. minutus	Lifou	1	1.20	1146.2	0	48	100	75	850
Z. rennellianus	Rennell	1	0.96	660.1	0	79	170	700	1550
Z. xanthochrous	New Caledonia	3	0.96	16648.4	400	88	1100	400	1200
Z. strenuus	Lord Howe Island	1	1.77	14.6	0	73	600	600	600
Z. griseotinctus .all	Louisade and Bismarks	12	1.04	202.5	85	54	85	150	1050
Z. murphyi	Kulambangrae	1	1.03	2036.7	0	71	60	600	1500
Z. f. yellow clade	Vanuatu	5	1.88	899.5	340	62	75	340	1200
W. superciliosa	Rennell	1	1.88	660.1	0	79	170	700	1550
Z. flavifrons .eastern.dark	Vanuatu	12	1.58	2041.3	440	59	14	440	1200
Z. flavifrons .western.dark	Santo and Malo	2	1.58	3955.5	320	56	14	320	1200
Z. gibbsi	Vanikoro	1	1.90	173.2	0	66	30	200	2150
Z. stresemanni	Malaita	1	1.40	3836.2	0	76	45	700	1800
Z. metcalfi .all	North Solomons	7	1.40	2970.7	50	69	50	500	1600
Z. explorator	Fiji	6	2.06	10531	800	88	60	800	2700
Z. oleagineus	Yap	1	1.80	105.4	0	80	100	400	2500
Z. cinereus .all	Caroline and Palau Islands	7	1.80	10531	60	88	60	800	2700
Z. fuscicapillus .all	New Guinea and Goodenough	2	2.77	785753	155	37	155	155	155
Z. luteus .all	Australia	12	2.44	7686850	0	0	72	150	0
Z. citrinellus .all	Australia and Indonesia	23	0.83	10710.7	50	40	50	50	650
Z. parvula	Java, Bali, Sumbawa and Flores	4	0.83	138793.6	25	47	25	25	1400
Z. u. ugiensis & oblitus	Mak and Gau	2	2.84	3190.5	45	75	45	700	1750
Z. u. hamlini	Bouganville	1	2.92	9317.8	0	61	50	220	1500
Z. kulambangrae	New Georgia group	4	1.25	2036.7	60	71	60	600	1500
Z. tetiparius	Tetepare	1	0.40	118.4	0	72	30	400	2150
Z. rendovae	Rendova	1	0.40	411.3	0	66	10	600	1500
Z. splendidus	Ranongga	1	1.41	147.9	0	64	10	500	1500
Z. luteirostris	Ghizo	1	2.04	35	0	67	15	600	1500
Z. vellalavella	Vellalavella and Bagga	2	2.72	628.9	25	66	25	500	1500

Appendix Table 4.1.C Morphological data for the species in the Incipient Species Tree gathered from Mees (1957; 1961; 1969) and used in the trait analysis. PC scores from the principal component analysis (see Chapter 4) are also included.

