Ecological and genetic responses of avifauna in species depauperate island ecosystems.

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Abstract

Understanding patterns in species abundance, distribution, and assemblages is an important component of biogeographical ecology, species diversity, and conservation. Ecological release and the taxon cycle are two theories proposed to describe patterns in species distribution and abundance on islands. These interlinked theories attempt to explain what happens to species when they enter novel, species-depauperate island ecosystems and how they change and evolve over time and space. Developing our knowledge of these two processes is not only important to understanding the evolutionary history of taxa but could help us understand how invasive species respond to island environments, how species may respond under changing conditions of climate change, and species susceptibility to extinction.

The aim of this study is to test for the presence of ecological release and the taxon cycle across Macaronesia. The thesis addresses criticisms of previous studies by using novel tools such as the availability of large-scale datasets of species distribution, biodiversity, and modern molecular tools to provide a temporal scale to the study and modern statistical techniques to model the taxon cycle and alternative models. Predictions associated with ecological release and the taxon cycle are tested across multiple island groups, species, and at different scales, using genetic, morphological, and ecological data, comparable species, habitats, and climates.

The results identified a consistent trend in niche expansion and density compensation in many of the focal species across a number of islands compared to mainland populations, thus supporting the presence of ecological release. Density compensation was also found when examining published estimates of abundance across European islands. A significant non-linear relationship between species age, abundance, and distribution was found in the birds across Macaronesia. Models for both distribution and abundance show a complex, consistent pattern of increase then decrease with lineage age. Trends throughout the thesis supported the presence of the taxon cycle across the Macaronesian islands, with patterns of expansion in distribution and abundance (ecological release) in more recent, younger colonists and contraction in range, niche shift, and decrease in abundance in more established, older species. Both ecological release and the taxon cycle may be important to better understand species invasions,

speciation, and susceptibility to extinction. However, further research is needed into the factors that drive these mechanisms and influence the magnitude in species responses.

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Chapter 1. Introduction

The island ecosystem has been the focus of much research since the early description of diversity patterns by Darwin and Russell in the 19th century (Losos and Ricklefs, 2010) and have provided the insights necessary to develop our understanding of many aspects of ecology and evolution. The Theory of Island Biogeography (TIB), developed by MacArthur and Wilson (1967), is crucial to our current understanding of a variety of insular processes, including species dispersal, colonization, speciation, and extinction (Lomolino and Brown, 2009; Spironello and Brooks, 2003). Islands provide a unique opportunity to investigate these processes and are often regarded as natural laboratories due to their geographical isolation, simplified biota, habitat heterogeneity, and relative youth (Spironello and Brooks, 2003; Losos and Ricklefs, 2009).

The work undertaken by MacArthur and Wilson (1967) revolutionised the discipline of biogeography and their ideas expanded into related areas of ecology and conservation (Lomolino and Brown, 2009). The MacArthur and Wilson equilibrium model (1967) is a simple model that describes the relationship between the number of species on an island and the rates of colonisation and extinction, providing the framework with which to investigate species richness dynamics in island or insular-type systems (Losos and Ricklefs, 2010; Heaney, 2000). This in turn has stimulated research into the dynamics of species richness and the evolution of biodiversity (Heaney, 2000).

The purpose of this chapter is to evaluate evidence for two interlinked hypotheses within TIB, which form an evolutionary paradox: ecological release and the taxon cycle. Both hypotheses are considered very important in ecology as they provide a predictive framework for taxonomic differentiation, species distribution, and extinction dynamics based on the evolutionary and ecological interactions between colonising and resident species (Ricklefs and Bermingham, 1999; Ricklefs and Bermingham, 2002). However, both concepts are also controversial, due primarily to the difficulty in testing the theories empirically (Pielou, 1979; Pregill and Olson, 1981; Blondel *et al*., 1988). This chapter will also consider how new genetics tools might be used to interrogate these island processes.

1.1 Ecological release

Ecological release is supposedly a process that occurs when a species colonises a species-depauperate island ecosystem and is released from resource partitioning constraints through the absence of predator and competitive pressures (Bolnick et al., 2010; Losos and Ricklefs, 2010). As a consequence of this release, a species may undergo density compensation and niche expansion, becoming more abundant and generalised in order to incorporate resources not utilised in their ancestral environment (MacArthur *et al.,* 1972; Feinsinger and Swarm, 1982; Losos and Ricklefs, 2010).

Release from competitive, predator, or host-parasite constraints is regarded as an important mechanism in explaining insular species abundance, niche width, and geographical distribution (Ricklefs, 2010; Carrascal *et al.,* 2008). The process of ecological release in the form of density compensation and niche expansion was initially observed for avifauna (MacArthur *et al.,* 1972; Mesquita *et al.,* 2007). However, the process has also been shown across a number of taxa, including lizards, (Bennett and Gorman, 1979; Buckley and Jetz, 2007; Mesquita *et al.,* 2007), herpetofauna (Rodda and Dean-Bradley, 2002), mammals (Rosenier and Flaspohler, 2006; Sara and Morand, 2002), molluscs (Kohn, 1978), and fish (Bolnick *et al.,* 2010). Despite the support for ecological release across a broad range of taxa, there are studies which suggest that density compensation and niche expansion may not be that common (Mesquita *et al.,* 2007), with studies showing greater (Palomino and Carrascal, 2005), similar, and lower species densities (MacArthur *et al.,* 1972; Vassalo and Rice, 1981) on islands than their mainland counterparts, with little evidence of niche expansion (Eaton et al, 2002). The ecological release hypothesis has been criticised based on difficulties in testing empirically, lack of comparable studies and inconsistencies in application (Blondel *et al.,* 1988). These criticisms suggest that further research is needed into ecological release using a comparison of ancestral populations with island species that may have undergone ecological release (Yoder *et al.,* 2010)

1.2 Release of invasive species

Species which invade island communities and undergo ecological release may impact upon resident species and, as such, are thought to be one of the primary drivers of species loss (Keane and Crawley, 2002; Sax *et al.,* 2002; 2007). Natural colonisations are thought to rare, especially long distance dispersal events limited to adjacent regions by dispersal ability and smaller in magnitude in contrast to human assisted invasions (Ricciardi, 2007). Human-assisted invasions occurring over large spatial scales are likely to have a greater effect than natural colonisers as they may encounter ecosystems with no analogous organisms (Ricciardi, 2007). Therefore, it is important to understand the ecological and evolutionary properties of these invasive species (Ricklefs and Bermingham, 2002). In addition, research into the early stages of species invasions and the factors that influence species colonisation success enables the prediction and limitation of the effects of invasive species (Marisico *et al.,* 2010). Species invasions also provide an opportunistic experiment in which to further understand evolutionary processes such as ecological release, adaption, and extinction (Sax et al, 2007). As a consequence of the immense and often irreversible (IUCN, 2000) ecological and economic effects of invasive species, the United Nations aims to prevent, control, and eradicate invasive species (Veitch and Clout, 2002).

1.3 Niche expansion and adaptive radiation

Evidence also suggests that ecological release is a likely precursor of adaptive radiation (Losos and Ricklefs, 2009), as a colonizing species will expand and evolve to utilise many resources in a novel habitat. After repeated episodes of speciation, each species may then specialise to a particular resource (Losos and Queiroz, 1997; Ricklefs and Bermingham, 2007). The diversification of Anole lizards in the Caribbean provide an example that links ecological opportunity, ecological release and adaptive radiation (Yoder *et al.,* 2010), with the evolution of habitat specialist types or ectomorphs (Losos and Queiroz, 1997). The link between ecological release and adaptive radiation has also been supported by fossil records following mass extinctions, as the absence of established biota permits rapid expansion and diversification through the filling of vacant niches (Ricklefs, 2010).

A number of recent papers have investigated the dynamics of niche expansion and niche filling (Bolnick *et al.,* 2007; Bolnick *et al.,* 2010). These studies have investigated the two hypothesised methods of niche expansion (under ecological release). The first predicts that a species has expanded its realised niche to incorporate the full breadth of available resources; the second predicts that individuals within a species will continue to utilise a narrow set of resources but diverge from conspecific competitors, reducing niche overlap and competition (Van Valen, 1965; Bolnick *et al.,* 2007). The second concept , known as the Niche Variation Hypothesis (NVH),has been documented in more than 100 taxa (Araujo *et al.,* 2009) and is advocated as a major cause of species diversification and speciation, enabling the maintenance and generation of biodiversity (Bolnick *et al.,* 2007; Agashe and Bolnick, 2010). However, empirical evidence to test the NVH is not strong and conceptually it is not universally accepted (Bolnick *et al.,* 2007).

Past studies have focused not only on morphological traits (previous tests of NVH) but also behavioural phenotypic traits (Bolnick *et al.,* 2007). These studies have identified ecological heterogeneity in generalist species occupying an increased niche breadth (Bolnick *et al.,* 2007; Araujo *et al.,* 2009). They have also suggested that there are multiple niche expansion responses (increased individual or among-individual niche width) dependent on the type of competition from which a species is released (Bolnick *et al.,* 2010).

Experimental work into niche expansion has also been used to determine the relative impacts of genetic variation and competition (Agashe and Bolnick, 2010). This research supports the role of intraspecific competition as a driver in niche expansion and evolution but highlights the importance of genetic variation for the maintenance of individual niche variation. The identification of this relationship between competition and genetic variation enhances our understanding of niche dynamics, especially in relation to how species diversify and fill ecological space (Agashe *et al.,* 2010, Ricklefs, 2010). Although this is a relatively well-researched area, attempts to understand species proliferation and diversification remain a constantly evolving topic (Ito and Dieckmann, 2007). The models produced by Ito and Dieckmann (2007) predict similarities with the taxon cycle (Wilson, 1961) in regard to a developmental cycle for a species; an idea that makes predictions about development and life history micro-evolution.

1.4 Taxon cycles: An evolutionary paradox

Expansion in niche width and distribution through ecological release provides the initial stage of the Taxon cycle coined by Wilson (1961) to describe sequential episodes of expansion and contraction in the Melanesian ant fauna (Wilson, 1961; Ricklefs and

Bermingham, 2002). Ecological release predicts that island immigrants initially undergo niche expansion and density compensation (expansion stage) as a consequence of reduced predation and competitive pressures (Losos and Queirioz, 1997; MacArthur *et al.,* 1972; Feinsinger and Swarm, 1982). However, over evolutionary time, species are predicted to become specialised to a particular habitat with a lower abundance and distribution (contraction stage), thus increasing its susceptibility to extinction (Ricklefs and Bermingham, 1999; 2002; Jones *et al.,* 1987). The two interlinked concepts of ecological release and the taxon cycle provide the basis of an evolutionary paradox. However, the mechanisms to explain why species initially become widespread and unspecialised and then rare, restricted, and highly specialised remain unknown (Ricklefs and Cox, 1978; Ricklefs and Bermingham, 2002).

Wilson (1961) identified three stages of the taxon cycle. Stage 1 species (expanding) show little differentiation from their mainland counterparts and display a continuous distribution. Stage 2 and 3 (contracting) show increasing degrees of differentiation and restricted ranges (Wilson, 1961; Jones *et al.,* 1987). Wilson (1961) suggested that the driver of this shift from expansion to contraction was the arrival of new colonists in marginal habitats and the associated increase in competition (Wilson, 1961; Ricklefs and Bermingham, 2002). A study of the distribution patterns of West Indies birds by Ricklefs and Cox (1972) provided empirical support for the taxon cycle sequence of evolutionary changes which an insular species undergoes, building on Wilson's (1961) theory by identifying four stages that a species may exhibit based on distribution and differentiation (Ricklefs and Cox, 1972). Stages 1 and 2 are expected to show widespread distributions, with stage 2 species being highly differentiated. Stage 3 species distribution is restricted and fragmented, whereas stage 4 species are endemic to a single island (Ricklefs and Cox, 1972). Ricklefs and Cox (1972) identified these stages as representing a temporal sequence of events and suggested that the arrival time of a species could be determined based on their distribution and differentiation (Ricklefs and Cox, 1972; Ricklefs and Bermingham, 1999).

Studies by Ricklefs and Cox (1972, 1978) in the West Indian Islands also supported Wilson's (1961) suggestion that competition was driving mechanism of the taxon cycle. The role of competition was predicted to progressively reduce as a species passes through the taxon cycle stages as a consequence of the counter-adaption of insular biota (Ricklefs and Cox, 1972; Ricklefs and Bermingham, 1999), presumably by the build-up of genetic correlations between the focal species and predators, prey, and parasites. A newly colonising species may have the competitive advantage over exiting species due to the release from competition, predation, or parasitism (Ricklefs and Cox, 1972, Jones *et al.,* 1987). Ricklefs and Cox (1972) identified coevolution and counter-adaptation of island biota and selection pressures such as competition from the arrival of new colonists as the driver of the taxon cycle. Further work examining species abundance and habitat occupancy on the West Indian Islands by Ricklefs and Cox (1978) noted that changes in species density and niche width on individual islands mirrored the patterns of geographical distribution and species differentiation of the taxon cycle.

The patterns in niche width and abundance associated with the taxon cycle have been identified on islands in a number of taxa other than ants (Wilson, 1961), including birds (Greenslade, 1968; Ricklefs and Cox, 1972, 1978), insects (Greenslade, 1969), rodents (McFarlane and Lunberg, 2002), and freshwater shrimp (Cook et al, 2007). However, studies of spiders (Gillespie *et al.,* 2008), birds, and butterflies (Jones *et al.,* 1987) have failed to identify any taxon cycle signal in distributions. Attempts to explain the absence of evidence to support the taxon cycle have identified anthropogenic disturbance as a possible mask for any natural processes (Pregill and Olson, 1981; Ricklefs and Bermingham, 2002) or may have created the evidence that supports the taxon cycle existence (Jones *et al.,* 1987).

1.5 Criticisms of the taxon cycle model

Scepticism surrounding the validity of the taxon cycle model and its attempts to explain species distribution is present within the academic community (Ricklefs and Bermingham, 1999; 2002). The strongest opposition to the taxon cycle's validity was expressed by Pielou (1979) and, more extensively, by Pregill and Olson (1981). Pielou (1979) suggests that a more probable and simplified explanation for the taxon cycle patterns observed on island and archipelagos may be the effect of sporadically occurring climatic 'bad years'. Pielou suggests that as a consequence of insular species isolation there is little chance of escape from harsh conditions other than the movement into sheltered habitats (species contraction). The movement into sheltered habitats improves species survival and provides an explanation for why late-stage species are often restricted and adapted to interior habitats (Pielou, 1979 pg 198). Insular populations according to Pielou (1979) remain in this state even during climatic 'good years' as the isolation of islands inhibits reinvasion from unaffected surrounding areas, as would occur on the mainland.

Pregill and Olson (1981) also proposed an alternative to the taxon cycle to explain the distribution of species across the Lesser Antilles. Through the synthesis of current species distributions, fossil records, and existing literature on the Pleistocene climatic and sea level conditions in the Antilles, Pregill and Olson suggested that, from a historical perspective, climatic cycles and sea level changes during the Pleistocene could account for the distribution and composition of species in the West Indies. In addition, Pregill and Olson (1981) identified a number of issues regarding the taxon cycle's validity, giving strength to their alternative hypothesis. These criticisms are aimed at two areas of the theory; the first is the stages themselves. Pregill and Olson (1981) suggested that the taxon cycle stages were 'tautological in origin' and were simply a set of criteria to describe species distributions that would apply to any species in an archipelago. In addition, Pregill and Olson suggested that the cycle's stages did not present a temporal sequence and identified a number of cases where different evolutionary histories could yield similar distributional patterns. This last criticism was aimed at the two extremes of the cycle, with some endemic species being found to be widespread (Stage 1) with other stage 4 species (single-island endemics) created through inter-island differentiation of a single radiation, not a relic of a widespread species and others representing species that are not relict but are indigenous (autochthons) to a single island (not formerly widespread) (Pregill and Olson 1981, Ricklefs and Bermingham, 2002).

The second aspect of the taxon cycle that has been criticised is the role of counter-adaption and coevolution as the driving mechanisms of the cycle (Ricklefs and Bermingham, 2002), described by Pregill and Olson (1981) as an artificial construct to explain the non-existent taxon cycle phenomenon. The opposition towards this mechanism stems from resistance to the idea that a well-adapted resident species would be at a competitive disadvantage to a new colonist, a notion that would require a newly arrived species for every resident species that has progressed to the second stage of the cycle (according to Pregill and Olson, 1981). In this respect, Pregill and Olson suggest that the taxon cycle is unsupported.

Liebherr and Hajek (1990) used cladistic hypotheses concerning the relationship of eight Carabidae taxa across the Antilles, Mexico, and Central America to investigate the taxon cycle and ‘taxon pulse’ from a reconstructed historical perspective (in lieu of a detailed fossil record). This method of phylogenetic reconstruction used the predicted habitat utilisation and cladistic transformation of the 8 study taxa but failed to identify a significant taxon cycle pattern in all but 1 species (Liebherr and Hajek, 1990). However, Ricklefs and Bermingham (2002) suggest that this test was inconclusive as it assumed that the taxon cycle proposes irreversible habitat change and that a derived phylogenetic position indicates a late stage species, which in both cases it does not.

Roughgarden and Pacala (1989) also identified the strong historical and phylogenetic component of insular community structure but, unlike Liebherr and Hajek (1990), Roughgarden and Pacala identified a pattern in *Anolis* lizard distribution and body size shift from large to small *Anoles* in the Lesser Antilles, consistent with the taxon cycle. However, there are a number of Anole species and islands within the Lesser Antilles that do not conform to the taxon cycle hypothesis, suggesting that the taxon cycle is only occurring in a limited area and may be rare and could be anthropogenically induced (Roughgarden and Pacala, 1989). A more recent paper by Losos (1990) examined Roughgarden and Pacala’s (1989) taxon cycle model and utilised a phylogenetic approach to incorporate variety in biochemical, karyotypic, and morphological characteristics (Losos, 1990; Ricklefs and Bermingham, 2002). Losos (1990) suggested that the taxon cycle is plausible, a conclusion supported by Taper and Case (1992), using various modelling techniques. However, the study by Losos (1990) found little evidence in Anoles size shifts and phylogenetic relatedness on the different islands to support the cycle’s presence (Losos, 1990).

1.6 Historical theories in the age of genomics

New genetics and genomic tools continue to revolutionize the study of evolution and ecology (Emerson, 2002; Suarez *et al.,* 2009; Venditti and Pagel, 2009). While evolutionary theory has traditionally been difficult to test empirically without a detailed fossil record (Liebherr and Hajek, 1990), molecular genetics now allows the direct query of evolutionary history (Blondel, 2000). Molecular phylogenetic studies (Ricklefs and Bermingham 1999, 2001, and 2002) have provided support for the taxon cycle and a degree of rebuttal to the initial objections by Pielou (1979) and Pregill and Olson (1981). This genetic work has enabled a test of the taxon cycle by estimating the timing of expansion and contraction phases of the cycle in accord with genetic diversification (Ricklefs and Bermingham, 1999). Thus, the so-called "molecular clock" can be used to estimate time since evolutionary divergence based on the similarity of gene sequences (Freeland, 2005). For example, in birds, a 1.6-2% sequence divergence in the cytochrome b gene is widely accepted to represent divergence time of approximately a million years (Packert *et al.,* 2007).

Based on the genetic distance between island populations and their mainland sister taxon, the taxon cycle stages (1 - 4) have been shown to represent a temporal sequence and a chronology of taxon age occurring over hundreds of thousands to millions of years (Ricklefs and Bermingham 1999). The results of this research indicate that birds progress through phases of expansion and contraction and that some species have undergone multiple expansions (Ricklefs and Bermingham, 2002). Species phases of expansion and contraction were also not found to be correlated between taxa or clearly related to the physical environment, such as glacial climatic shifts based on species age estimates and Pleistocene climatic cycles (Ricklefs and Bermingham, 1999, 2002). Molecular phylogenetics analysis also indicated that Stage 4 species had sister-taxa present on the mainland in addition to representing the oldest species in the archipelago and, as such, are relics consistent with the taxon cycle (Ricklefs and Bermingham, 2002, Ricklefs, 2005).

Molecular evidence used in a study by Cook et al (2008) into freshwater decapod shrimps in the Caribbean supported the presence of sequential colonisation and taxon cycling. They analysed Cytochrome Oxidase I mtDNA in shrimp, calculating genetic differences consistent with the taxon cycle. In relation to the possible drivers of Caribbean shrimp assemblage structure and taxon cycling, Cook *et al.* (2008) suggest a marginal role of Pleistocene aridity as proposed by Pregill and Olsen (1981) in facilitating certain species adaptations (*Atya lanipes*). As a result of the lack of congruence between species expansions and historical climatic changes, Cook *et al.* (2008) support the role of ecological factors such as competition, in addition to environmental disturbances (hurricanes and volcanoes) as the drivers of the taxon cycle and shrimp biogeographical distributions. Support for the taxon cycle has also been identified in a single genus of bird (*Pachycephala*) in the Indo-Pacific using molecular data, species distributions, habitat and elevational ranges (Jonsson et al., 2014). Jonsson et al (2014) identified evidence that supports cycles of expansion and contraction shaping species diversity and distribution. Recent colonists (stage 1 and 2 or expanding species) were widely distributed across large and small islands, while older relictual taxa (stage 4 - contracting species) were found only on the largest and highest islands. Where both expanding (stage 1 and 2) and contracting (Stage 4) species were present on the same island, expanding species were found at lower elevations and disturbed habitats and contracting species were found at higher elevations and undisturbed habitats supporting the taxon cycle concept (Jonsson et al., 2014). A study by Economo and Sarnat (2012) also observed a similar a similar pattern as Jonsson et al (2014) while revisiting the ant fauna of Melanesia. Shifts to higher elevation and primary habitats, in addition to rarity and habitat specialism with increasing endemism was found across the Melanesian ant fauna, consistent with the taxon cycle hypothesis (Economo and Sarnat, 2012).

1.7 Birds and their enemies – Co-evolution

Ricklefs and Bermingham (2002) indicate that the patterns of expansion and contraction demonstrated by the taxon cycle are most likely a function of the evolutionary interactions of a species and its ‘enemies’. However, the potential driver of the taxon cycle remains speculative (Cook *et al.,* 2008; Ricklefs and Bermingham, 2002). Ricklefs and Bermingham (2002) suggest that the release of a species from parasites or pathogens (or genetic change in virulence or resistance), in addition to the introduction of pathogens that become virulent in resident populations (Conquistador effect), may allow a colonist to undergo a phase of expansion and increased productivity. However, over time the co-evolution of parasites and pathogens exploit these new colonists, reducing productivity and competitive ability. This may stop the phase of expansion and may cause a phase of contraction in a species (Ricklefs and Bermingham, 2002). Distribution of blood parasites and evidence of host switching observed in the Lesser

Antilles are features that should be present if novel host-parasite variation were to be a driving mechanism behind the taxon cycle (Fallon *et al.*, 2005; Ricklefs and Bermingham, 2002). Torchin *et al.* (2003) investigated the variation in parasite prevalence in introduced and native species and supported Ricklefs and Bermingham's (2002) theory, with introduced species being less parasitised (around 50% of native population's parasite species) both in terms of average prevalence of each species and total prevalence of all parasite species. The investigation of parasite load was beyond the scope of this thesis, but further research should investigate the relationship between taxon cycle rank, colonization time, and parasite and pathogen load.

1.8 Extinction risk

An area of research intrinsically linked to the taxon cycle is extinction; a potential termination of a species' cycle as a result of reduced abundance, restricted distribution, and competitive ability and susceptibility to stochastic and anthropogenic influences (Ricklefs and Bermingham, 2002). Ricklefs and Bermingham (2002) suggest that the average life span of aspecies is 3.6 - 4.8 million years, which indicates that the probability of extinction increases with the age of an island population (Losos and Ricklefs, 2009). The correlates associated with extinction risk were investigated by Jones *et al.* (2001) for the birds of Indonesian islands. This study assessed the impact of ecological and historical traits on species abundance with reference to the species' evolutionary history and evolutionary phenomena (Jones *et al.,* 2001). In relation to the taxon cycle, Jones *et al* observed higher densities in older, more distinct sub-speciated bird populations than in recent colonists. Although initially this appears to conflict with taxon cycle expectations, the work by Jones *et al* concentrated on indigenous forest alone and, as such, could reflect a secondary expansion associated with specialisation and increased productivity of a later stage species to an interior habitat (Jones *et al.,* 2001; Ricklefs and Bermingham, 1999). The age or evolutionary development of a species is cited by Jones *et al.* (2001) as the most useful measure to predict local species abundance. The taxonomic differentiation, specialisation, and endemism associated with the increasing age of a species and a later stage of the taxon cycle has also been advocated by Duncan and Blackburn (2004) and Boyer (2008) in the susceptibility of species to extinction based on a synthesis of existing data. However, Duncan and Blackburn (2004) suggest that different traits associated with endemic species may affect their susceptibility to extinction in different circumstances. Small geographical range and population size have been identified as the main predictors of extinction risk (Purvis *et al.,* 2000; O'Grady *et al.,* 2004) making island species particularly susceptible to extinction. The taxon cycle represents a natural process that results in species being restricted in distribution and low in abundance and therefore prone to extinction.

1.9 Macaronesia and the taxon cycle

The two interlinked theories, ecological release and the taxon cycle, have received a varied response from the academic community, with a number of extensive and in-depth criticisms of the theory and application of both concepts. However, both remain firmly within the theoretical framework of island biogeography and are integral to our understanding of insular species assemblages, distribution, and extinction dynamics. Molecular genetics has enabled many of the previously assumed and extensively criticised aspects of the taxon cycle to be investigated and assessed, providing further support and validity to the existence of the taxon cycle. However, the general application and drivers of these evolutionary mechanisms remain unclear and speculative. As a consequence, further work is required to determine the general application of both ecological release and the taxon cycle using molecular data to calibrate the timing of the taxon cycle with ecological data. Additional research should also ensure that a quantitatively comparative study is conducted, with similar mainland and island habitats and climate. A study incorporating these two aspects would provide a novel molecular based mainland-island comparative study of the concept of ecological release and the taxon cycle.

The Macaronesian Islands of the Atlantic, which include the Canary Islands, Cape Verde Islands, the Azores, and the Madeiran archipelago provide the ideal environment to study these processes due to their isolation, volcanic origin (known age) and ecological heterogeneity (Suarez *et al.,* 2009) (Figure 1.1). In addition, the source population (sister taxon) of colonisers based on prevailing wind and sea current has been narrowed down to the Iberian Peninsula or Northern Africa for Macaronesian avifauna (Juan *et al.,* 2000; Illera et al, 2012). Although for the Cape Verde archipelago the lower latitude, close proximity to Africa and species composition suggest a semi-arid African mainland origin (Illera *et al.,* 2012).

The four island groups range in geological age from 0.8 million years (my) to over 20 my old (Dietzen *et al.,* 2008). The islands range in distance from the European and African continent between 95 to 1600km and are situated between 15° to 40° N latitude (Kim *et al.,* 2008). Altitude across the islands varies from 130 to 3700m above sea level (Illera *et al.,* 2012). The climate across the four archipelagos varies from temperate maritime in the Azores, Mediterranean across the Canary Islands and Madeira and tropical (with a dry and humid season) in the Cape Verdes (Clarke, 2006).

The broad range of latitude, age, altitude and distance to mainland variation creates a broad diversity of ecological conditions across the island groups with habitats ranging from deserts to cloud forests (Clarke, 2006; Illera *et al.,* 2012). Each archipelago also exhibits a broad range of habitats. The Cape Verde habitats are categorised as rocky coast, saltpans, lagoons, dunes, desert, dry woodland and shrub, and urban areas (Hazevoet, 1995). Habitat across the Azores include coastal, lakes, agriculture, plantations and remnants of laurel forest on inaccessible slopes (Clarke, 2006). Madeiran habitats have been classed as agriculture, pasture, residential, managed forest, non-native (*Eucalyptus globules* and *Pinus pinaster*) and natural laurel and health forest (Jones *et al*., 1987). The Canary Islands coastal regions are characterised by palm and semi-arid habitats, agriculture on lower slopes and laurel, health and pine forest at higher altitudes (Clarke, 2006).

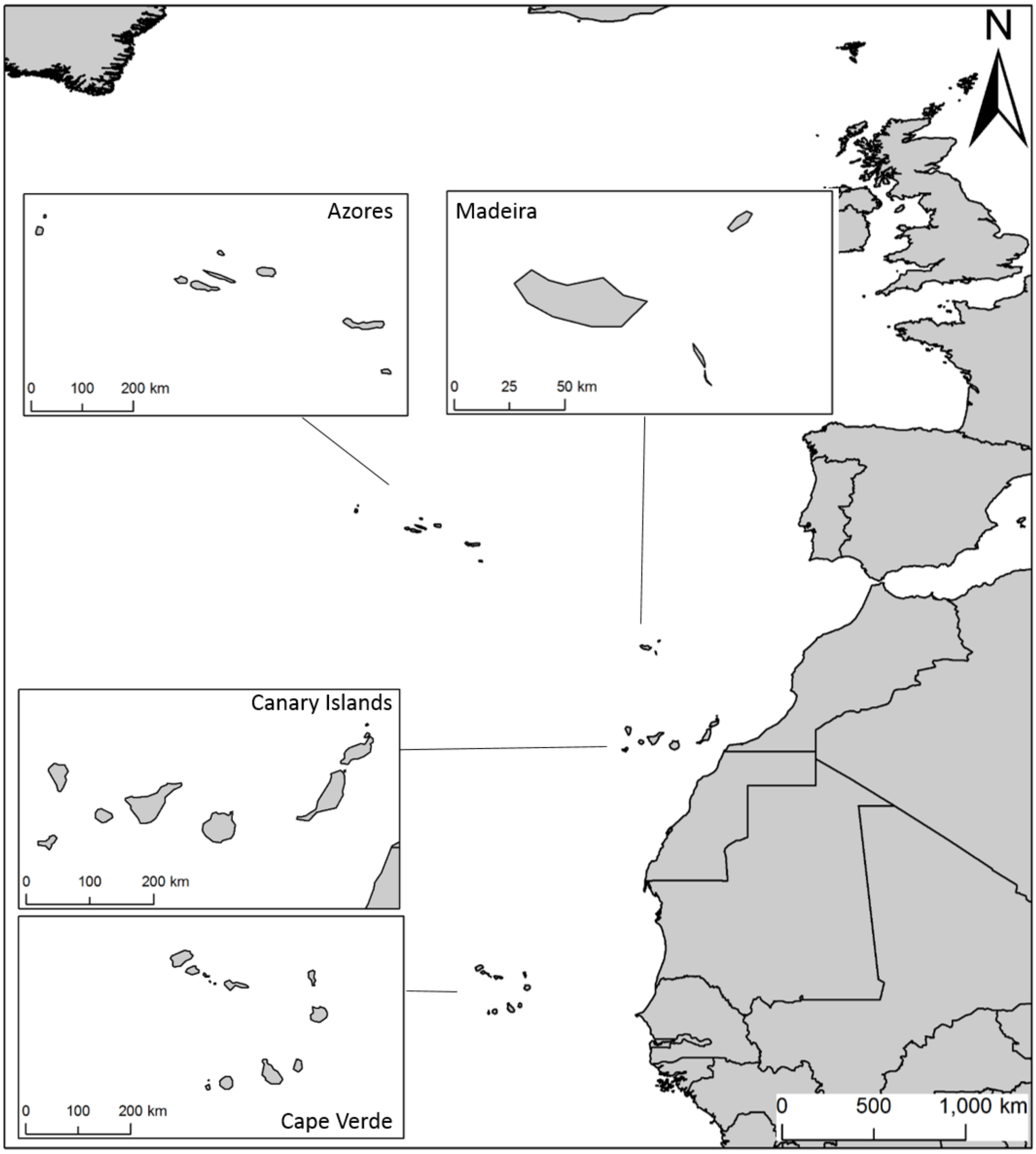

Figure 1.1. Map of Macaronesia with archipelagos in boxes.

1.10 Thesis Aims

The overall aim of this PhD thesis is to assess evidence of two interlinked theories, ecological release and the taxon cycle, which have been proposed to explain species abundance and distribution on islands. This thesis will address criticisms of previous studies by using large-scale datasets of species distribution, biodiversity, and novel modern molecular tools to provide a temporal scale to the study and modern statistical techniques to model the taxon cycle. Bird species across the Macaronesian islands will be used to test these theories. Both theories will be tested across multiple island groups and at varying scales over the following chapters, as well as being used to inform conservation of a newly recognised species.

1.11 Chapter Overview

Chapter 2. Ecological opportunity and ecological release in Madeiran birds.

This chapter tests a number of predictions arising from the theory of ecological release on the birds of Madeira. This study provides an island – mainland comparative study of six species found on Madeira and mainland Portugal. Abundance, density, and niche width are compared between the island and mainland populations to identify if species have become more abundant and have broadened their niche under ecological release on Madeira. This chapter also analyses published data to determine whether higher bird densities on islands is a consistent trend.

Chapter 3. Evidence for the taxon cycle in the avifauna from a single island.

Understanding patterns in species assemblage, abundance, and distribution is a central component of biogeographical ecology, biological diversity, and species conservation. Taxon cycles have been prosed as a theory to explain patterns in species distribution, abundance, and habitat use on islands. This chapter uses genetic, morphological, and ecological data from Madeira to test for the presence of taxon cycle. Patterns in abundance and distribution are related to proposed taxon cycle ranks, data on genetic and morphological differentiation are used to test taxon cycle predictions.

Chapter 4. Investigating the presence or absence of ecological release and the taxon cycle across multiple island chains.

Ecological release and the taxon cycle have been proposed as theories to explain patterns in species abundance and distribution across islands. The theories are relevant to mechanisms of island speciation, but also to understand species invasions, responses to climate change, and susceptibility to extinction. This chapter will test the both theories using the novel availability of large scale datasets from breeding bird surveys and breeding bird atlas programs. This chapter will use distribution and abundance datasets collected for the Azores, Madeira, Canary Islands, and the Cape Verde Islands, as well as published mitochondrial genetic data for a subset of species, to test a number of predictions based on ecological release and the taxon cycle.

Chapter 5. Habitat association and population size of the Madeira Firecrest (*Regulus madeirensis*)

The Madeira Firecrest is a recently recognised single island endemic. As a recently recognised species, details of population size, habitat preference, and distribution are poorly known. The Madeira Firecrest is also thought to have undergone ecological release on Madeira (Chapter 3). This chapter uses data collected to test for ecological release and the taxon cycle to provide a novel, an assessment of the Madeira Firecrest population size, distribution, and habitat associations.

Chapter 6. Discussion.

The main findings of the thesis are discussed in this chapter along with the potential for further research and the application of these theories to better understand species invasion, impacts of climate change, conservation, and patterns of extinction.

Chapter 2. Ecological opportunity and ecological release in Madeiran birds

Abstract

Island systems have played an important role in our understanding of evolutionary and ecological theories. Ecological opportunity present in species depauperate island environments is thought to play an important role in species diversification. The response of species to ecological opportunity is called ecological release. This chapter examines the response of six focal species to the species-poor environment of Madeira. The chapter tests whether the two components of ecological release, density compensation, and niche expansion are present in the focal species when compared to mainland counterparts. Five species were found to be at higher density in indigenous forest on Madeira than on the mainland using field data. Three of these species were consistently higher on islands when analysing published estimates. The study also indicates that five of the focal species have a broader niche on Madeira than on the mainland. These results provide evidence for the presence of ecological release on Madeira for a number of the focal species.

2.1 Introduction

Island systems have played an important role in our understanding of evolutionary and ecological theories (Warren *et al.,* 2014). Ecological opportunity found in novel and species depauperate environments, such as islands, is thought to link ecological population dynamics to species diversification (Yoder *et al.,* 2010). The ecological causes of species diversification and adaptive radiation have received renewed attention (Nosil and Reimchen, 2005) with focus on the role of ecological opportunity (Yoder *et al.,* 2010).