Species	**Wing length**		**Tail length**		**Tarsus length**		**Bill length**		**PC scores**			
	No. records	**Mean (mm)**	**No. records**	**Mean (mm)**	**No. records**	**Mean (mm)**	**No. records**	**Mean (mm)**	**PC1**	**PC2**	**PC3**	**PC4**
Z. l. lateralis .Tasmania	17	62.09	17	43.65	17	17.62	17	13.09	-0.15	-0.12	0.00	0.03
Z. l. lateralis .Norfolk Island	25	61.73	23	42.72	0	17.44	24	13.13	-0.17	-0.10	0.00	0.03
Z. l. lateralis.New Zealand	36	62.44	35	45.14	33	17.45	33	13.01	-0.15	-0.16	0.01	0.03
Z. l. cornwalli	45	60.54	45	41.57	42	16.62	43	12.84	-0.22	-0.09	0.03	0.04
Z. l. chlorocephalus	2	66.50	2	46.50	2	18.25	2	14.38	-0.02	-0.14	0.02	0.05
Z. l. vatensis	44	68.55	44	50.44	43	20.78	41	15.65	0.14	-0.16	-0.03	0.00
Z. l. valuensis	7	65.07	7	45.93	7	19.97	6	15.00	0.04	-0.10	-0.04	-0.01
Z. l. tropicus	28	63.46	28	45.02	27	19.67	26	15.27	0.03	-0.07	-0.02	-0.02
Z. l. tephropleurus	15	60.33	15	45.10	15	19.32	15	15.52	0.01	-0.06	0.01	-0.07
Z. l. flaviceps	84	61.15	84	44.15	80	18.37	76	13.66	-0.11	-0.11	-0.01	-0.01
Z. l. griseonotus	22	62.80	22	46.27	22	18.89	21	13.36	-0.08	-0.16	-0.04	0.00
Z. l. nigrescens	33	62.71	33	47.03	32	19.27	32	14.62	0.00	-0.13	-0.01	-0.03
Z. l. melanops	11	63.45	11	47.41	10	19.35	11	14.30	-0.01	-0.15	-0.02	-0.02
Z. lateralis. south & west Australia	142	57.26	145	41.68	140	16.82	137	12.68	-0.25	-0.09	0.02	-0.01
Z. f. majuscula	12	61.29	12	44.08	11	20.07	12	16.40	0.06	-0.01	-0.01	-0.07
Z. inornatus	31	73.13	30	49.17	31	21.72	30	20.73	0.37	0.00	0.04	0.00
Z.albogularis	19	77.21	18	53.20	19	23.07	20	18.83	0.39	-0.13	-0.04	0.03
Z. tenuirostris	12	66.92	12	47.08	11	20.95	12	18.00	0.21	-0.03	0.01	-0.04
Z. minutus	29	54.58	29	40.47	29	18.07	29	13.84	-0.18	-0.02	0.00	-0.09
Z. rennellianus	3	64.00	3	38.83	3	19.92	3	16.42	0.03	0.09	-0.04	0.00
Z. xanthochrous	8	60.31	8	44.44	8	19.19	8	15.06	-0.02	-0.06	0.00	-0.06
Z. strenuus	74	71.02	73	52.03	74	21.76	74	23.23	0.47	0.01	0.11	-0.06
Z. g. eichhorni	14	61.69	14	38.32	14	19.86	14	15.82	-0.02	0.09	-0.05	-0.02
Z. g. longirostris	3	63.00	3	39.33	2	19.25	3	17.50	0.06	0.11	0.02	-0.02
Z. g. griseotinctus	14	62.89	14	41.36	14	19.09	14	16.07	0.01	0.03	0.01	-0.01
Z. g. pallidipes	13	64.23	13	40.65	13	19.90	13	17.62	0.10	0.09	0.01	-0.02
Z. murphyi	5	66.30	5	44.30	5	19.40	5	17.80	0.14	0.02	0.05	0.00
Z. f. gauensis	11	64.55	11	42.86	10	20.55	10	16.05	0.07	-0.01	-0.05	-0.02
Z. f. efatensis	24	61.63	24	40.88	23	19.61	23	16.02	0.01	0.04	-0.02	-0.03
Z. f. flavifrons	6	65.83	6	45.33	6	20.88	4	17.81	0.18	0.00	0.00	-0.04
W. lacertosa	15	83.17	15	49.40	15	25.62	15	24.33	0.61	0.06	-0.04	0.03
W. superciliosa	22	77.18	22	46.91	22	23.69	20	21.24	0.43	0.04	-0.04	0.03
Z. f. brevicauda	9	59.11	9	36.67	8	19.22	7	14.64	-0.12	0.09	-0.07	-0.02
Z. f. perplexa	44	61.52	44	39.93	41	19.71	39	15.28	-0.03	0.03	-0.05	-0.02
Z. f. macgillivrayi	7	59.36	7	38.29	6	19.33	7	15.21	-0.07	0.07	-0.04	-0.04