Ecological opportunity occurs when a population is released from the selection pressures of competition and predation (Des Roches *et al.,* 2011). The ecological and evolutionary response that occurs when a species encounters ecological opportunity is known collectively as ecological release (MacArthur and Wilson, 2001; Yoder *et al.,* 2010; Losos and DeQueiroz, 1997; Cox and Ricklefs, 1977). Species having undergone ecological release due to ecological opportunity are predicted to exhibit (1) higher densities than their mainland or source counterparts, known as density compensation (MacArthur *et al.,* 1972), (2) niche expansion with a broadened niche to incorporate resources not used by their mainland counterpart (MacArthur and Wilson, 2001).

Ecological release has been observed across a number of taxa. Density compensation was initially observed in birds (MacArthur *et al.,* 1972; Mesquita *et al.,* 2007; Ricklefs and Cox, 1972; Terborgh and Faaborg, 1973) and, more recently, amphibians and reptiles (Rodda and Dean-Bradley, 2002). Many studies also support the theory that island species occupy a broader niche than their mainland counterparts (Cox and Ricklefs, 1977; MacArthur *et al.,* 1972). However, for both niche expansion and density compensation, there are studies that have not observed these responses to available ecological opportunity on depauperate islands (Lizards: Losos and Queiroz, 1997; birds: Vassallo and Rice, 1982).

The ecological release hypothesis has received criticism based on difficulties in testing the theory empirically and inconsistencies in application. Lack of support for ecological release in some studies has caused suggestions that density compensation and niche expansion may not be that common (Mesquita *et al.,* 2007; Losos and Queiroz, 1997; Vassallo and Rice, 1982). The study of ecological release has been criticised because of a lack of properly matched habitats and species in addition to only comparing results between single mainland-island pairs (Blondel *et al.,* 1988). Ambiguity in the role of ecological opportunity in ecological release and adaptive radiation suggest further work is needed and, in particular, with studies using comparisons of ancestral populations with species having experienced ecological opportunity (Yoder *et al.,* 2010).

This chapter tests predictions arising from ecological release theory using a comparative mainland-island study looking at mainland and island ecological characteristics in six species pairs. The study overcomes the limitation of previous studies by using comparable habitats and species. We test two predictions: 1. Island species will be at higher densities on the island of Madeira than in mainland Portugal, and 2. Island species will occupy a broader niche than their mainland counterparts. Density estimates obtained from this study were also compared to published density estimates from islands across Europe to identify if patterns of density compensation were consistent across multiple studies and European islands.

2.2 Methods

2.2.1 Study site

The insular element of the study was conducted on Madeira; a volcanic island approximately 5.2 million years old, located in the eastern Atlantic, 900km south-west of Portugal, 440km north of the Canary Islands, and 565km from western Africa (Dietzen *et al.,* 2008; Jones *et al.,* 1987; Oliveira *et al.,* 1999). The Madeiran Archipelago is situated between 30°01' and 33°80'N and 15°51' and 17°16'W. Madeira has a total surface area of 742km^2 with a mountainous central ridge and a maximum elevation of 1861m. The climate on Madeira is classed as Mediterranean with wet winters and dry summers, with temperatures ranging from 14-23°C and rainfall in the laurel forest of >1700mm and up to over 3000mm annual rainfall (Clarke, 2006; Marrero and Nogales, 2005; Sim-Sim et al,. 2005). The land use is divided into agriculture, pasture, residential, managed forest, non-native (*Eucalyptus globules* and *Pinus pinaster*) and natural forest (Jones et al., 1987). Madeira's indigenous forest is the Laurisilva or laurel forest that once covered most of the island but now covers around 16% and is protected within the Madeiran natural park (Clarke, 2006; Jones, 1988).

The mainland element of the study was conducted in the Peneda-Geres National park (PGNP), covering around 72,000ha (latitude 41°36 to 42°07N and longitudes 7°44 to 8°27W), situated in north-western Portugal (Soares and Brito, 2006). The region is close to the transition between the Mediterranean and Euro-Siberian regions and is characterised by wet winters and hot summers, with an average rainfall of 3200mm/year and average temperatures ranging from 10 - 16^{o}C (Brito, 2003). The landscape is composed of deciduous forest (*Quercus robur* and *Quesrcus pyrenaica*), mixed deciduous and coniferous forest (*Pinus pinaster*), shrubland dominated by heaths (*Erica sp.*), gorses (*Ulex sp.*), and agricultural land. Data collection in the PGNP, Portugal was focused on comparable habitats types to those observed in Madeira with surveys undertaken in Oak forest, mixed forest, shrubland, and shrubland forest mix habitats. The mainland site was chosen as it has a similar Mediterranean climate, similar altitudinal range (Madeira: max elevation = 1861m a.s.l, PGNP: 50-1500m a.s.l) (Soares and Brito, 2006; Jones *et al.,* 1987) and similar forest and shrubland types. Both sites also contain broadleaf forest (laurel or oak), pine forest, and shrubland dominated by heaths (*Erica sp.*), gorses (*Ulex sp.*) in addition to supporting all six of the focal species used in this study.

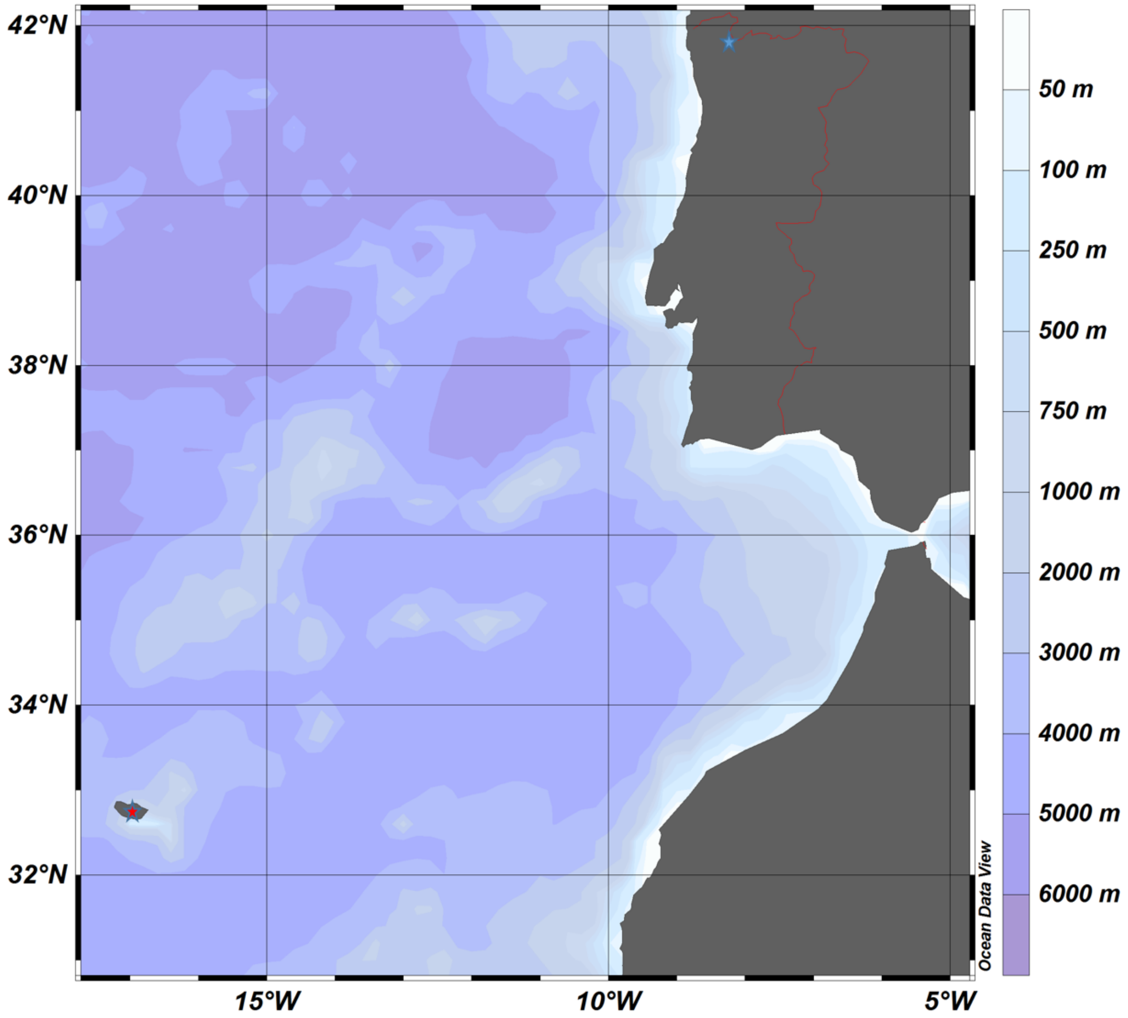

Figure 2.1. Map of island (red star - Madeira) and mainland site (blue star - Peneda-Geres National park).

2.2.2 Focal species

The focal species were the Blackcap (*Sylvia atricapilla*), Blackbird (*Turdus merula*), Robin (*Erithacus rubecula*), Chaffinch (*Fringilla coelebs, Fringilla coelebs madeirensis*), Firecrest (*Regulus ignicapillus / Regulus madeierensis*), Madeiran Laurel Pigeon, and European Woodpigeon (*Columba trocaz* and *Columba palumbus*). These species were chosen because they represent species proposed to have colonised Madeira at different times (different stages of the taxon cycle – Chapter 3). Blackcap, Robin, and Blackbird on

Madeira show little differentiation from mainland populations based on wing length and roundedness (Hounsome, 1993; Jones *et al.,* 1987) and represent species that are likely to have colonised Madeira recently. In comparison, Chaffinch, Madeira Firecrest, and Laurel Pigeon represent species that are highly differentiated from their mainland counterparts, representing sub-species (*F. coelebs*) and separate species thought to have colonised Madeira and become isolated on Madeira less recently (Hounsome, 1993; Jones *et al.,* 1987). In addition, all focal species exhibit a sister taxon on the mainland to allow a comparison of both species abundance and habitat utilisation.

2.2.3 Bird surveys

Focal species abundance was obtained using a point transect distance sampling method (Buckland *et al.,* 2001). Surveying was undertaken in the breeding season between March and June, with transects conducted between 07:00 and 11.00 to coincide with peak activity levels. However, surveys were not conducted during inclement weather such as heavy rain, mist, or strong winds (see Marsden and Whiffin, 2003). Point counts were positioned systematically in order to survey the main forest types on Madeira and comparable forest on the mainland. Point counts were conducted at intervals of 200m with the start of each point transect randomly selected (using a stopwatch), conducted over a 4-min period with a minimum of 50 points per habitat type and 80-100 contacts per species consistent with Buckland *et al.* (2001) and Bibby *et al.* (1998). Where points were positioned along paths, roads, or watercourses to avoid an edge effect, points were positioned 10-30m perpendicular to the transect (Lee and Marsden, 2008). A single observer (John Norrey) was used throughout the study although a recorder (either in the form of a dictaphone or a research assistant) was used to record observations. When two persons were present, each individual maintained the same role to reduce observer bias and the effect of inter-observer variability (Lee and Marsden, 2008). Birds in flight were ignored unless their original position (alighting) could be identified; however, birds disturbed or flushed before the counts were recorded as present (Marsden and Whiffin, 2003). Point counts were conducted immediately after arrival (Marsden and Whiffin, 2003), as the use of a settling down period has been shown to reduce the number of contacts (Lee and Marsden, 2008). Distances to each contact were measured using a range finder (Bushnell-yardage pro) and the method of contact recorded (Visually (Si) or aurally (So) or both). The contacts identified aurally were placed in distance bands if an accurate distance could not be taken due to the likelihood of error in the estimation.

Habitat characteristics were recorded at each site to infer niche width. Data collected included an assessment of habitat type (Laurel or Oak Forest, Mixed / Exotic and Pine forest, and Upland Shrubland (400-1800m ASL)), habitat score (percentage of each habitat type at a point – 30m radius), vegetation cover (%) at ground (<1m), mid (1-5m) and high canopy (>5m), species composition, tree DBH and height of the two tallest trees within the 30m radius. All measurements were taken by a single observer to avoid bias.

2.3 Analysis

2.3.1 Bird species density

Species densities were calculated using Distance software 6.2 (Thomas *et al.,* 2010). Distance sampling analysis followed the guidelines suggested by Buckland *et al.* (2001). Briefly, an initial exploratory analysis was undertaken on the data; histograms were created for each habitat type in order to identify the presence of outliers and variation in detectability based on the method used (sight or sound). Within Distance, data were manipulated where appropriate to remove outliers (removal of furthest 10%) and placed into distance bands to fit detection curves (Buckland *et al.,* 2001; Thomas *et al.,* 2010). For each species and habitat type, four key functions were applied (uniform, half-normal, hazard rate, and negative exponential) with a cosine series adjustment (Thomas *et al.,* 2010; Lloyd, 2008) in addition to half-normal with hermite polynomial and hazard rate with simple polynomial adjustment as suggested by Thomas et al (2010). Detection curves, AIC, and chi-square were used to determine the best key function fit to each habitat type (Lloyd, 2008; Thomas *et al.,* 2010). In addition, visual and aural contacts were analysed collectively and independently. Density estimates were expressed as the number of individuals per km^2. As some species did not reach the minimum of 40-80 records needed to estimate densities (Bibby *et al.,* 1999; Buckland *et al.,* 2001, the relative abundance (number of individuals per point) of the species in each habitat were also calculated to allow comparisons between species pairs. This was done for the Laurel Pigeon and Woodpigeon in exotic and pine forest and for all species in the Shrubland habitats. Independent sample T-tests were used to test for a significant difference in density and relative abundances between species pairs and similar habitat types.

2.3.2 Diversity, distribution, and species richness

The statistical package R (R Development Core Team, 2013) and the package Vegan was used to calculate the species richness and diversity (Shannon-Weiner index) of each habitat type in Portugal and Madeira (Magurran and McGill, 2014; Lloyd, 2008). Both species richness and diversity were calculated to compare the possible level of competition difference between the mainland and island habitats.

2.3.3 Niche width and position

Niche width in comparable indigenous forest were compared using a PCA (Principal Component Analysis) to measure the niche occupied by mainland and island species pairs to allow information on niche centres and width to be compared. Percentage cover (Ground, Mid-canopy, and High), DBH, average tree height, and contact position within the canopy were used in the PCA. Principal components were chosen that presented 80% of the variance explained and were used in further analysis. Niche position was compared between species pairs using a Wilcoxon-test. Niche width was compared using the Bartlett Test for homogeneity of variance (Fernández *et al.,* 2013). Statistical analysis was carried out using R 3.1.2.

2.3.4 General trends in density compensation

Estimates of density and abundance for all forest species (in addition to the Madeiran focal species used in this study) found across the Macaronesian islands were collected for islands (Azores, Canary Islands, Corsica, and the Aland Islands) and mainland Europe sites from published studies. Identification of relevant papers was achieved using Web of Knowledge (WOK) and Google Scholar, using scientific and common names. Species name, location, forest type, survey method, abundance / density estimates, and measure of error were recorded from each study. Studies without a measurement of area, mention of survey type or non-forest studies were excluded from the study. Independent sample T-test were used to test for differences between species pairs.

2.4 Results

2.4.1 Density compensation

Five of the six focal species showed a higher density (individuals per square kilometre) in the native Madeiran laurel forest than in the oak forest of Portugal. For three of the species - Blackbird, Chaffinch, and the Madeira Firecrest, the densities were significantly higher than on the mainland (Table 2.1). In contrast, the Robin was found at a significantly higher density on the mainland than on Madeira. The comparison of the exotic forest in Madeira and the mixed pine forest of Portugal highlighted two species, Blackbird and Robin, which were at significantly higher densities on the mainland than on Madeira (Table 2.1). Due to insufficient contacts, estimates of density for the focal species in the shrubland habitat were not calculated and relative abundance were compared. All six of the focal species were observed at higher relative abundances in upland areas of Madeira than in shrubland in Portugal, with four of the species showing significantly higher abundances (Table 2.1). All three habitat types on the mainland show higher levels of species richness and diversity than their island counterparts (Table 2.1). Across the 18 comparisons, 13 showed higher density on Madeira compared to the mainland Portugal ($X^2 = 3.56$, DF = 1, P = 0.06).

Table 2.1: Density estimates (individuals km^{-2} ± SE with 95% confidence limits in parenthesis) for focal species on Madeira and mainland Portugal across three habitat pairs. Bird species richness and Shannon species diversity of each habitat type also recorded per habitat type. Relative abundance are recorded without 95% confidence limits in parenthesis. * next to a species and habitat denotes a significantly higher density between species pairs at p<0.05, ** p<0.01, *** p<0.001.