Appendix Table 4.1.C continued

	Wing length		**Tail length**		**Tarsus length**		**Bill length**		**PC scores**			
Species	**No. records**	**Mean (mm)**	**No. records**	**Mean (mm)**	**No. records**	**Mean (mm)**	**No. records**	**Mean (mm)**	**PC1**	**PC2**	**PC3**	**PC4**
Z. gibbsi	3	67.67	3	42.67	3	19.00	2	17.50	0.11	0.04	0.05	0.03
Z. stresemanni	9	68.72	9	43.56	9	20.42	9	17.44	0.15	0.02	-0.01	0.02
Z. m. exigua	18	58.83	18	37.78	18	16.93	17	14.41	-0.18	0.05	0.04	0.01
Z. m. metcalfi	4	59.38	4	38.38	4	16.75	4	14.00	-0.20	0.02	0.04	0.02
Z. m .floridana	8	59.38	8	37.75	8	16.56	8	14.56	-0.18	0.06	0.06	0.02
Z. explorator	17	61.00	16	36.22	17	18.51	16	15.00	-0.11	0.11	-0.03	0.01
Z. cinereus cinereus	2	63.50	2	34.25	2	20.25	2	15.13	-0.07	0.16	-0.12	0.04
Z. cinereus ponapensis	2	60.50	2	35.75	2	19.38	2	13.25	-0.19	0.06	-0.13	0.02
Z. cinereus finschii	20	66.05	19	40.18	20	21.35	17	16.75	0.10	0.07	-0.08	0.00
R. ruki	10	81.00	10	48.20	10	23.80	9	20.42	0.44	-0.01	-0.06	0.07
Z. oleagineus	3	70.67	3	43.83	3	20.33	3	17.83	0.18	0.02	0.00	0.04
R. longirostra	21	70.60	20	42.08	21	21.72	18	23.26	0.38	0.19	0.06	-0.02
Z. fu. crookshanki	2	60.50	2	42.25	2	17.25	2	15.00	-0.09	-0.02	0.07	-0.01
Z. fu. fuscicapillus	17	58.62	17	36.81	15	16.30	15	12.95	-0.28	0.02	0.02	0.04
Z. luteus.all	76	55.36	75	37.78	73	17.32	70	12.53	-0.29	-0.01	-0.03	-0.03
Z. citrinellus citrinellus	13	56.88	13	37.40	12	17.10	13	12.75	-0.28	0.00	-0.02	0.00
Z. citrinellus harterti	5	58.20	5	39.50	5	17.25	5	13.25	-0.22	-0.03	0.00	0.00
Z. citrinellus albiventris	55	60.05	55	40.20	53	18.61	53	14.70	-0.09	0.01	-0.01	-0.02
Z. palpebrosus melanura	53	52.45	9	32.38	8	15.03	9	12.14	-0.46	0.11	0.03	0.01
Z. palpebrosus unica	4	52.25	4	30.38	4	15.06	4	11.83	-0.50	0.15	0.00	0.02
Z. u. oblitus	19	66.79	19	45.68	18	17.57	12	15.04	-0.01	-0.10	0.07	0.06
Z. u. ugiensis	7	68.00	7	42.86	7	20.04	6	15.92	0.07	-0.02	-0.04	0.04
Z. u. hamlini	2	67.50	2	43.75	2	20.38	2	16.00	0.09	-0.03	-0.04	0.02
Z. kulambangrae	7	62.93	7	39.71	7	18.54	7	16.54	0.00	0.08	0.03	0.00
Z. tetiparius	5	63.90	5	42.40	5	17.55	5	16.30	0.00	0.01	0.09	0.02
Z. rendovae	6	65.75	6	43.67	6	18.29	6	17.04	0.07	0.00	0.08	0.02
Z. splendidus	6	61.25	6	40.75	6	17.33	6	16.21	-0.04	0.05	0.09	0.00
Z. luteirostris	7	60.64	7	36.36	7	17.18	7	15.57	-0.12	0.12	0.05	0.02
Z. vellalavella	9	63.22	9	39.61	9	17.50	9	16.00	-0.04	0.06	0.07	0.03

Appendix Table 4.1.D Island data for islands inhabited by species in the Incipient Species Tree. The data comes from the UN system-wide Earthwatch website (http://islands.unep.ch/Tiarea.htm). Species age is the branch length calibrated for time in millions of years taken from the Four Gene Tree. Dist. = the maximum dispersal distance, based on how far each taxa was likely to have dispersed in its current form. UN index = UN Isolation index: sum of the square roots of the distances to the nearest island of at least equivalent size, the nearest island group and the nearest continent. If one of these three measures is invalid the next highest distance is used.