Rank	Species	Laurel Forest (Madeira)	Oak Woodland (Portugal)	Exotic / Mixed Woodland (Madeira)	Pine / Mixed Woodland (Portugal)	Upland Shrubland (Madeira)	Shrubland (Portugal)
1	*Turdus merula*	63.36 ± 8.2 ** (49.04-81.87)	20.96 ± 4.35 (13.81-31.83)	24.24 ± 5.82 (15.10-38.86)	52.1 ± 16.25 * (28.01-96.9)	1.378±1.206***	0.163±0.426
2	*Sylvia atricapilla*	169.63 ± 24.71 (127.19 -226.23)	121.27 ± 26.25 (78.72-186.82)	73.23 ± 8.82 (57.68-92.96)	69.18 ± 14.8 (45.05-106.26)	0.429±0.849	0.245 ±0.522
3	*Erithacus rubecula*	72.91 ± 17.33 (45.66-116.41)	135.69 ± 18.63 * (103.15-178.5)	20.88 ± 4.53 (13.56-32.14)	165.41 ± 36.38 *** (106.35–257.35)	1.205±1.533***	0.127±0.336
4	*Fringilla coelebs*	147.28 ± 19.36 * (113.41-190.71)	62.93 ± 9.26 (46.91-84.45)	29.29 ± 6.02 (19.53-43.92)	53.21 ± 14.34 (31.08-91.12)	1.010±1.126***	0.184±0.391
5	*Regulus madeirensis /regulus*	945.80 ± 95.29 ** (776.04-1152.69)	109.37 ± 18.51 (77.82-153.7)	113.99 ± 31.89 (65.81-197.46)	171.37 ± 48.04 (97.54-301.06)	0.776±1.108***	0.143±0.435
6	*Columba trocaz/ palumbus*	49.32 ± 27.67 (16.98-143.24	12.89 ± 3.52 (7.25-22.61)	0.205±1.525	0.111±0.317	0.071±0.613	0.020±0.143
Species Richness		9	26	12	28	15	26
Shannon Diversity		1.74	2.62	1.98	2.68	1.98	2.82

2.4.2 Niche expansion

Niche centre and niche width comparisons

The first four PCA components for each of the focal species explained greater than 80% variation in the data (Blackbird – 83.8%, Blackcap – 82.6%, Robin – 85.1%, Chaffinch – 86%, Firecrest – 85.8%, Laurel Pigeon – 83.2%). Subsequent analyses were based on these axis / components. All six species demonstrated significant differences in niche centres (median scores from PCA) on at least one axis (Blackbird - 3, Blackcap - 2, Robin - 2, Chaffinch – 3, Firecrest - 3, Laurel Pigeon – 1). Significant differences in niche width using a Bartlett test for homogeneity were found for five of the six focal species in at least one axis with a broader niche shown in all six Madeiran species across the first two principal components (Figure 2.2). No significant differences were shown in PC3 or PC4 in any of the focal species and were not included in Figure 2.2.

Blackbird

Blackbird showed significant difference in niche width in PC1 (29.5% variation explained, Bartlett test $p < 0.001$) and PC2 (23.4% variation explained, Bartlett test $p = 0.016$) with a broader niche shown in the Madeiran populations across both axis (Figure 2.2). PC1 showed a positive relationship with average tree height and DBH. PC2 showed a negative relationship with mid-canopy cover and a positive relationship with high canopy cover.

Blackcap

Blackcap showed no significant difference (Bartlett test $P > 0.05$) in niche width across principal components.

Robin

Niche width was found to be significantly different in PC1 (30.6% variation explained, Bartlett test $p < 0.001$) and PC2 (23.8% variation explained, Bartlett test $p < 0.001$) in Robins with a broader niche shown across both axis for the Madeiran Population (Figure 2.2). PC1 shows a positive relationship with average tree height and average DBH and PC2, showing a positive relationship with mid-canopy cover and a negative relationship with high canopy cover.

Chaffinch

Chaffinch showed significant differences in PC1 (32.5% variation explained, Bartlett test $p < 0.001$) and PC2 (22.9% variation explained, Bartlett test $p < 0.001$) with a broader niche shown across both axis for the Madeiran Population (Figure 2.2). PC1 shows a positive relationship for average tree height, DBH, and ground cover, and a positive relationship for mid-canopy cover and a negative relationship in high canopy cover in PC2 (Figure 2.2).

Firecrest

Firecrest showed a significant difference in PC1 (34.8% variation explained, Bartlett test $p < 0.001$) and PC2 (22% variation explained, Bartlett test $p < 0.001$) with a positive relationship with DBH and a negative relationship with high canopy cover shown in PC1 and PC2 respectively. The Madeira Firecrest shows a broader niche across both axis (figure 2.2).

Laurel / Wood pigeon

Niche width were found to be significantly different in PC2 (23.9% variation explained, Bartlett test $p = 0.008$) for Laurel Pigeon and Woodpigeon with a positive relationship with mid-canopy cover and negative relationship with high-canopy cover. Niche width is broader for PC2 in the Laurel pigeon (figure 2.2).

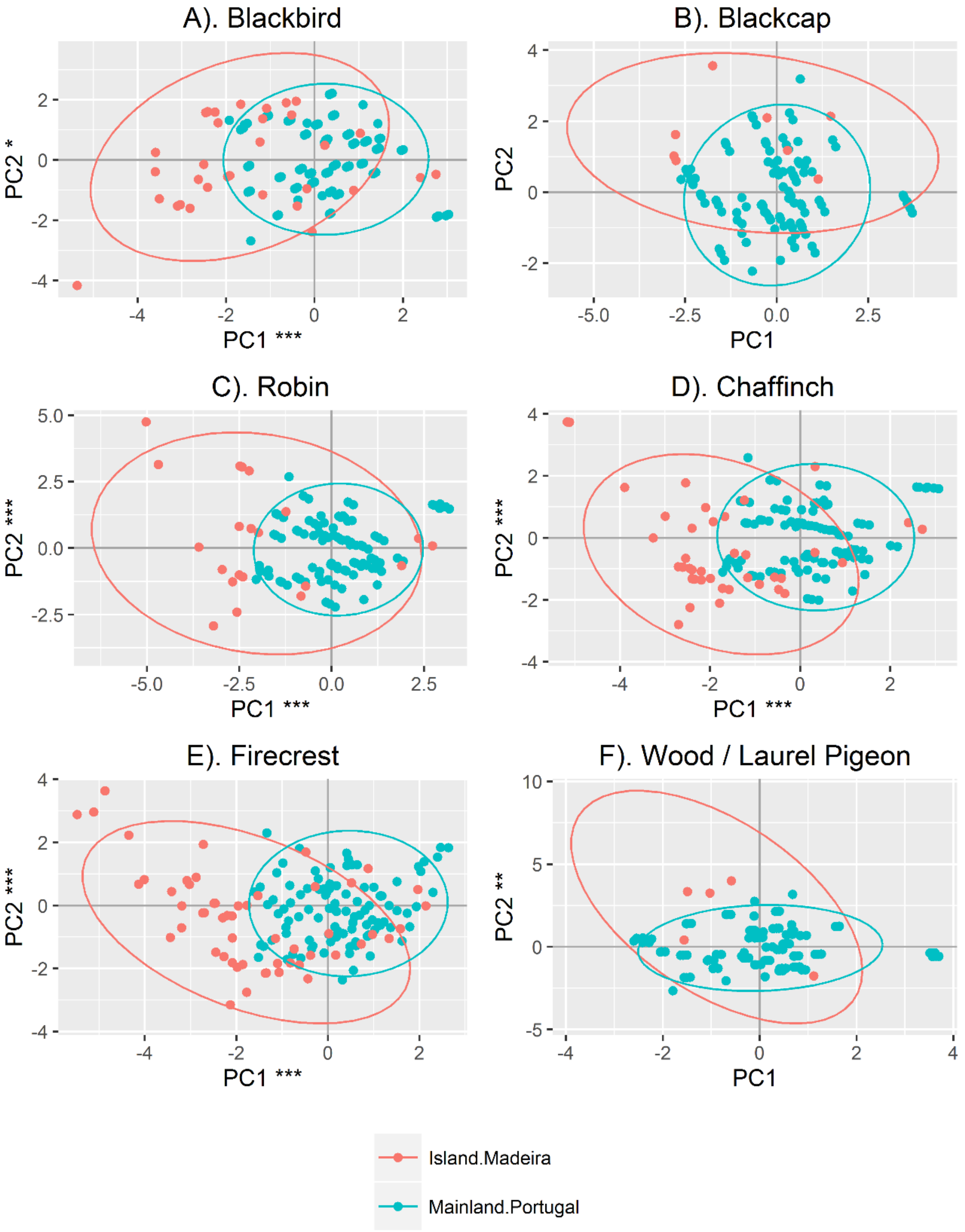

Figure 2.2: Niche width comparisons between mainland and island indigenous forests. PC 1 and 2 with 95 % confidence interval ellipses. An * next to an axis denotes a significant difference in niche width calculated using a Bartlett test for each principle component axis at p < 0.05, ** p < 0.01, *** p < 0.001.

2.4.5 General trends in density compensation

Density estimates collected from Madeira were compared to those of the focal species elsewhere in Macaronesia and mainland and island sites across Europe (Figure 2.3). In addition, data were also collected for other forest species across Macaronesia. Data have been analysed at four levels to reduce the effect of different habitats and methods of data collection. The first level of comparison uses all data collected (Figure 2.3A), the next level analysed only indigenous forest data (Figure 2.3B), the third level of analysis uses only data collected from indigenous forests using point counts methods (Figure 2.3C). This is the same method of data collection used in this chapter. The final level uses data collected from indigenous forest habitats using point counts and analysed using distance sampling (Figure 2.3D). The final level uses the same method of data collection and analysis used earlier in this chapter.

Published research on *Columba*, *Fringilla*, *Phylloscopus*, *Pyrrhula*, *Regulus*, and *Turdus* species demonstrated higher densities on islands than mainlands across all forest data (Figure 2.3 A) and indigenous forest (Figure 2.3 B). This is consistent with the higher density estimates collected in Madeiran laurel forest compared to mainland forest in this study for Blackbird (*Turdus*), Chaffinch (*Fringilla*), Laurel Pigeon (*Columba*), and Madeira Firecrest (*Regulus*) (Table 2.1). *Cyanistes*, *Sylvia,* and *Erithacus* species demonstrated lower average published densities on islands than the mainland (Figure 2.3 A and B). Lower densities of *Erithacus rubecula* is consistent with the results found on Madeira. In contrast to published estimates, Blackcap (*Sylvia*) were found at higher densities on Madeira in this study than the mainland (Table 2.1).

Fringilla, *Pyrrhula*, and *Regulus* species densities remained higher on islands than mainlands when broken down by different data collection methods (Figure 3 C and D). *Columba* and *Turdus* species were found at lower densities and *Cyanistes* and *Sylvia* species at higher densities when broken down by methods (Figure 2.3 C and D). *Erithacus* species densities remained lower on islands across the 4 levels of comparison (Figure 2.3 C and D).

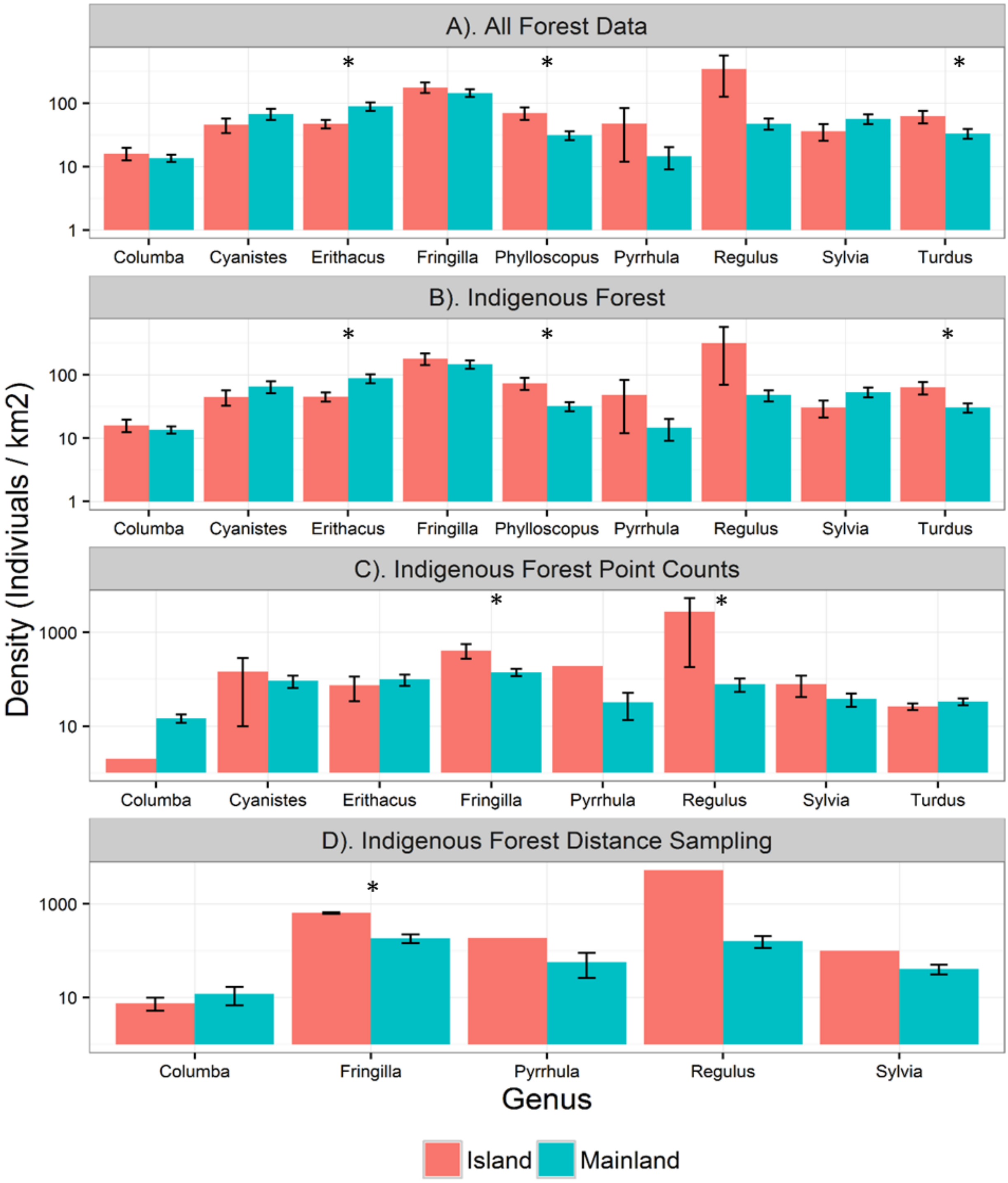

Figure 2.3: Comparison of published estimates of island and mainland density (mean individuals per km^2 ± SE across the studies) for focal species across Europe. Comparison broken down to four levels from all forest data collected (A) to only using data from indigenous forest and collected and analysed using the same methods used in this paper (D). Levels used to explore consistency in trends and remove sources of habitat and method bias. * next to a species denotes a significant difference between the pair at p<0.05.

2.5 Discussion

This paper tested the ecological release hypothesis using comparable habitats on Madeira and mainland Portugal. This was supplemented with additional mainland-island comparisons across Europe using published data. The research also attempted to address previous criticisms of the study of the ERH (Blondel *et al.,* 1988). The ERH predicts that species colonising a depaurperate ecosystem will increase in density (density compensation) and broaden their niche (niche expansion) (Feinsinger and Swarm, 1982; Losos and Queiroz, 1997).

2.5.1 Density compensation

Five of the six focal species were found at higher densities, three of which were significantly higher in density in the indigenous laurel forest on Madeira relative to equivalent habitat in Portugal. This is consistent with the density compensation aspect of the ERH (MacArthur *et al.,* 1972). Two of these significant species found at higher densities on Madeira (Chaffinch and Firecrest) represent species that would be expected to be older Madeiran species having colonized Madeira less recently as they have become differentiated enough, both genetically and morphologically, to be recognised as an endemic subspecies and species respectively (Clarke, 2006). The remaining significant species, the Blackbird, shows little morphological difference and would be predicted to have colonized Madeira relatively recently (Hounsome, 1993). The laurel forest also showed both lower species richness and diversity consistent with the species depauperate nature of islands as a consequence of their isolation (Jones *et al.,* 2001; Vassallo and Rice, 1982) and may be an indicator that there is reduced competition and more available ecological space or opportunity for Madeiran species to occupy (Bolnick *et al.,* 2010; Feinsinger and Swarm, 1982; Mesquita *et al.,* 2007). Relatively low species richness and species diversity is consistent across all three habitat types on Madeira. Higher abundances were also observed in all focal species in the upland scrubland on Madeira compared to Portugal with four of the species significantly higher.

In contrast, higher densities of four of the focal species were observed in the mixed / pine forest of Portugal compared to the equivalent habitat on Madeira. There is mixed support for the ERH in the exotic forest of Madeira, and previous research has suggested that this may be a result of masking through human disturbance with the exotic forest on Madeira replacing the indigenous laurel forest (Jones et al., 1987). The recent change in natural habitat state caused by humans on Madeira could have lowered the density of some species that have not adapted (Jones *et al.,* 1987). However, the creation of new habitats could also provide an opportunity for a second phase of expansion for species that are able to adapt as suggested by Wilson (1961) and Ricklefs and Cox (1972), although there is currently no evidence for this on Madeira.

2.5.2 Niche width and centre

Density compensation is often seen as a response to a shift in a species' ecological parameters (Vassallo and Rice, 1982) or a broadening of its realised niche as newly available resources that may have been used by competitors are accessed (Bolnick *et al.,* 2010; Feinsinger and Swarm, 1982). This niche expansion is predicted to occur in species-poor ecosystems such as oceanic islands (Losos and Queiroz, 1997). Significant differences in niche centre in all species across at least one axis and significant differences in niche width in at least one PCA axis for five of the six focal species were found in the focal species on Madeira compared to their mainland counterpart in Portugal. All but one species showed larger niche widths in the first PC (Laurel and Woodpigeon) and second PC (Blackcap) supporting the increase in niche width associated with the ecological release hypothesis. This is consistent with previous research that has recorded ecological release in the form of niche expansion (Bolnick *et al.,* 2010; Feinsinger and Swarm, 1982).

2.5.3 Density compensation in context

The differences in density identified in the island–mainland comparison of Madeira and Portugal could be attributed to habitat differences between sites. However, analysis of previous density estimates of forest species across Macaronesia support the presence of density compensation in certain species on Madeira and similar Atlantic islands. This support from published literature for density compensation was also present when data was broken down from all forest data to just indigenous forest data, then by survey technique from all methods, to point counts and distance sampling data only, to limit the effect of habitat and surveying method bias. Three species (*Fringilla, Regulus,* *Pyrrhula* Species) were consistently higher in density on islands using both field and published data.