Species	Island(s)	Subspecies Age (myr)	Area (km2)	Dist.	UN index	Distance to nearest (km)		
						Island	Group	Continent
Z. l. lateralis .Tasmania	Tasmania	0.200	65021.1	200	35	50	200	200
Z. l. lateralis .Norfolk Island	Norfolk Island	0.030	36.8	670	101	1400	670	1400
Z. l. lateralis.New Zealand	New Zealand	0.030	145836	1800	86	50	1800	1600
Z. l. cornwalli	Seaus	0.090	7686850	0	0	72	150	0
Z. l. chlorocephalus	Heron Island	0.090	0.16	0	35	72	72	72
Z. l. vatensis	Vanuatu	0.200	555	220	54	35	220	1100
Z. l. valuensis	Motalava	0.120	24	0	54	14	200	1300
Z. l. tropicus	Vanuatu	0.120	3955.5	320	56	14	320	1200
Z. l. tephropleurus	Lord Howe Island	0.330	14.6	0	73	600	600	600
Z. l. flaviceps	Vanuatu	0.280	10531	800	88	60	800	2700
Z. l. griseonotus	Grande Terre	0.170	16648.4	0	88	1100	400	1200
Z. l. nigrescens	Mare & Ouvea	0.140	656.6	0	44	40	75	850
Z. l. melanops	Lifou	0.140	1146.2	0	48	100	75	850
Z. lateralis. south & west Australia	Australia	1.830	7686850	0	0	72	150	0
Z. f. majuscula	Aneityum	2.940	159.2	0	55	63	200	1100
Z. inornatus	Lifou	1.520	1146.2	0	48	100	75	850
Z.albogularis	Norfolk Island	1.520	36.8	0	101	1400	670	1400
Z. tenuirostris	Norfolk Island	1.490	36.8	0	101	1400	670	1400
Z. minutus	Lifou	1.200	1146.2	0	48	100	75	850
Z. rennellianus	Rennell	0.960	660.1	0	79	170	700	1550
Z. xanthochrous	Grandterre, Ile de Pins & Mare	0.960	16648.4	0	88	1100	400	1200
Z. strenuus	Lord Howe Island	1.770	14.6	0	73	600	600	600
Z. g. eichhorni	Nissan, Nauna & Long	0.125	500	50	42	50	50	800
Z. g. longirostris	Heath, East Hastings & Alcester	0.125	10	40	51	40	150	1050
Z. g. griseotinctus	Misima, Panasesa, Deboyne and Panepompo	0.250	202.5	85	54	85	150	1050
Z. g. pallidipes	Rossel	0.500	262.5	0	57	35	335	1070
Z. murphyi	Kulambangrae	1.030	687.8	0	65	10	550	1500
Z. f. gauensis	Gaua	0.730	328.2	0	58	25	290	1300
Z. f. efatensis	Nguna, Efate & Erro	0.270	888.1	35	56	35	270	1100
Z. f. flavifrons	Tanna	0.270	555	0	54	35	220	1100

Appendix Table 4.1.D continued

Species	Island(s)	Subspecies Age (myr)	Area (km2)	Dist.	UN index	Distance to nearest (km)		
						Island	Group	Continent
W. lacertosa	Ndeni	0.940	505.5	0	70	70	250	2100
W. superciliosa	Rennell	0.940	660.1	0	79	170	700	1550
Z. f. brevicauda	Santo & Malo	1.580	3955.5	14	56	14	320	1200
Z. f. perplexa	Vanuatu	0.660	334.3	25	57	25	240	1300
Z. f. macgillivrayi	Malekula	0.660	2041.3	0	59	14	440	1200
Z. gibbsi	Vanikoro	1.900	173.2	0	66	30	200	2150
Z. stresemanni	Malaita	1.400	3836.2	0	76	45	700	1800
Z. m. exigua	Shortland, Choisel, Bougainville & Buka	0.350	9317.8	50	61	50	220	1500
Z. m. metcalfi	Ysabel & Sanjorge	0.350	3664.8	0	75	80	600	1700
Z. m .floridana	Florida	0.700	386	0	73	25	700	1750
Z. explorator	Fiji	2.060	10531	60	88	60	800	2700
Z. cinereus cinereus	Kusaie	0.450	110	0	126	250	1500	5100
Z. cinereus ponapensis	Ponape	0.450	334	0	108	20	1350	4500
Z. cinereus finschii	Peleliu, Garakayo Ngabad, Koror & Babelthua	0.900	374	2	81	2	850	2500
R. ruki	Truk	0.450	8.8	0	95	50	900	3400
Z. oleagineus	Yap	0.450	105.4	0	80	100	400	2500
R. longirostra	Ponape	0.900	334	0	108	20	1350	4500
Z. fu. crookshanki	Goodenough	1.380	686.7	0	36	5	30	820
Z. fu. fuscicapillus	New Guinea	1.380	785753	0	37	155	155	155
Z. luteus.all	Australia	2.440	7686850	0	0	72	150	0
Z. citrinellus citrinellus	Timor, Roti, Sawu & Sumba	0.207	28418.9	30	32	30	30	450
Z. citrinellus harterti	Alor	0.207	2119.7	0	32	30	30	450
Z. citrinellus albiventris	Goenoengapi, Wetar, Kisser, Roma etc	0.413	3600	56	38	56	56	550
Z. palpebrosus melanura	Java & Bali	0.413	138793.6	25	47	25	25	1400
Z. palpebrosus unica	Sumbawa & Flores	0.413	14386	15	39	15	25	900
Z. u. oblitus	Guadalcanar	1.420	5352.9	0	75	55	700	1700
Z. u. ugiensis	Makira	1.420	3190.5	0	75	45	700	1750
Z. u. hamlini	Bouganville	2.920	9317.8	0	61	50	220	1500
Z. kulambangrae	Kulambangra, Newgeorgia, Vanunga & Gatuka	1.250	2036.7	60	71	60	600	1500
Z. tetiparius	Tetepare	0.400	118.4	0	66	10	600	2000
Z. rendovae	Rendova	0.400	411.3	0	66	10	600	1500
Z. splendidus	Ranongga	1.410	147.9	0	64	10	500	1500
Z. luteirostris	Ghizo	2.040	35	0	67	15	600	1500
Z. vellalavella	Vellalavella & Bagga	2.720	628.9	25	66	25	500	1500