2.5.4 Ecological Release Hypothesis (ERH)

The results of this study suggest that some species may have undergone ecological release in the form of density compensation and niche expansion in the native laurel forests of Madeira. This is consistent with previous studies (MacArthur *et al.,* 1972; Ricklefs and Cox, 1972; Terborgh and Faaborg, 1973) and is further supported by comparisons from published literature in this paper. This release may occur as a result of the lack of limiting interspecific competition on islands and the availability of novel resources that may have been monopolised by competitors in a more competitive mainland environment (Bolnick *et al.,* 2010). Ecological factors such as competition and predation are cited as being the most important factors affecting species assemblage (Diamond, 1978; Mesquita *et al.,* 2007). However, evolutionary history has also been recognised as a factor affecting community structure and assemblage with ecological differences rooted in a species history (Losos, 1995; Mesquita *et al.,* 2007). For example, Mesquita et al (2007) found little evidence of increased density and niche expansion associated with ecological release in lizards and suggest that lizard species are highly conservative in ecological traits. Low variation in niche breadth among populations suggests that evolutionary history of some species may be important in assemblage structure (Mesquita *et al.,* 2007).

Chapter 3. Evidence for the taxon cycle in the avifauna from a single island

Abstract

Understanding patterns in species assemblage, abundance, and distribution is a central component of biogeographical ecology, biological diversity, and species conservation. The taxon cycle has been proposed as a theory to explain biogeographical dynamics of species in time and space. Taxon cycles are phases of expansion and contraction in species distribution, abundance, and niche width. The taxon cycle theory is not only important for understanding the historical evolution of taxa but is also important to understanding species susceptibility to extinction, responses to climate change, and species invasions. There has been a renewed interest in applying the concept of the taxon cycle to a number of taxa supported by application of modern tools to a historical theory. This chapter combines genetics tools and large ecological datasets to conduct a novel test of the taxon cycle. Genetic, morphological and ecological data were obtained for the birds of Madeira. This study presents support for the taxon cycle on Madeira, with the earliest colonists being closely associated with interior, montane forest habitats. In contrast, newer colonists and early stage species were present more widely and were more abundant in disturbed, marginal island habitats. Both findings are consistent with the taxon cycle theory.

3.1 Introduction

Understanding patterns in species assemblage, abundance, and distribution is a central component of biogeographical ecology and biological diversity. The taxon cycle hypothesis proposed by Wilson (1961) provides an explanation for species biogeographic dynamics over time and space (Wilson, 1961; Economo and Sarant, 2012). Taxon cycles are phases of expansion and contraction in species distribution, abundance, and niche width with associated shifts in distribution and adaptations (Ricklefs and Bermingham, 1999; 2002). The taxon cycle theory is not only important for understanding the historical evolution of taxa but is also important for the understanding of species susceptibility to extinction, responses to climate change, and species invasions (Ricklefs and Bermingham, 2002; Economo and Sarant, 2012).

The concept of the taxon cycle was developed to describe a shift of Melanesian ant fauna from island edge and marginal habitat to interior forest habitats (Wilson, 1961). Evolutionary “movement” of species through the taxon cycle is argued to be driven by competition with species undergoing change in geographical range, habitat distribution, and population density, in addition to evolutionary differentiation and local extinction of island populations (Ricklefs and Cox, 1978; Ricklefs and Bermingham, 1999). Cycles of expansion and contraction in a number of insect and bird species distribution across island groups have supported the taxon cycle theory (Greenslade, 1968, 1969; Ricklefs and Cox, 1972; 1978). Wilson (1961) proposed interspecific competition as the main mechanism behind the cycle. Alternatively, coevolution of predator populations and pathogens of a species and counteradapatiaon of local fauna to a new colonist may be involved in the cycles (Ricklefs and Cox, 1972; Ricklefs and Bermingham, 1999; 2002).

Ricklefs and Cox (1972; 1978) hypothesised that species would experience four stages. In a temporal sequence during the taxon cycle: (1) expanding or widespread in distribution with little or no differentiation or sub-speciation, largely confined to marginal coastal habitats, and (stage 2) species in the next stage are predicted to be widespread in distribution with widespread sub-speciation. Species at the second stage may also be more specialized and inhabit higher elevations. Stage 3 species are fragmented in distribution and differentiated, with some populations becoming extinct. The final stage (stage 4) is a single island endemic with a small range and restricted to higher elevation and mature forest (Ricklefs, 1970; Ricklefs and Cox, 1972; 1978; Ricklefs and Bermingham, 2002).

The presence of the taxon cycle has been difficult to test empirically and there have been questions over the existence of taxon cycle (Pregil and Olson, 1981; Losos, 1992). However, work on the taxon cycle reoccurs frequently and there is suggestion that the theory may be more relevant in the current era of biodiversity science with increasing links between ecological and evolutionary perspectives over time and space (Economo and Sarnat, 2012). Advances in molecular techniques now allow the construction of phylogenies that can be used to estimate the timings of evolutionary events, relative ages of populations, and provide a temporal context to the taxon cycle (Ricklefs and Bermingham, 2002; Jonsson *et al.*, 2014). In addition, advances in statistical inference, geographical information systems, and the availability of large-scale datasets of species distribution and biodiversity provide novel tools to understand patterns in species distribution, diversity, and complex processes (Economo and Sarnat, 2012). There has been a renewed interest in the concept of the taxon cycle across a number of taxa (Economo *et al*, 2015; Jonsson *et al.*, 2014) but few studies have tested the theory using novel, modern approaches (Jonsson *et al.*, 2014).

This study will collate existing data on abundance, habitat use, and distribution of bird fauna for the Madeiran Archipelago and combine it with morphological and genetic data to test for the taxon cycle using modern approaches. The aim of this study is to determine whether patterns of species abundance, distribution, and niche width on Madeira relate to species taxonomic status, morphological and genetic differentiation, therefore directly testing the central tenet of taxon cycle theory. Species will be placed in putative taxon ranks based on their taxonomic status and distribution. These ranks will be tested by assessing genetic and morphological differences across the ranks for pairs of species present on Madeira and the mainland. Taxon cycle rank for all species on Madeira will then be used to look at predicted patterns in abundance and distribution. Specifically, this paper will investigate the following predictions based on the taxon cycle: (1) Genetic and morphological difference will increase with increasing taxon cycle rank. (2) Abundance in indigenous, interior habitats will increase at later stages of the taxon cycle. (3) Abundance in exotic, marginal habitats will decrease at later stages of the taxon cycle. (4) Niche width will decrease at later stages of the taxon cycle. (5) Overall distribution across the archipelago will decrease at latter stages of the taxon cycle.

3.2 Methods

3.2.1 Study area

The study area is the Madeiran Archipelago situated between 30°01’ and 33°80’N and 15°51’ and 17°16’W (Figure 1.1). The archipelago is made up of Madeira, Porto Santo, Ilhas Derertas, and Ilhas Selvagens. The largest of the islands, Madeira, is a volcanic island approximately 5.2 million years old, located in the eastern Atlantic, 900km south-west of Portugal, 440km north of the Canary Islands, and 565km from western Africa (Dietzen *et al.*, 2008; Jones *et al.*, 1987, Zhou *et al.,* 2012). The surface area of Madeira is 741km^2 rising to a maximum elevation of 1862m. The land use on Madeira is divided into agriculture, pasture, residential, managed forest, non-native (*Eucalyptus globules* and *Pinus pinaster*) and natural forest (Jones *et al*., 1987). The indigenous laurel forest covers around 20% (15,000ha) of the islands surface but once covered most of the island and is protected within the Parque Natural da Madeira (Clarke, 2006; Marrero *et al.*, 2004).

3.2.2 Bird census data

To identify trends in species distribution, abundance, and habitat use across Madeira, data for all species on Madeira were provided by the Parque Natural da Madeira. This was from a systematic survey of Madeira that was conducted over three breeding seasons (2009 - 2011). Surveying was conducted within a grid system composed of 291 grid of 2x2 km^2 quadrats covering all of the Madeira archipelago. The Madeiran archipelago occupies a total of 291 quadrats, of which 181 were on Madeira. Each quadrat was surveyed at least once with a transect that lasted 1-hour split into six 10-minute increments, walked at a constant speed (2.5-3km/hour) using a GPS and a stopwatch (Atlas das Aves do Arquipélago da Madeira, 2009). Surveys were conducted in the three hours after sunrise and the three hours before sunset to coincide with peaks in bird activity (Bibby *et al.*, 1999). During each of the six transect increments, the total number of individuals observed, habitat type (classified based on appendix 1), and any indication of breeding were noted.

3.2.3 Taxon cycle rank

A previous study by Jones *et al.* (1987) used a subset of the Madeiran species and placed them on an ordinal scale to represent species positions within the taxon cycle, this study has adopted this taxon cycle rank. Briefly, species were ranked 1-12, with recent species immigrants that are presumably identical to the mainland stock given low ranks. Older species, such as endemic subspecies on an archipelago, single island subspecies, and single island endemics represented the oldest species with the higher ranks (Jones *et al.*, 1987). Species were also placed on an ordinal scale 1-4 representing the four stages of the taxon cycle outlined by Ricklefs and Cox (1972; 1978), with recent colonists or introduced species assigned the value 1, 2 for endemic subspecies to Macaronesia, 3 for endemic subspecies to the Madeira Archipelago, and 4 to single island Madeiran endemic species (similar to Carrascal *et al.*, 2008; Economo and Sarnat, 2012) (Appendix 5). Wintering, passage and occasional species were not included in my analysis. Species were ranked, in addition to using genetic distances, to enable all 29 terrestrial bird species (37 including seabirds and waders) to be used in the analysis, as genetic data was only available for 8 of the species pairs.

3.2.4 Morphological measurements

Morphological measurements were obtained from a number of focal species pairs (Madeiran / Mainland samples), collected from mist-netting birds on Madeira (collected by and published in Hounsome, 1993) and from the mainland supplied by ARocha bird ringing station in Portugal between 2011 and 2012. These records have also been supplemented with measurements taken from museum species from various Mainland European locations and from published estimates (collected by and published in Hounsome, 1993). Focal species included Blackbird (*Turdus merula*), Blackcap (*Sylvia atricapilla*), Laurel and Wood Pigeon (*Columba trocaz / Columba palumbus*), Firecrest (*Regulus madeirensis / Regulus ignicapillus*), Goldfinch (*Carduelis carduelis*), Chaffinch (*Fringilla coelebs*), Robin (*Erithacus rubecula*), Linnet (*Carduelis cannabina*), Canary / Serin (*Serinus canaria / Serinus serinus*), Spectacled Warbler (*Sylvia conspicillata*), Grey Wagtail (*Motacilla cinerea*), and Rock Sparrow (*Petronia petronia*). Measurements of wing length, bill width, depth and length, tarsus length, tail length and weight were collected for each species in addition to sex and age of each individual.

3.2.5 Genetic differentiation

Several Madeiran focal species were used to determine genetic differentiation from their mainland counterparts as an indication of taxon age based on the idea of the molecular clock. These species represent the entire range of taxon cycle stages. Published sequences for Robin, Blackcap, Canary and Serin, Spectacled warbler, Berthelot's Pipit and Tawny Pipit (*Anthus berthelotti / Anthus campestris*), Chaffinch, Firecrest, and Laurel and Wood Pigeon were obtained for the mitochondrial Cytochrome b (cytb) gene using the NCBI GenBank database using BLAST in MEGA6 (Tamura *et al.*, 2013) (Table 3.1). Sequences were aligned with MUSCLE using default settings and trimmed to the same length (528bp). Average between and within group genetic uncorrected p-distances and corrected Tamura and Nei distances were calculated for each species pair between island populations and their mainland counterpart using default settings (similar to Dietzen *et al.,* 2006). The mutational model that best fit the data was identified using FINDMODEL (Posada and Crandall, 1998). A GTR+G (General Time Reversible + Gamma) model was selected using the Akaike Information Criterion (AIC) in FINDMODEL and was used to create a Maximum Likelihood (ML) tree in MEGA 6.0 (Tamura *et al.*, 2013). Robustness of the tree was assessed with 1000 replicates.

3.2.6 Relative Abundance, distribution and niche width analysis

Species relative abundance was quantified by calculating the average number of individuals seen per 2x2km^2 of each habitat type. Average species abundance was also calculated for each species in marginal (within two quadrats of the coast) and interior areas of Madeira. Species distribution was quantified as the total number of unique 2x2 km^2 quadrats occupied by each species. Using the average abundance of each species per habitat type, niche width was calculated using the Levins index (Levins, 1968) and the Shannon and Simpson's biodiversity indices.

3.2.7 Morphological analysis

Mean percent difference for each morphological measurement for each species pair were calculated and an average of all morphological measurements combined was also calculated for each species between the mainland and island population. Principal Component Analysis (PCA) was performed for each species to reduce dimensionality of the morphological data (Jonsson *et al.,* 2014). PC1 and PC2 were used as a measure of overall morphological difference for a subset of the species on Madeira (similar to Jonsson *et al.*, 2014). A discriminant function analysis (DFA) was applied to test whether mainland and island populations could be distinguished and classified correctly (similar to Dietzen *et al.*, 2008; Illera *et al.*, 2014). The DFA was recorded as overall accuracy of classifying both populations and also the average accuracy of the species pairs.

3.2.8 Taxon cycle analysis

Spearman's rank correlation was applied to test for a relationship between morphological and genetic differentiation. Kruskal-Wallis tests were applied to test for differences in genetic and morphological divergence across taxon cycle ranks. Maximum distribution and average abundance was calculated per species and compared across the taxon cycle ranks. Distribution, abundance, and niche width across the 4 taxon cycle ranks were also compared using Kruskal-Wallis tests. Wilcoxon signed-rank tests were used to test for differences between early and late stage species. All analysis and calculations were performed using R (R Development Core Team, 2015). Distribution and abundance data were mapped using QGIS 2.1.2.3 (QGIS Development Team, 2015). All species present on Madeira were analysed together including seabirds, waders and waterfowl, as it is unknown whether these groups pass through stages of the taxon cycle. This study also analysed land birds separately to allow direct comparison with previous studies that have focused on this group (Ricklefs and Cox, 1978; Prodon *et al.,* 2002).

Table 3.1: Source locations and number of sequences from GenBank for each species used in genetic analysis

	Genbank Sequences (N)	
Species	**Madeira**	**Mainland Europe**
Anthus berthelotii / Anthus campestris [a]	1	2
Columba trocaz / Columba palumbus [b]	4	6
Erithacus rubecula	9	13
Fringilla coelebs	7	9
Regulus madeirensis / Regulus ignicapillus [c]	13	4
Sylvia atricapilla	2	2
Sylvia conspicillata	1	6
Serinus canaria / Serinus serinus [d]	3	1

Where two different species are listed, the mainland sister species has been used as a comparison with the sister species identified from previous studies (a = Illera *et al.,* 2007, b = Dourado et al., 2014, c = Päckert *et al.,* 2003, d = Arnaiz-Villena *et al.,* 1999).

3.3 Results

Morphological and molecular data were collected for 12 and 8 species pairs respectively. An increase in morphological (Figure 3.1A) and genetic difference (Figure 3.1B) was identified across taxon rank on Madeira. A significant positive correlation was identified in genetic distance (Spearman Rank Correlation (one tailed), rho = 0.79, p = 0.009) but not in average morphological difference (Spearman Rank Correlation (one tailed), rho = 0.4, p = 0.09) across taxon ranks. No significant difference was found in average morphological difference across taxon cycle rank (Kruskal-Wallis, X^2 = 2.08, df = 3, p = 0.56) or between early and late stage species (Wilcoxon signed-rank, W = 11, p = 0.34). However, an increase in mean (rank 1. 3.49, rank 2. 6.01, rank 3. 7.14, and rank 4. 13.01) and median (rank 1. 3.49, rank 2. 4.69, rank 3. 8.05, and rank 4. 13.01) was identified with increasing rank and stage. No significant difference was found in genetic distance across rank (Kruskal-Wallis, X^2 = 5.5, df = 3, p = 0.14). An increase in both mean (rank 1. 0.004, rank 2. 0.01, rank 3. 0.035, and rank 4. 0.06) and median (rank 1. 0.004, rank 2. 0.002, rank 3. 0.035, and rank 4. 0.06) genetic distance was shown with increasing taxon cycle rank. When grouped into early (rank 1 and 2; mean = 0.009, median = 0.003) and late (rank 3 and 4; mean = 0.047, median = 0.035) stage species a significant difference in genetic distance was found (Wilcoxon signed-rank, W = 0, p = 0.03). Phylogenetic analysis of the species pairs support this trend with higher levels of divergence in higher ranked species (rank 3 and 4) compared to lower ranked species (rank 1 and 2, Figure 3.2).

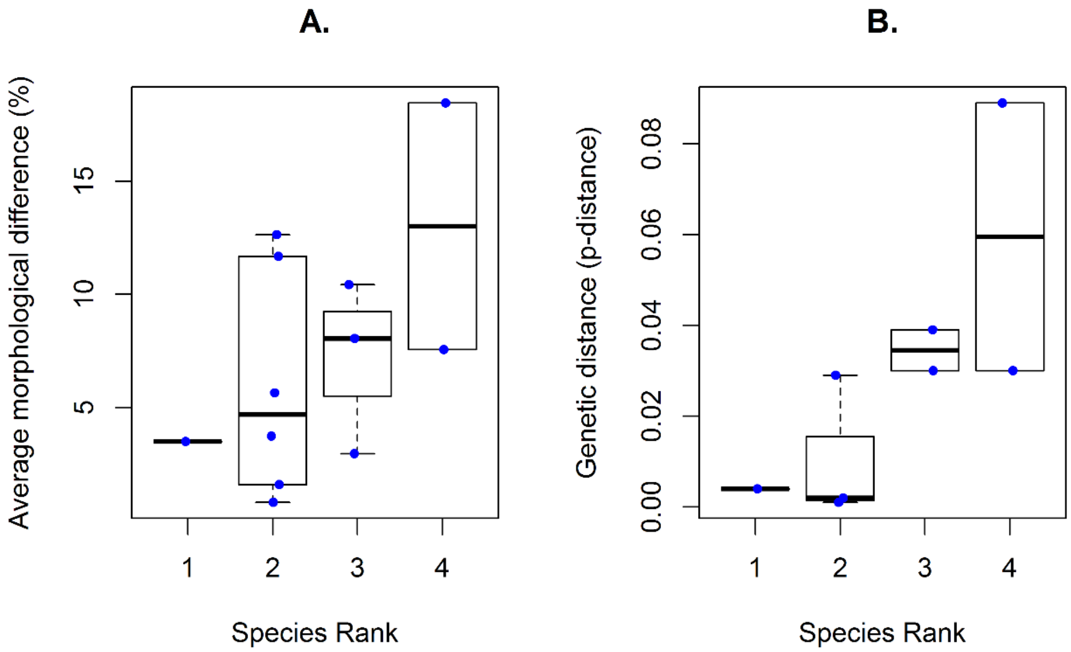

Figure 3.1: A) Average morphological difference (%) and B) genetic distance (p-distance) across taxon cycle stage based on existing species classifications. A. Rank 1 (n=1), rank 2 (n=6), rank 3 (n=3), rank 4 (n=2). B. Rank 1 (n=1), rank 2 (n=3), rank 3 (n=2), rank 4 (n=2).