Appendix 4.2

Procedure and R code for testing if trait differences between congeneric sympatrics are significantly greater than expected by chance.

Appendix 4.2.A Testing character displacement using absolute standardized contrasts

Brownian simulations were performed using both the Reciprocally Monophyletic Tree and the Incipient Species Tree, for both trees the simulations were performed with and without *Z. lateralis* included. Trait simulations were performed for the first two principal components as well as for all four of the measured morphological traits separately (wing length, tarsus length, tail length and bill length). As a worked example, this code demonstrates the process in R for the Reciprocally Monophyletic tree and principal component one (PC1). The description of what each piece of code does appears first and the code itself is indented.

The CAIC package was read into R

```
library(CAIC)
```

The phylogenetic tree was read into R, into an object called ‘observed’.

```
observed<-read.nexus("TRAITspeciestree.nex",tree.names=NULL)
```

The trait data was read into R, into an object called ‘trait.data’ ensuring that the row names exactly matched the tip labels of the phylogenetic tree.

```
trait.data<-read.table("TRAIT.species.PCA.txt",header = TRUE)
```

The trait data required, in this case the column for PC1, was taken from the object ‘trait.data’.

```
observed$phenotype<-trait.data$Comp.1
```

First, observed values had to be calculated for the data. A list was therefore created assigning all the sympatric species in the phylogeny to their particular island. For the simulations excluding *Z. lateralis* the islands with two species, including one *Z. lateralis*, were not included at this point and only the endemic were included on islands with three species.

```
sympatric.taxa<-list()
sympatric.taxa[["santo"]]<-c("Z.f.dark.west.part","Z.lateralis.pacific")
sympatric.taxa[["epi"]]<-c("Z.f.dark.east.plus","Z.lateralis.pacific")
sympatric.taxa[["tanna"]]<-c("Z.f.yellow","Z.lateralis.pacific")
sympatric.taxa[["fiji"]]<-c("Z.explorator","Z.lateralis.pacific")
```

```
sympatric.taxa[["rennell"]]<-c("W.superciliosa","Z.rennellianus")
sympatric.taxa[["australia"]]<-c("Z.luteus.all","Z.lateralis.east")
sympatric.taxa[["lifou"]]<-c("Z.inornatus","Z.minutus","Z.lateralis.pacific")
sympatric.taxa[["gt"]]<-c("Z.xanthochrous","Z.lateralis.pacific")
sympatric.taxa[["norfolk"]]<-c("Z.albogularis","Z.tenuirostris","Z.lateralis.pacific")
sympatric.taxa[["lhi"]]<-c("Z.strennuus","Z.lateralis.pacific")
sympatric.taxa[["bou"]]<-c("Z.u.hamlini","Z.metcalfi")
sympatric.taxa[["kul"]]<-c("Z.kulambangrae","Z.murphyi")
```

For each of these islands in turn, the sympatric taxa were selected from the tree and the remaining tips dropped. The trait data for the selected tips was then placed in an object called ‘pruned.tree$phenotype’.

```
observed.numerator<-c()
for(x in 1:12){
        wanted.tips<-pmatch(sympatric.taxa[[x]],observed$tip.label)
        pruned.tree<-drop.tip(observed,observed$tip.label[-wanted.tips])
        pruned.tree$phenotype<-observed$phenotype[wanted.tips]
```