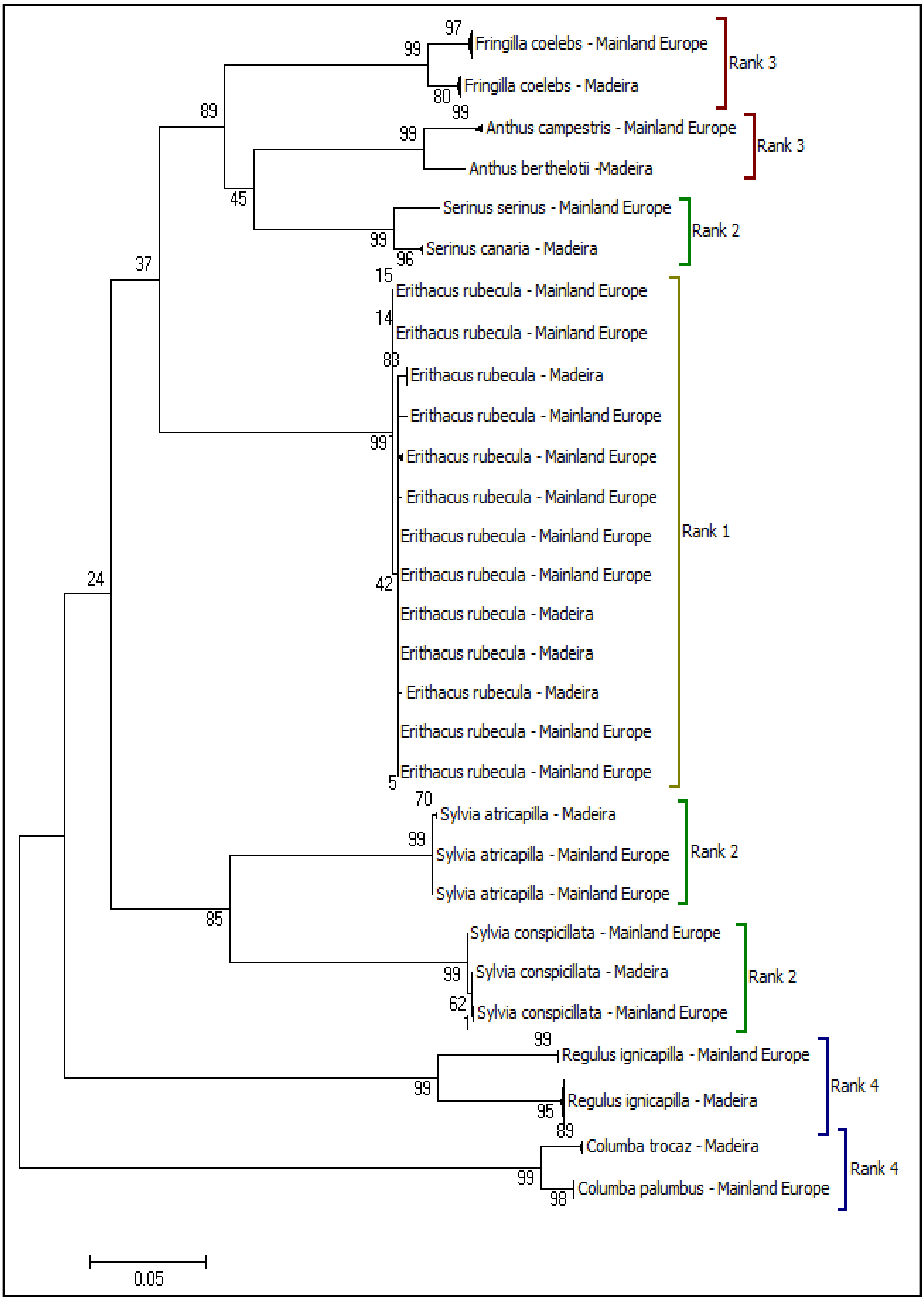

Figure 3.2: Maximum likelihood (ML) topology for Cytb across focal species. The numbers on the branches indicate the percentage of trees the associated taxa clustered together. Sub-group brackets indicate which taxon cycle rank each species pair have been placed in.

Figure 3.3 shows the relationships between genetic and morphological difference and species distribution, niche width and abundance on Madeira. Genetic distance (p-distance) showed positive correlations with Laurel forest, indigenous and interior habitat abundance. Negative correlations were found between genetic distance and species distribution (number of quadrats), number of habitats, niche width (Levins), exotic forest and disturbed habitat abundance. Overall average morphological difference, PCA component 2, and DFA accuracy also showed a negative correlation with niche width, distribution, and number of habitats occupied respectively. PCA component 1 showed a positive correlation with exotic forest and disturbed habitat abundance (Figure 3.3). In addition, using the subset of Madeiran species (16) and the continuous ranks used by Jones *et al* (1987), no significant correlation was identified between these continuous ranks (1-12) and species distribution and abundance across Madeira ($p > 0.05$).

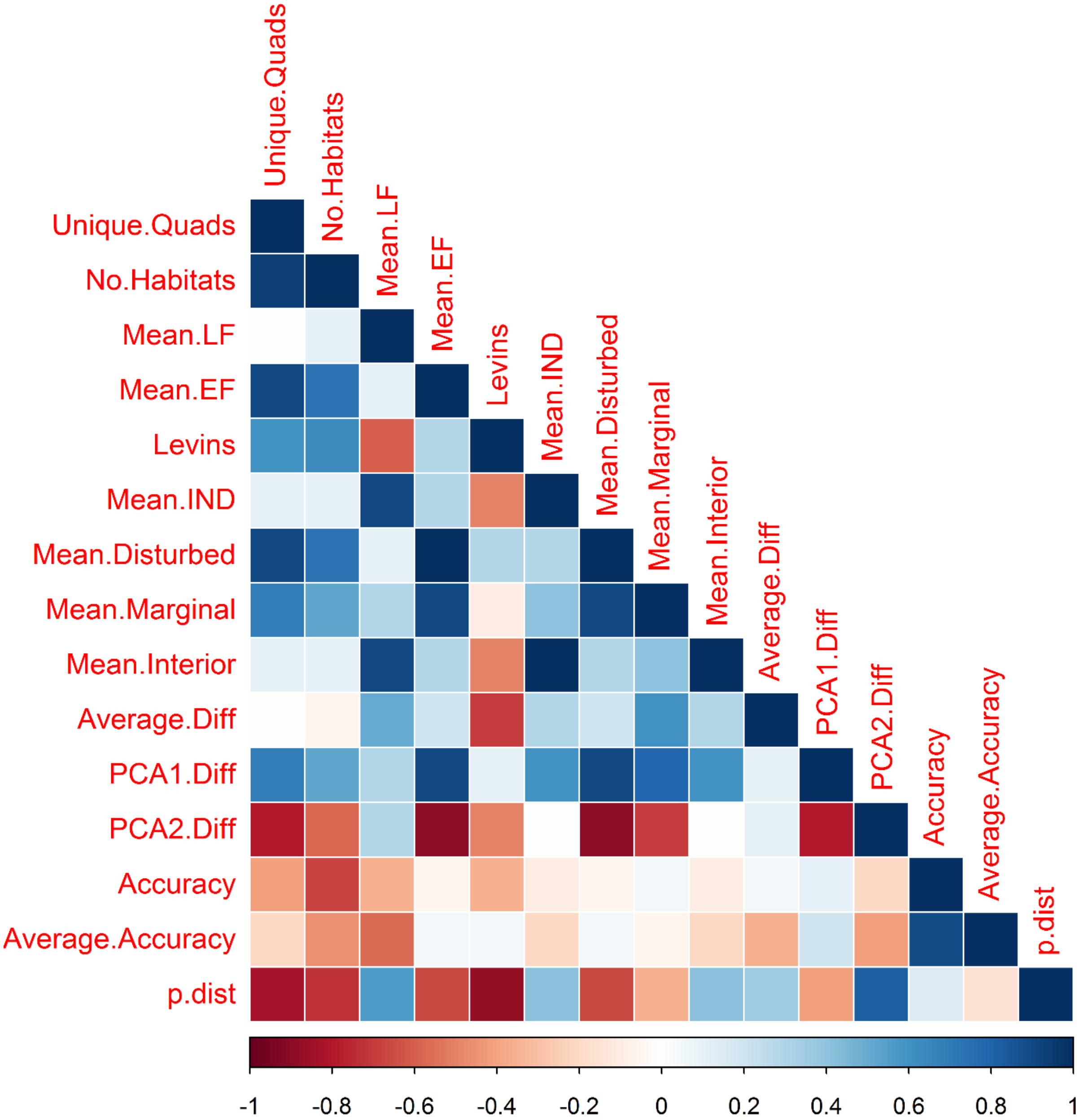

Figure 3.3: Correlation of genetic and morphological differences with species distribution, niche width, habitat use and abundance on Madeira. Distribution measured in number of quadrats present (Unique Quads), Niche width measured in the number of habitats present (No.Habitats) and Levins index. Mean abundance calculated for the laurel forest (LF), exotic forest (EF), indigenous (IND), disturbed, marginal and interior habitats. Morphological difference was calculated across all measurements (Average.Diff), using PCA (PCA1 and PCA2) and DFA as the overall accuracy and the average accuracy (Accuracy and Average.Accuracy). Genetic distance between species pairs represented by p-distance (p.dist).

3.3.1 Distribution and abundance across taxon cycle ranks

Data for 37 species were used to identify differences in distribution and abundance across taxon cycle rank. A significant difference in distribution (Kruskal-Wallis, X^2 = 14.98, df = 3, P = 0.002), habitat breadth (Kruskal-Wallis, X^2 = 13.89, df = 3, P = 0.003), abundance in Laurel (Kruskal-Wallis, X^2 = 13.33, df = 3, P = 0.004), Exotic forest (Kruskal-Wallis, X^2 = 8.45, df = 3, P = 0.038), and average abundance across indigenous undisturbed habitats (Kruskal-Wallis, X^2 = 16.05, df = 3, P = 0.001) were detected between species rank (figure 3.4). No significant difference was detected in disturbed habitat abundance between species rank (Kruskal-Wallis, X^2 = 5.51, df = 3, P = 0.14). Increases in habitat breadth and in abundance in laurel forest and undisturbed habitats were observed with increasing species rank, with exotic forest showing the highest abundance also in the highest rank. Distribution increased in the early stage (Rank 2) and remained high in species in the later stages (Figure 3.4). Disturbed habitat abundance was highest in the earlier stages of the species ranking.

The same pattern across species ranks was also observed when waders, seabirds, and waterfowl were excluded from the analysis (figure 3.5, n=29). Only abundance in undisturbed habitats remained significant (Kruskal-Wallis, X^2 = 7.99, df = 3, P = 0.046). However, distribution (Kruskal-Wallis, X^2 = 7.34, df = 3, P = 0.062), habitat breadth (Kruskal-Wallis, X^2 = 7.49, df = 3, P = 0.058), and abundance in Laurel forest (Kruskal-Wallis, X^2 = 7.34, df = 3, P = 0.062) remained almost significant.

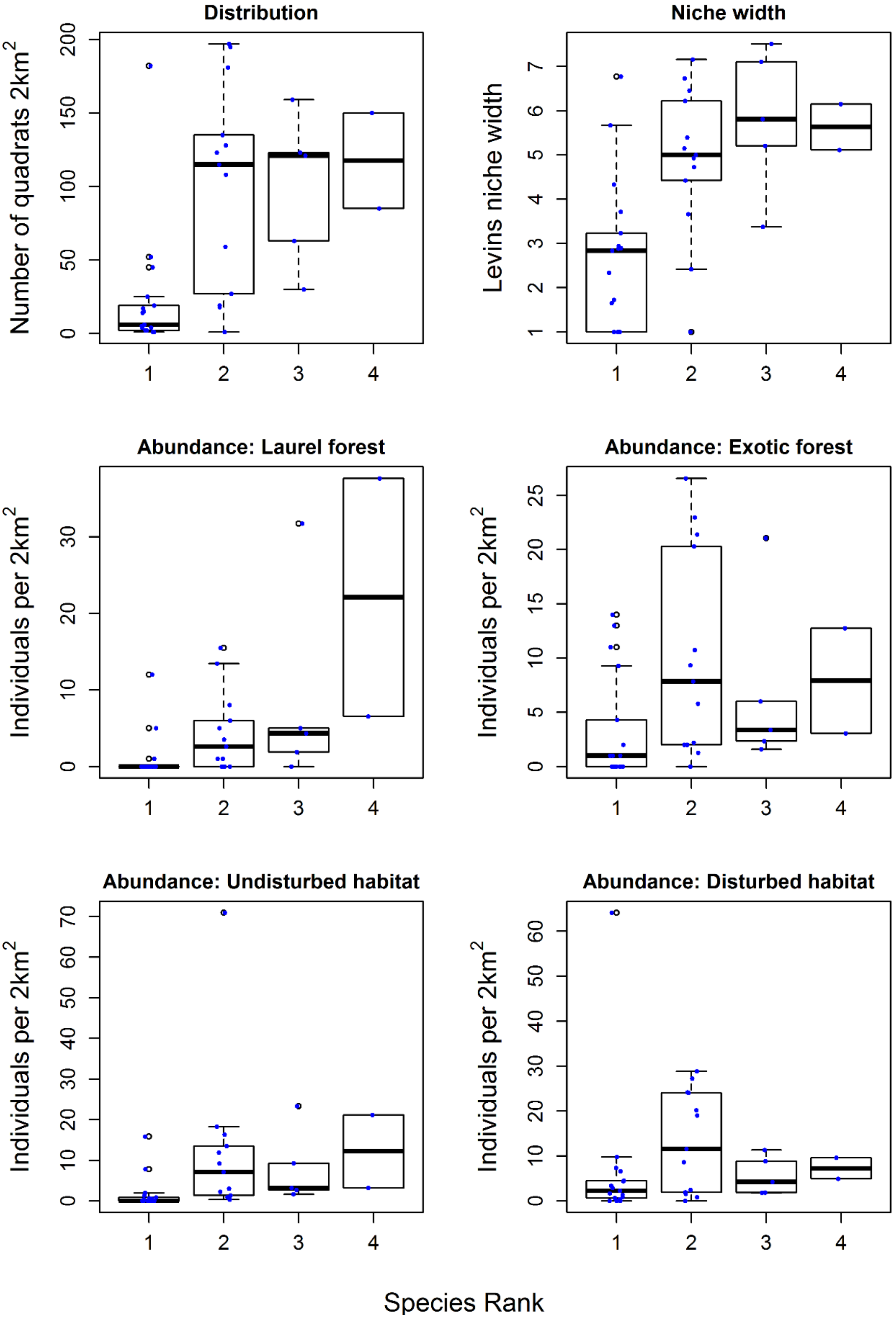

Figure 3.4: Distribution, Habitat breadth and abundance across taxon cycle ranks for all species on Madeira. Rank 1 (n=17), 2 (n=13), 3 (n=5), 4 (n=2).

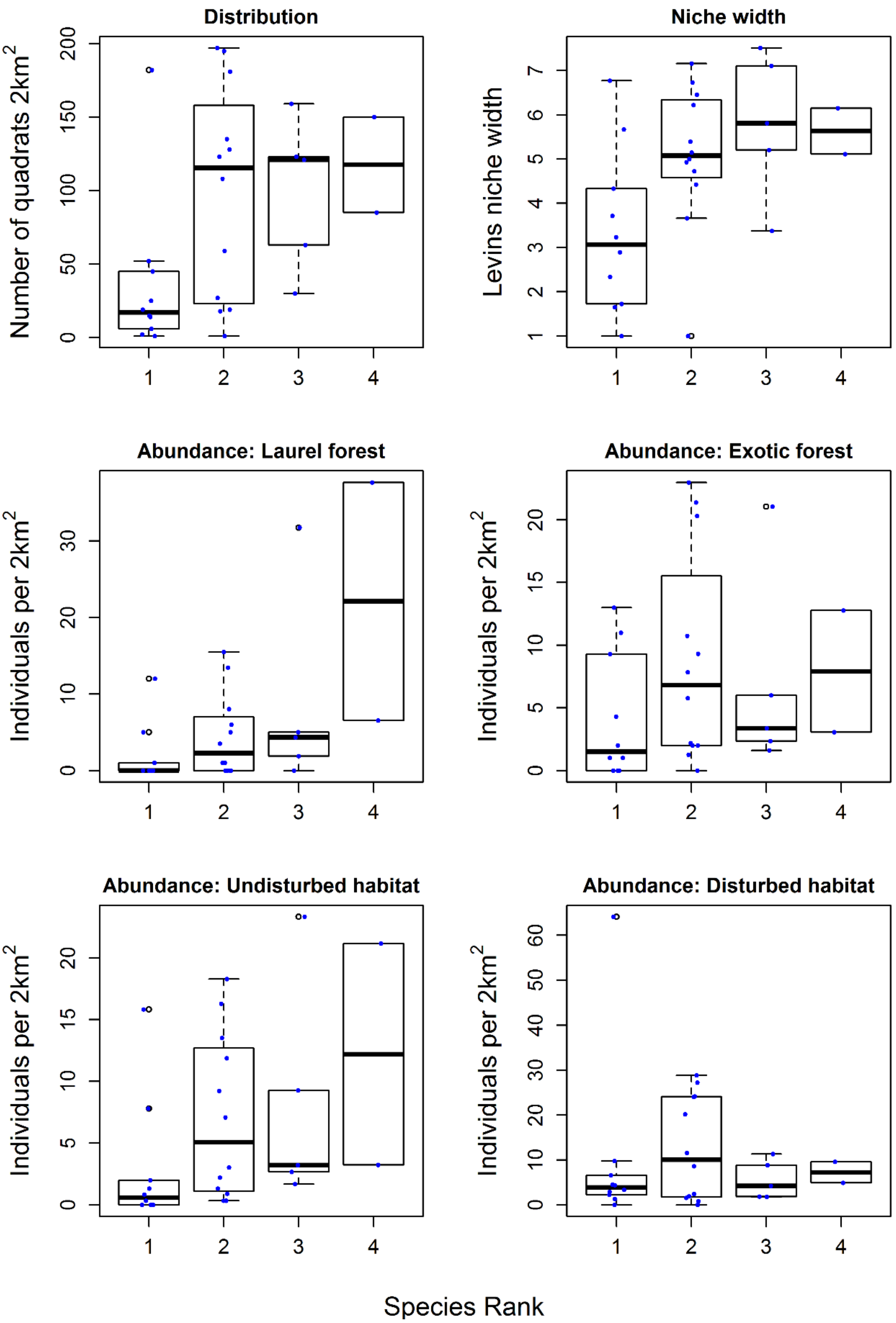

Figure 3.5: Distribution, habitat breadth and abundance across taxon cycle ranks (excluding seabirds, waders and waterfowl). Rank 1 (n=10), 2 (n=12), 3 (n=5), 4 (n=2).

Species distribution and abundance across the Madeiran archipelago for each taxonomic rank are shown in figure 3.6 (including all species, n=37). Rank 1 species were found to be present across most of the archipelago with some absent quadrats (n=17). Rank 2 species were also found widely across the archipelago with the highest densities in the Desertas and the outer quadrats of Madeira (n=13). Rank 3 species were also found across the islands and in higher densities in the North and Central areas of Madeira (n=5). Rank 4 species were only present on Madeira and were absent from the south coast of Madeira. Rank 4 species were found at highest densities in Central and North-west regions of Madeira (n=2).

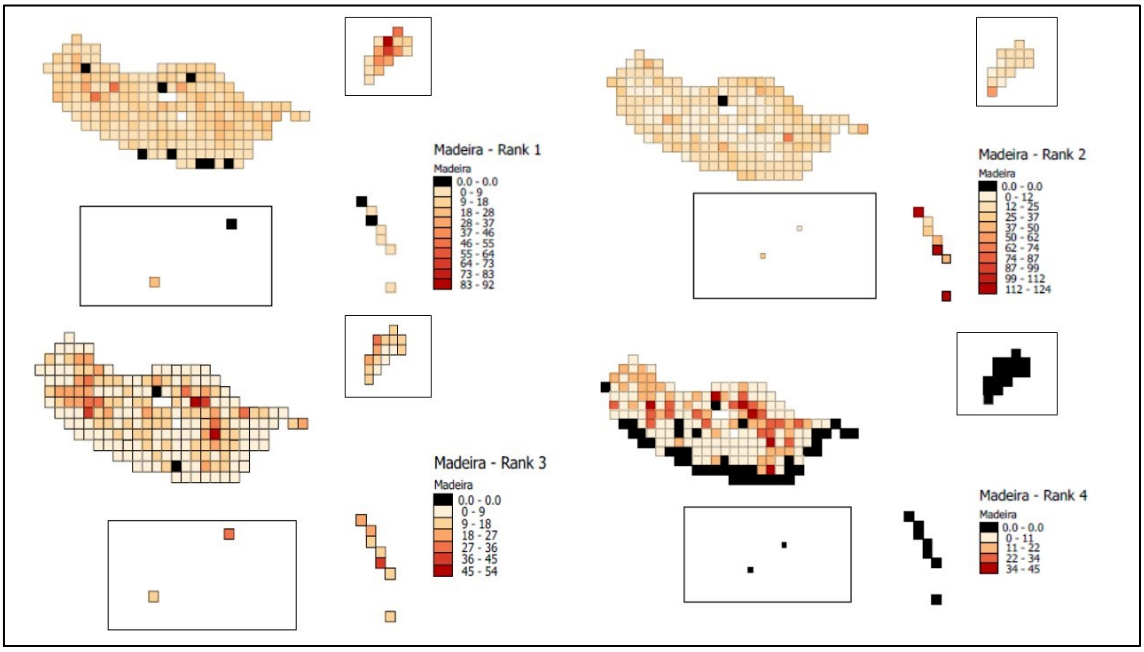

Figure 3.6 : Distribution and abundance (individuals per 2x2km^2 quadrat) of species classified as Rank 1 (recently colonist or introduced species), Rank 2 (endemic subspecies to Macaronesia), Rank 3 (endemic subspecies to the Madeira Archipelago), and Rank 4 species (Endemic Species) across Madeiran archipelago 2x2km^2 quadrats (Porto Santo – top right inset, Madeira, Desertas, Salvagens – bottom inset).

Using all species data, a significant difference was shown in abundance in coastal densities (within two quadrats of the coast) across species rank (Kruskal-Wallis, X^2 = 197.17, df = 3, P < 0.001). The highest median and mean abundance in marginal quadrats were shown in rank 2 (mean = 20.31, median = 11). No significant difference was found in interior abundance across species rank (Kruskal-Wallis, X^2 = 5.66, df = 3, P = 0.13). The highest median abundance were shown in rank 1 (10) and 3 (8.5) and the highest means in rank 3 (12.32) and 4 species (14.38).

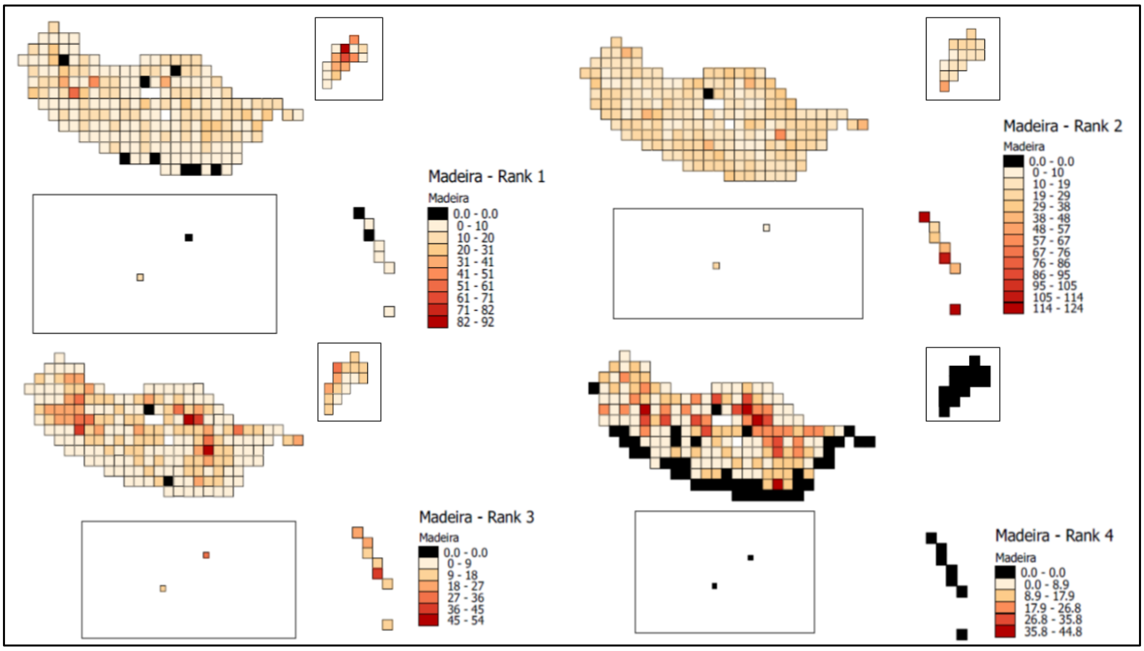

Figure 3.7 : Distribution and abundance (individuals per 2x2km^2 quadrat) of species (excluding seabirds, waders and waterfowl) classified as Rank 1 (recently colonist or introduced species), Rank 2 (endemic subspecies to Macaronesia), Rank 3 (endemic subspecies to the Madeira Archipelago), and Rank 4 species (Endemic Species) across Madeiran archipelago 2x2km^2 quadrats (Porto Santo – top right inset, Madeira, Desertas, Salvagens – bottom inset).

Seabirds, waders, and waterfowl were removed and the distribution and abundance of each rank were calculated (Figure 3.7, n=29). These species were removed as previous studies have focused on land birds only. Species distribution and abundances were similar between the two analyses. Rank 1 species were present across most of Madeiran archipelago with some absent quadrats (n=10). Higher densities were found in North-west Quadrats on Madeira. Rank 2 species were also found widely across the archipelago with the highest densities in the Desertas and the outer quadrats of Madeira (n=12). Rank 3 species were also found across the islands and in higher densities in the North and Central areas of Madeira and the outer quadrats of Madeira (n=5). Rank 4 species were only present on Madeira and were absent from the south coast of Madeira (n=2). Rank 4 species were found at highest densities in Central and North-west regions of Madeira.

A significant difference in abundance in marginal sites was shown across the sites (Kruskal-Wallis, $X^2 = 197.17$, df = 3, $P < 0.001$). The highest median and mean abundance in coastal quadrats were shown in rank 2 (mean = 19.5, median = 12). Interior abundance across species rank was almost significant (Kruskal-Wallis, $X^2 = 7.02$, df = 3, $P = 0.07$. The highest median abundance were shown in rank 1 (10) and the highest means in rank 3 (12.32) and 4 species (14.38).

3. 4 Discussion

3.4.1 Taxon cycle rank

The results from the chapter provide the first evidence for the taxon cycle on Madeira using genetic distance and ecological data. A significant increase in genetic distance was identified with increasing taxon cycle rank and between early stage (recent colonists) and late stage species (endemic sub-species and species). This supports the placement of species into broader taxon cycle ranks that reflect the stages identified by Ricklefs and Cox (1972, 1978). A similar trend of increasing genetic distance and taxon rank was also found by Ricklefs and Birmingham (1999), identifying the sequence of ranks 1-4 as a chronology of taxon age. An increase in morphological difference across the 4 stages was also found. Genetic distance from mainland counterpart was found to be negatively correlated with species distribution, number of habitats occupied, niche width and exotic forest, and disturbed habitat abundance. Average morphological difference was found to be negatively correlated with Levin's niche width and PCA (component 2) negatively correlated with distribution, exotic forest, and disturbed habitat abundance. This is consistent with predictions from the taxon cycle as species are expected to become reduced and fragmented in distribution, shifting from marginal and disturbed to interior and forested habitats and become more specialized (Wilson, 1961; Ricklefs and Cox, 1972; 1978; Ricklefs and Bermingham, 2002).

The higher abundance in laurel forest located in the interior of Madeira, with increasing genetic distance from mainland counterpart is consistent with findings from previous studies that identified a movement to interior forest habitats and higher elevations with progression through the later stages of the taxon cycle (Wilson, 1961; Ricklefs and Cox, 1972; 1978; Ricklefs and Bermingham, 2002). Positive correlations were also observed between the results from the morphological PCA (PC1) and abundance in exotic forest and marginal habitats. Older, contracting range species are expected to occupy forest habitats (Wilson, 1961; Ricklefs and Bermingham, 2002), which may support the correlation of morphological difference with both forest habitats (Exotic and indigenous Laurel). In addition, some species may also experience a new phase of expansion in the later stages of the taxon cycle into marginal habitats (Wilson, 1961; Ricklefs and Bermingham, 2002). Ricklefs and Cox (1972) suggested that late stage species could undergo secondary expansion if they escaped from predator or parasite pressure by becoming rare. Genetic change under these conditions may free a species from a predator or parasite driving a new phase of expansion (Ricklefs and Bermingham, 2002).

3.4.2 Abundance and distribution

Species in the later stages of the taxon cycle on Madeira were found at significantly higher levels of abundance in laurel, exotic, and all undisturbed forest, and they also occupied a larger distribution and a broader niche. These patterns were consistent when seabirds, waders, and waterfowl were removed from the analysis (similar to Ricklefs and Cox, 1978; Prodon *et al.,* 2002). The higher abundance in forest habitats are consistent with taxon cycle predictions from previous studies (Wilson, 1961; Ricklefs and Bermingham, 2002). Disturbed habitat abundance was found at higher levels in the early stages of the taxon cycle on Madeira and is consistent with stages defined by Wilson (1961) and Ricklefs and Cox (1972; 1978). A broader niche width and increased distribution in the later stages of the taxon cycle is not consistent with predictions for older species, although re-expansion of older species into marginal habitats has been proposed as being part of the latter stages of the taxon cycle, which may explain the trend seen here (Wilson, 1961; Ricklefs and Bermingham, 2002). In contrast, de Moraes Weber *et al.* (2014) also found a broader range in older species when looking at the ecological niche of phyllostomid bats In South America, suggesting that older species have reached suitable areas and then remained stable.

The distribution and abundance analysis in this chapter is consistent with the taxon cycle, with older species (rank 4) being absent from some coastal areas and at higher abundance in the higher elevation montane central areas and the North-West of the island both dominated by forest. Early stage (rank 1 and 2) species were present widely across the archipelago (all species) and Madeira (excluding seabirds, waders, and waterfowl). This is consistent with prediction for species at the early and late stages of the taxon cycle (Wilson, 1961; Ricklefs and Cox, 1972; 1978; Ricklefs and Bermingham, 2002). Occupancy of primary montane habitats by relictual taxa (late stage species) has also been supported recently by Jonsson *et al.* (2014) in Indo-Pacific passerine birds. Differences were observed across ranks for both exterior and interior abundances. Marginal abundances (within two quadrats of the coast) were highest in early stage species (Rank 2) consistent with expectations from movement through the taxon cycle.

Understanding the movement of species through the taxon cycle and the associated changes in distribution, abundance and adaptation is important to our understanding of both natural and anthropogenic extinctions. Previous studies have identified small population size, endemism and small geographic range as the main predictors of extinction risk (Purvis *et al.,* 2000; O'Grady *et al.,* 2004). As species pass through the taxon cycle they are likely to exhibit traits such as habitat and niche specialism, restricted distribution and low abundance that make them susceptible to extinction. This study provided the first evidence of the taxon cycle on Madeira, tested using existing data sources. A similar method could be applied, where existing data is available, to identify the presence of taxon cycle on other island groups and relate to extinction threat.

3.4.3 Conclusion

In summary, this study uses a large comprehensive dataset of the birds of Madeira and both genetic and morphological data to test for the presence of the taxon cycle in the bird taxa of a single island. The results provide the first support for the presence of the taxon cycle on Madeira with older species being closely associated with interior, montane, forest habitats. In contrast, newer colonists, early stage species were found present more widely and were more abundant in disturbed habitats. Patterns identified on Madeira that are consistent with the taxon cycle suggest that the theory may play an important role in explaining the distribution and abundance of species on a single island and could help understand natural and anthropogenic extinction, the impact of new colonists or invasive species and influence the conservation of single island endemics.

Chapter 4. Investigating the presence or absence of ecological release and the taxon cycle across multiple island chains.

Abstract

Ecological release and the taxon cycle are two interlinked theories that have been proposed to explain patterns in species distribution and abundance on islands. Both theories are important to understanding the evolutionary history of taxa, but ecological release is specifically important with respect to understanding how invasive species respond to novel environments. Cycles of expansion and contraction of species may also be important to understanding susceptibility to extinction and responses to climate change. This chapter uses species distribution and abundance data collated for the Azores, Madeira, Canary Islands, and the Cape Verde Islands, as well as published mitochondrial genetic data for a subset of species, to test for evidence of ecological release and the taxon cycle across Macaronesia. Nine of twelve focal species were found at higher abundance in the Azores and Madeira compared to the mainland. For three island groups (Madeira, Azores, and the Canary Islands), distribution and the proportion of point counts occupied were relatively low for late stage taxon cycle ranks. Distribution and abundance show a complex, consistent pattern of increase then decrease with lineage age. The results from this paper provide strong support for the presence of ecological release and the taxon cycle across the Macaronesian bird communities.

4.1 Introduction

The taxon cycle theory was proposed to explain biogeographical dynamics in space and time (Economo and Sarnat, 2012) and first developed to explain expanding and contracting populations of Melanesian ants (Wilson, 1961). Three stages along a continuum representing microevolutionary change were identified: Stage 1 species are wide spread or expanding occupying marginal habitats and island edges; Stage 2 species have increasingly fragmented and restricted ranges with a movement to interior forest habitat; Stage 3 species are more evolutionary distinct with few mainland relatives (Wilson, 1961).

A number of empirical studies provide support for the taxon cycle on diverse island taxa. Birds and insects of the Solomon Islands are consistent with predictions of the taxon cycle for expansion, differentiation, and contraction (Greenslade 1968, 1969). Ricklefs and Cox (1972; 1978) identified patterns that support the presence of the taxon cycle in birds of the West Indies and refined predictions arising from taxon cycle theory. They describe four stages species would exhibit: (1) widespread in distribution with little differentiation and confined to marginal coastal habitats; (2) widespread in distribution with differentiation and more specialized in inland habitat use; (3) fragmented in distribution and differentiated with some populations becoming extinct; (4) island endemic with restricted range (Ricklefs and Cox 1972; 1978). While there have been hypotheses posed that are alternative to the taxon cycle to explain island biogeographic phenomena (e.g., the influence of climate: Pielou, 1979; Pregill and Olson, 1981; the age-area model: Willis, 1992; Webb and Gaston, 2000, de Moraes Weber et al., 2014; the stasis model: Jablonski 1987; Figure 4.1), recent genetic evidence in West Indies birds strongly supports taxon cycle theory (Ricklefs and Bermingham, 1999), while strong support for alternative hypotheses has not emerged (de Moraes Weber et al., 2014).