The mean standardized contrast for each island was calculated and stored.

```
        observed.numerator[x]<-mean(abs(pic(pruned.tree$phenotype,pruned.tree)))
        }
```

The mean of all the individual island contrasts then gave the absolute standardized contrast across all the islands with sympatric species.

```
observed.numerator.av<-mean(observed.numerator)
```

The mean across the entire tree was then calculated.

```
observed.denominator<-mean(abs(pic(observed$phenotype,observed)))
```

The observed value is then obtained by dividing the mean contrast of sympatric taxa by the mean calculated across the entire tree. The size of this ‘obsval’ gives an indication of whether sympatric species have diverged faster (ratio >1) or slower (ratio <1) than expected.

```
obsval<-observed.numerator.av/observed.denominator
obsval
```

Values were then calculated for each island and an object was created to store the observed values for individual islands.

```
island.obs.val<-observed.numerator/observed.denominator
```

Finally, the observed variance across all the islands was calculated to check if that was different to what would be expected by chance.

```
    observed.contrast.var<-var(island.obs.val)
```

Next random tips were simulated under Brownian motion using ‘evolve.phylo’ in the APE package for R (Paradis *et al.* 2004).

Objects were created to store the average of the expected contrasts and the expected variance generated by the simulation.

```
    store.exp.vals.av<-c()
    store.exp.var<-c()
```

A matrix was created to store the expected values generated by the simulation. Here there are 12 different islands (columns), and 10000 simulations (rows).

```
    store.exp.islevals<-matrix(nrow=10000,ncol=12)
```

The simulation was repeated 10000 times with trait evolved by Brownian motion each time. The process of each simulation was similar to the one described above but with simulated instead of real trait data. Each simulation generated an expected trait value for each sympatric island.

```
    for(nullrep in 1:10000){
        expected <- evolve.phylo(observed, 1, 1)$tip.character$V1

        exp.numerator<-c()
        for(x in 1:12){
            wanted.tips<-pmatch(sympatric.taxa[[x]],observed$tip.label)
            pruned.tree<-drop.tip(observed,observed$tip.label[-wanted.tips])
            pruned.tree$phenotype<-expected[wanted.tips]
```

The mean standardized contrast for each island was calculated and stored.

```
            exp.numerator[x]<-mean(abs(pic(pruned.tree$phenotype,pruned.tree)))
            }
```

The mean of all the individual simulated island contrasts then gave the expected standardized contrast across each simulated set of sympatric islands.

```
    exp.numerator.av<-mean(exp.numerator)
```

The mean across the entire tree was then calculated for each simulation.

```
    exp.denominator<-mean(abs(pic(expected,observed)))
```

The mean of the contrasts for all the sympatric islands was then divided by the mean across the entire tree for each simulation to give an expected value for each simulation. These were stored in the object created earlier.

```
store.exp.vals.av[nullrep]<-exp.numerator.av/exp.denominator
```

For individual islands the expected numerator (rather than the average of the expected numerator) divided by the expected denominator gave the contrasts for individual islands.

```
island.contrasts<-exp.numerator/exp.denominator
store.exp.islevals[nullrep,]<-island.contrasts
```

The islands contrasts were used to calculate the expected variance.

```
store.exp.var[nullrep]<-var(island.contrasts)

}
```

Finally, the p-value was generated to test if the direction of the observed value for sympatric species was significantly divergent across the whole tree.

```
pval<-min(length(which(store.exp.vals.av<=obsval)),
        length(which(store.exp.vals.av>=obsval)))/10000
pval
```

By selecting individual islands it was possible to look at the significance of individual cases. In the code below island 1 is selected but by changing the ‘choose species’ value each island could be looked at in turn.

```
choose.species<-1
        pval<-min(length(which(store.exp.islevals[,choose.species]
                <=island.obs.val[choose.species])),length(which(store.exp.islevals[,choose.s
                pecies]>=island.obs.val[choose.species])))/10000
        pval
```

```
#this tests whether the variance is more or less than across the whole tree
        pval<-min(length(which(store.exp.var<=observed.contrast.var)),
                length(which(store.exp.var>=observed.contrast.var)))/10000
        pval
```

Appendix 4.2.B Testing character displacement using minimum Euclidian distance

The CAIC package was read into R

```
library(CAIC)
```

The phylogenetic tree was read into R, into an object called ‘usetree’.

```
usetree<-read.nexus("TRAITspeciestree.nex",tree.names=NULL)
```

The trait data was read into R, into an object called ‘TRAITZostPC’ ensuring that the row names exactly matched the tip labels of the phylogenetic tree.

```
TRAITZostPC<-read.table("TRAIT.species.PCA.txt",header=T)
```

The observed distances for PC1 and PC2 were placed in an object.

```
observed_1<-TRAITZostPC$Comp.1
observed_2<-TRAITZostPC$Comp.2
```

A list was created assigning all the sympatric species in the phylogeny to their particular island.

```
sympatric.list<-list()
sympatric.list[["1"]]<-c("Z.f.dark.west.part","Z.lateralis.pacific")
sympatric.list[["2"]]<-c("Z.f.dark.east.plus","Z.lateralis.pacific")
sympatric.list[["3"]]<-c("Z.f.yellow","Z.lateralis.pacific")
sympatric.list[["4"]]<-c("Z.explorator","Z.lateralis.pacific")
sympatric.list[["5"]]<-c("W.superciliosa","Z.rennellianus")
sympatric.list[["6"]]<-c("Z.luteus.all","Z.lateralis.east")
sympatric.list[["7"]]<-c("Z.inornatus","Z.minutus","Z.lateralis.pacific")
sympatric.list[["8"]]<-c("Z.xanthochrous","Z.lateralis.pacific")
sympatric.list[["9"]]<-c("Z.albogularis","Z.tenuirostris","Z.lateralis.pacific")
sympatric.list[["10"]]<-c("Z.strenuus","Z.lateralis.pacific")
sympatric.list[["11"]]<-c("Z.u.hamlini","Z.metcalfi")
sympatric.list[["12"]]<-c("Z.kulambangrae","Z.murphyi")
```

The minimum Euclidian distance was calculated as the minimum distance between the two species in each sympatric pair according to the co-ordinates on PC1 and PC1 (here observed_1 and observed_2).

```
minEuclids<-c()
for(symp in 1:length(sympatric.list)){
wanted.tips<-pmatch(sympatric.list[[symp]],usetree$tip.label)
minEuclids[symp]<-min(dist(cbind(observed_1,observed_2)[wanted.tips,]))
}
```

The observed value is the smallest Euclidian difference because the test is based on determining whether there is a minimum difference that species should be apart.

```
obsmin<-min(minEuclids)
obsmin
```

Next, expected values were generated as the mean minimum distance across 10000 trees simulated in a Brownian motion model. Again ‘evolve.phylo’ from the APE package for R (Paradis *et al.* 2004) was used to evolve the traits, in this case the two Principal Components.

```
expmin<-c()
store.island.mins<-matrix(nrow=10000,ncol=12)
simvar1<-fitContinuous(usetree,observed_1)$Trait1$beta
simvar2<-fitContinuous(usetree,observed_2)$Trait1$beta



for (rep in 1:10000){

sim_1<-evolve.phylo(usetree,1,simvar1)$tip.character[,1]
sim_2<-evolve.phylo(usetree,1,simvar2)$tip.character[,1]

minEuclidsexp<-c()
for(symp in 1:length(sympatric.list)){

wanted.tips<-pmatch(sympatric.list[[symp]],usetree$tip.label)
minEuclidsexp[symp]<-min(dist(cbind(sim_1,sim_2)[wanted.tips,]))
}

store.island.mins[rep,]<-minEuclidsexp
```

The expected minimum distance was calculated as the smallest of the simulated minimum Euclidian distance.

```
expmin[rep]<-min(minEuclidsexp)
}

pval<-min(c((length(which(expmin>=obsmin))*2)/10000),
((length(which(expmin<=obsmin))*2)/10000))
median(expmin)
hist(expmin)
abline(v=obsmin,col=2)
```

```
pval
```

Finally, each islands observed value was compared to the expected value.

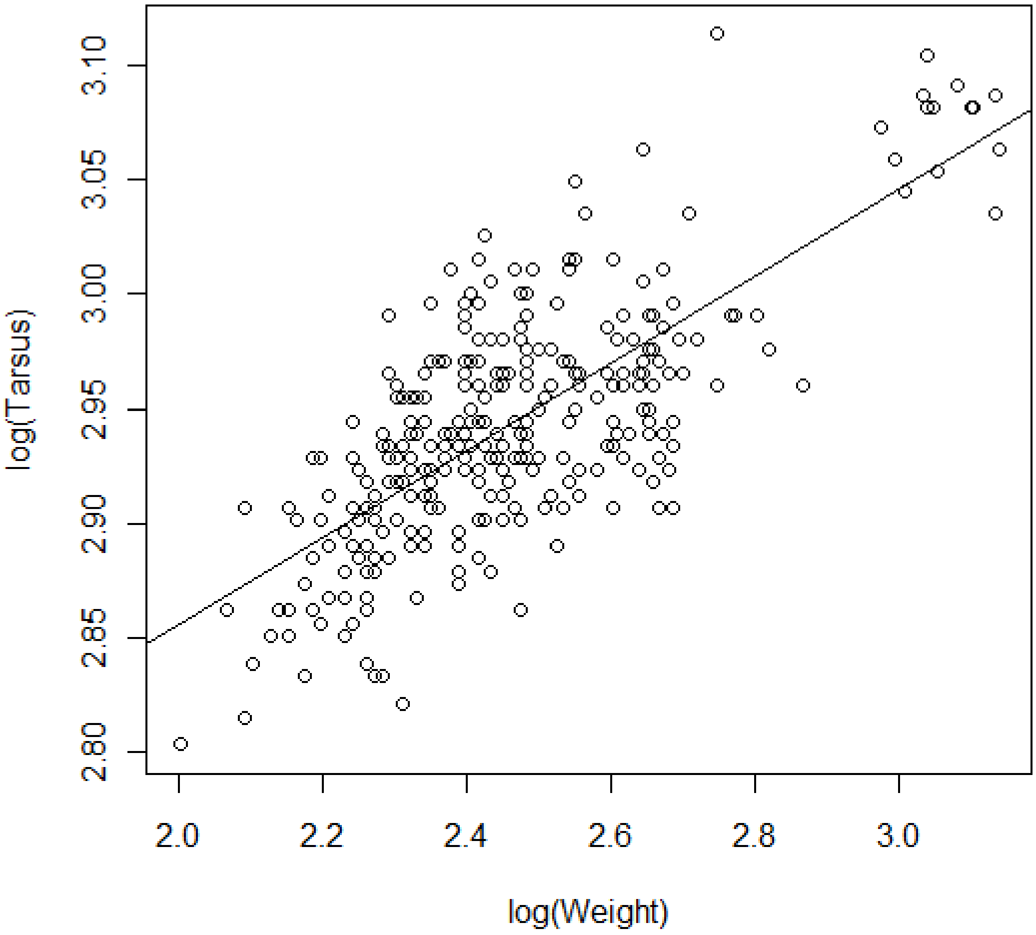
```
selectcol<-4
median(store.island.mins[,selectcol])
hist(store.island.mins[,selectcol])
abline(v=minEuclids[selectcol],col=2)
minEuclids[selectcol]
pval<-min(c((length(which(store.island.mins[,selectcol]
        >=minEuclids[selectcol]))*2)/10000),((length(which(store.island.mins
        [,selectcol]<=minEuclids[selectcol]))*2)/10000))
pval
```

Appendix 4.3

Appendix Table 4.3.A Loadings from a principal component analysis for the south west Pacific *Zosterops* based on four morphological measures per species: average maximum wing chord, average tarsus length, average tail length and culmen length (from bill tip to the anterior of the nostril). Part a) shows scores based on the Reciprocally Monophyletic Tree, and part b) those based on the Incipient Species Tree.

	a) The species tree				**b) the subspecies tree**			
Loadings:	PC1	PC2	PC3	PC4	PC1	PC2	PC3	PC4
log (average wing length)	0.383	-0.177		0.902	0.355	-0.195	-0.135	0.904
log (average tarsus length)	0.4	-0.333	-0.792	-0.319	0.388	-0.198	-0.841	-0.32
log (average tail length)	0.404	-0.665	0.58	-0.241	0.319	-0.812	0.428	-0.236
log (average bill length)	0.728	0.645	0.164	-0.165	0.789	0.513	0.301	-0.154
Proportion of Variance	0.81	0.12	0.05	0.02	0.81	0.13	0.04	0.01

Appendix 4.4



Appendix Fig 4.4.A Regression of logged weight against logged tarsus for *Zosterops* measurements taken in the field; N = 301, adjusted R2 = 0.55, p-value = <0.001 (RAB unpublished data).

Appendix 5

Appendix 5 is a CD containing the raw sequence and morphological data for all individuals.

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