An associated theory with the taxon cycle is ecological release. When a species-depauperate ecosystem (like an island) is colonised, niche expansion and increased density will be observed resulting from ecological release from competition and predation (MacArthur and Wilson, 1967; MacArthur *et al.,* 1972). This increase in abundance associated with ecological release is known as density compensation (MacArthur *et al.,* 1972). Consistent with the taxon cycle, there has been support for ecological release in a number of taxa (Birds: MacArthur *et al.,* 1972; Primates: Peres and Dolman, 2000; Lizards: Case, 1975; Herpetofauna: Rodda and Dean-Bradley, 2002; Microbial wood-webs: McGrady-Steed & Morin; 2000). While there has been criticism of ecological release based on difficulty in experimental design to detect the presence of the phenomenon (Wright, 1980; Blondel *et al.,* 1988), there is a strong base of evidence that is consistent with the basic predictions arising from it. Chapter 2 identified ecological release in the form of density compensation and niche expansion within the bird fauna of a single island. This chapter will test for the presence of ecological release across multiple islands and habitat types.

The aim of this study was to determine whether patterns in species abundance and distribution across Macaronesia relate to genetic differentiation and proposed taxon cycle rankings. Specifically, the objectives of this study were to test whether; (1) Having undergone ecological release, island species will be higher in abundance than mainland counterparts; (2) distribution, abundance, and genetic distance will differ between taxon cycle ranks; (3) abundance and distribution will show a positive or negative linear relationship with species age (Age-Area model; de Moraes Weber *et al.,* 2014) or else show a negative quadratic relationship with age (taxon cycle model; Ricklefs and Cox, 1972; 1978) (Figure 4.1). The results of this study will be discussed in the context of the most appropriate model that fits the distribution and abundance pattern of the avifauna of Macaronesia, relate to previous studies and also relate to species susceptibility to extinction.

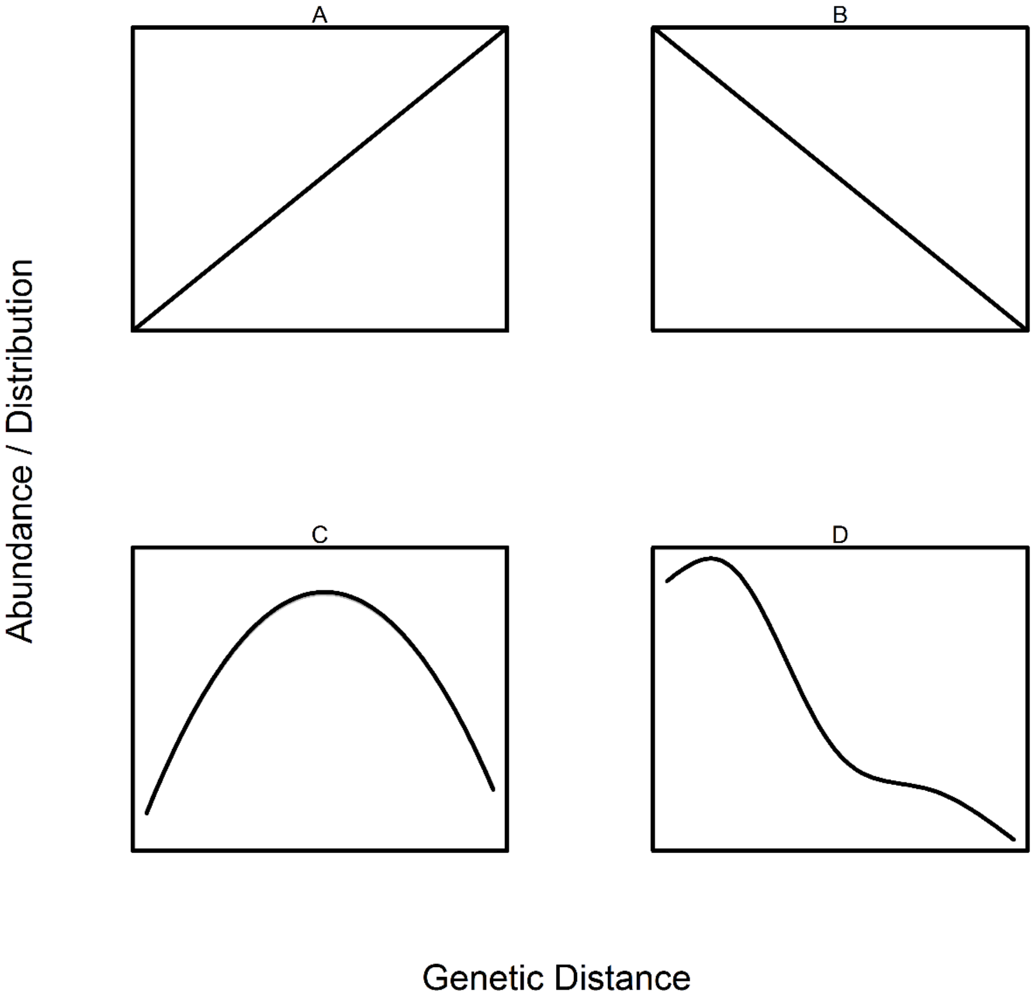

Figure 4.1: Prediction curves for the relationship between genetic distance (Taxon age) and species distribution and abundance; (A and B) Positive and negative linear relationship suggesting that species distribution may increase or decrease with age (Age-Area model; Willis, 1922; Webb and Gaston, 2000; Weber *et al.,* 2014); (C) negative quadratic model, which would show an increase in abundance or distribution with age, followed by a decrease with increasing species specialisation and distribution fragmentation (Taxon Cycle model – Ricklefs and Cox, 1972; 1978); (D) non-linear relationship.

4.2 Methods

4.2.1 Site study

Macaronesia consists of the Canary Islands, Madeira, the Azores, and the Cape Verde Islands. The Canaries consist of seven main islands (situated between 27°37`and

29°25`N, and 13°20` and 18°10`W) with a range of ages increasing East to West from >1m to 20m years old (Dietzen *et al.,* 2008). The Madeiran archipelago (situated between 30°01` and 33°80`N, and 15°51` and 17°16`W) is made up of Madeira, Porto Santo, Ilhas Desertas, and Ilhas Selvagens. The largest of the islands, Madeira, is a volcanic island approximately 5.2 million years old (Zhou *et al.*, 2012). The Azores consist of nine main islands (situated between 36°55 and 39°43`N, and 25º01 and 31º07`W) with ages ranging from 0.25 to 8.12 Myr (Triantis *et al.*, 2010). The Cape Verde Islands (situated between 14°48` and 17°12`N, and 22°40` and 22°22`W) consisting of ten main islands. The age of the Cape Verde Islands range from 5.9 to 25.6 Myr (Duarte *et al.*, 2007) (Figure 4.2).

4.2.2 Study species

Focal species included in this study consist of a focal species and a mainland counterpart for comparison of abundance and distribution. Species pairs for the Azores, Madeira, and the Canary Islands included: Blackbird (*Turdus merula*), Blackcap (*Sylvia atricapilla*), Laurel, and Wood Pigeon (*Columba trocaz / bollii / junionae / palumbus*)*,* Firecrest (*Regulus madeirensis / Regulus ignicapillus*)*,* Goldcrest (*Regulus regulus*), Goldfinch (*Carduelis carduelis*), Chaffinch (*Fringilla coelebs*) Blue Chaffinch (*Fringilla teydea / polatzeki*)*,* Robin (*Erithacus rubecula*)*,* Linnet (*Carduelis Cannabina*)*,* Canary / Serin (*Serinus canaria / Serinus serinus*)*,* Spectacled Warbler (*Sylvia conspicillata*), Grey Wagtail (*Motacilla cinerea*), Blue Tit (*Cyanistes caeruleus / Cyanistes teneriffae*), and Berthelot's / Tawny Pipit (*Anthus berthelotii* / *Anthus Campestris*). These species are represent putatively different taxon cycle stages, exhibiting various degrees of morphological differentiation from their mainland counterparts (e.g. sub-species or species level differences). All 34 species found across the Cape Verde Islands were used in this study, including a range of variation across the taxon cycle including recently introduced colonists and single island endemics (see list in Appendix 4).

4.2.3 Survey data

Data for species distribution and abundance across Portugal, Azores, and Madeira were collected between 2004 - 2010 by the Portuguese Society for the Protection of Birds (SPEA) in 10 x 10km squares. Within each square, 20 points at least 1km apart were surveyed across available habitat types. Bird species were recorded over a 5 minute period at each point. Surveys were conducted between dawn and 11am. Each square was visited twice per year with repeat census carried out at the same points. Data were also collected for the Canary Islands between 1985 - 2002, supplied by the Spanish Society of Ornithology (SEO) Breeding Bird Atlas. Presence of species in 10km squares were collected for all the focal species across the Canary Islands. Data for the Cape Verde Islands were collected by Hazevoet (1995) between 1988 and 1993. Presence and breeding status of each species was recorded in 5km squares. Each square was visited on multiple occasions at different times of the day. As this survey is at a different resolution, the data were analysed separately.

4.2.4 Taxon cycle ranks

Species were assigned a rank along an ordinal scale 1 - 4: rank 1 are recent colonists or introduced species (non-endemic species); rank 2 are subspecies or species endemic to Macaronesia; rank 3 are endemic subspecies or species found on a single group of islands; and rank 4 are single island endemic species (similar to Carrascal *et al.*, 2008; Economo and Sarnat, 2012). All wintering, passage, or occasional species were excluded from the analysis. Rank 1 and 2 species were considered “early” and rank 3 and 4 were considered “late” taxon cycle species for the purposes of this analysis.

4.2.5 Genetic data analysis

Based on available genetic data, a subset of all species across the Azores, Madeira, and the Canary Islands were used to estimate genetic differentiation from mainland counterparts in paired focal taxa as an indication of taxon age. Focal taxa represent species classed at all stages of the taxon cycle. Sequences for the Robin, Blackcap, Canary and Serin, Berthelot’s Pipit and Tawny Pipit, Chaffinch, Blue Chaffinch, Firecrest, Laurel and Wood pigeon, Goldcrest, and Blue Tit were obtained using the NCBI GenBank using BLAST in MEGA6 (Tamura *et al.*, 2013) (see Appendix 3 for BLAST results). Sequences were aligned using a Muscle in MEGA6 (default settings) and trimmed (528bp). Average uncorrected genetic p-distance and corrected Tamura and Nei distance were calculated for each species pair for each island using default settings in MEGA6 (after methods in Dietzen *et al.,* 2006).

4.2.6 Relative abundance and distribution analysis

Species abundance was quantified by calculating the average number of individuals seen per 10km square across each island and within each habitat on Madeira and mainland Portugal. Kruskal-Wallis tests were used to identify differences between island and mainland sites in abundance and distribution. Pairwise Wilcoxon tests were used to compare abundance between taxa pairs (objective 1). Distribution was quantified as the total number of 10x10 km^2 (or 5m squares - Cape Verde Birds) quadrats occupied for each species per islands on which the species is present. The number of points at which a species was noted was also calculated and, along with the quadrat presence, was converted into a percentage of total observations.

4.2.7 Taxon cycle analysis

Kruskal-Wallis tests were used to test for difference in species abundance, distribution, and genetic distance across the 4 taxon cycle ranks based on species taxonomic status (objective 2). Data were analysed collectively for the Azores, Canary Islands, and Madeira and analysed separately for the Azores and Madeira, which had species abundance data. Cape Verde data were analysed separately as they were collected at a different spatial scale. Generalized linear models (GLM) were used to test for the presence of a positive or negative linear trend between species age using genetic distance between species pairs (genetic distance between island and mainland sister taxa) and abundance and distribution (objective 3: Willis, 1922; Webb and Gaston, 2000; de Moraes Weber *et al.,* 2014). All statistical analysis was performed in R (R Development Core Team, 2015). GLM with quadratic terms was used to test the prediction that under the taxon cycle (objective 3), species will increase in distribution and abundance with age, using a broader range of resources, and then decreasing in abundance and distribution as species become specialised and fragmented in distribution. Semi-parametric generalized additive models (GAM) were used to test the relationship between lineage age, abundance, and distribution (objective). GAM were fitted using the R package {mgcv} (Wood, 2006). GAMs were applied here as they provide a more flexible model that would allow investigation of non-linear relationships (Zuur, 2007). Alternative models were compared using corrected AIC (corrected for small sample size) and considering measures of explanatory power.

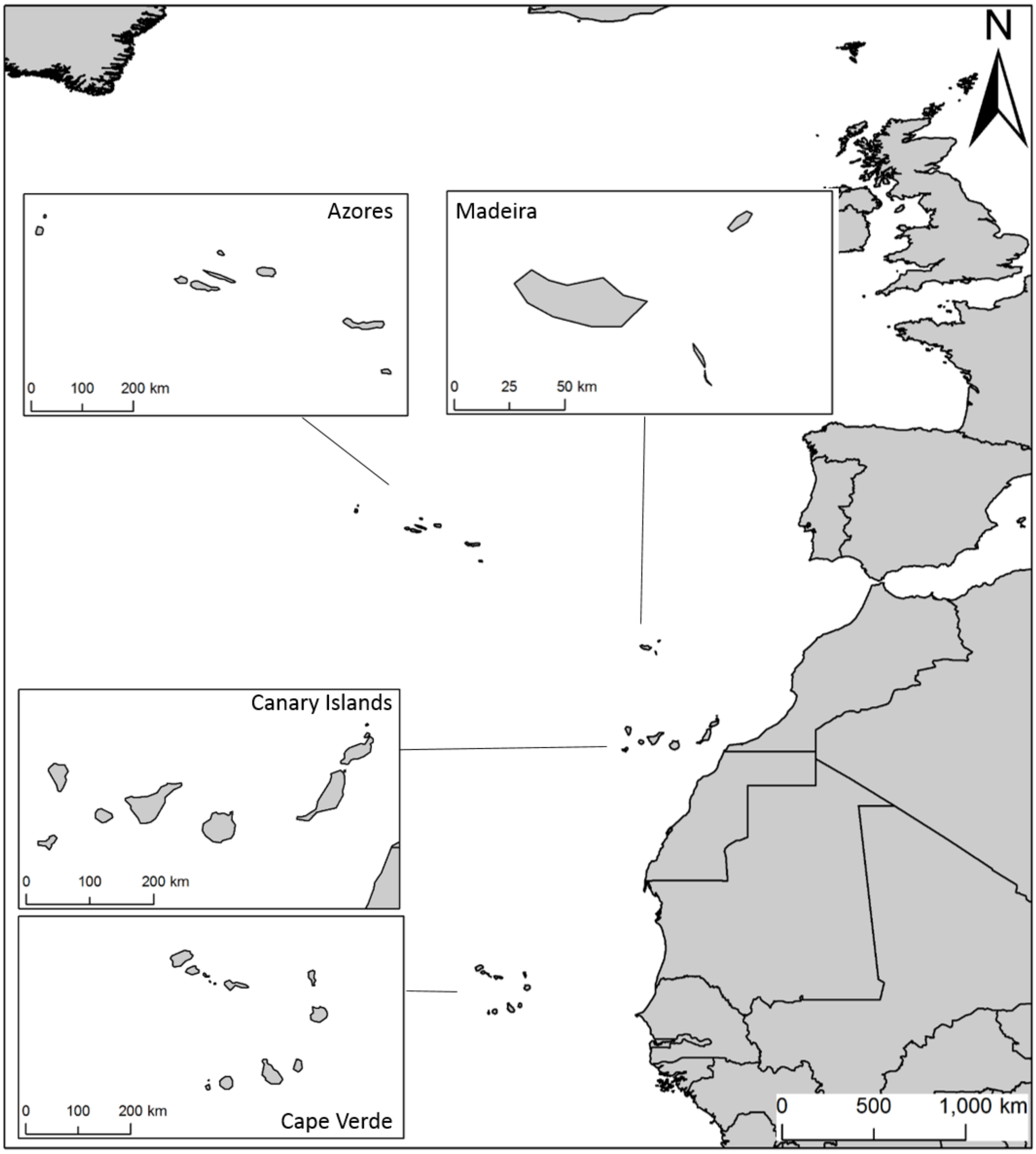

Figure 4.2 Map of Macaronesia with archipelagos in boxes.

4.3 Results

4.3.1 Density compensation, distribution, and abundance patterns (Azores and Madeira)

Significant differences in abundance were shown for all species when compared between the Azores, Madeira, and mainland Portugal (Kruskal-Wallis, $P < 0.05$). The Blackcap, Chaffinch, Blackbird, Grey Wagtail, and Berthelot's Pipit were found frequently at significantly higher abundances on islands than their mainland counterparts (Wilcoxon test, $P < 0.05$; Figure 4.3). The Firecrest, Robin, Canary, and Wood Pigeon were also found at significantly higher abundance on some of the islands (Wilcoxon test, $P < 0.05$; Figure 4.3). The Linnet, Goldfinch, and Goldcrest were not observed at significantly higher abundances on Madeira and the Azores than on the mainland (Wilcoxon test, P > 0.05; Figure 4.2).

Significant differences were observed when abundance was calculated for each habitat type for Madeira. Blackcap, Chaffinch, Blackbird, Grey Wagtail, Firecrest, Robin, and Canary were found to be significantly higher in agriculture and forest in comparison to mainland counterparts (Wilcoxon test, P < 0.05; Figure 4.4). With the exception of the Firecrest and Robin, these species were also found at significantly higher density in urban habitats (Wilcoxon test, P < 0.05; Figure 4.4). Blackbird and Robin were found to be significantly higher in abundance in bush, whereas Blackbird, Linnet, and Berthelot's Pipit were found at higher abundance in in Pasture, and Blackcap and Grey Wagtail in wetland on Madeira compared to the same habitats on the mainland (Wilcoxon test – P < 0.05; Figure 4.4).

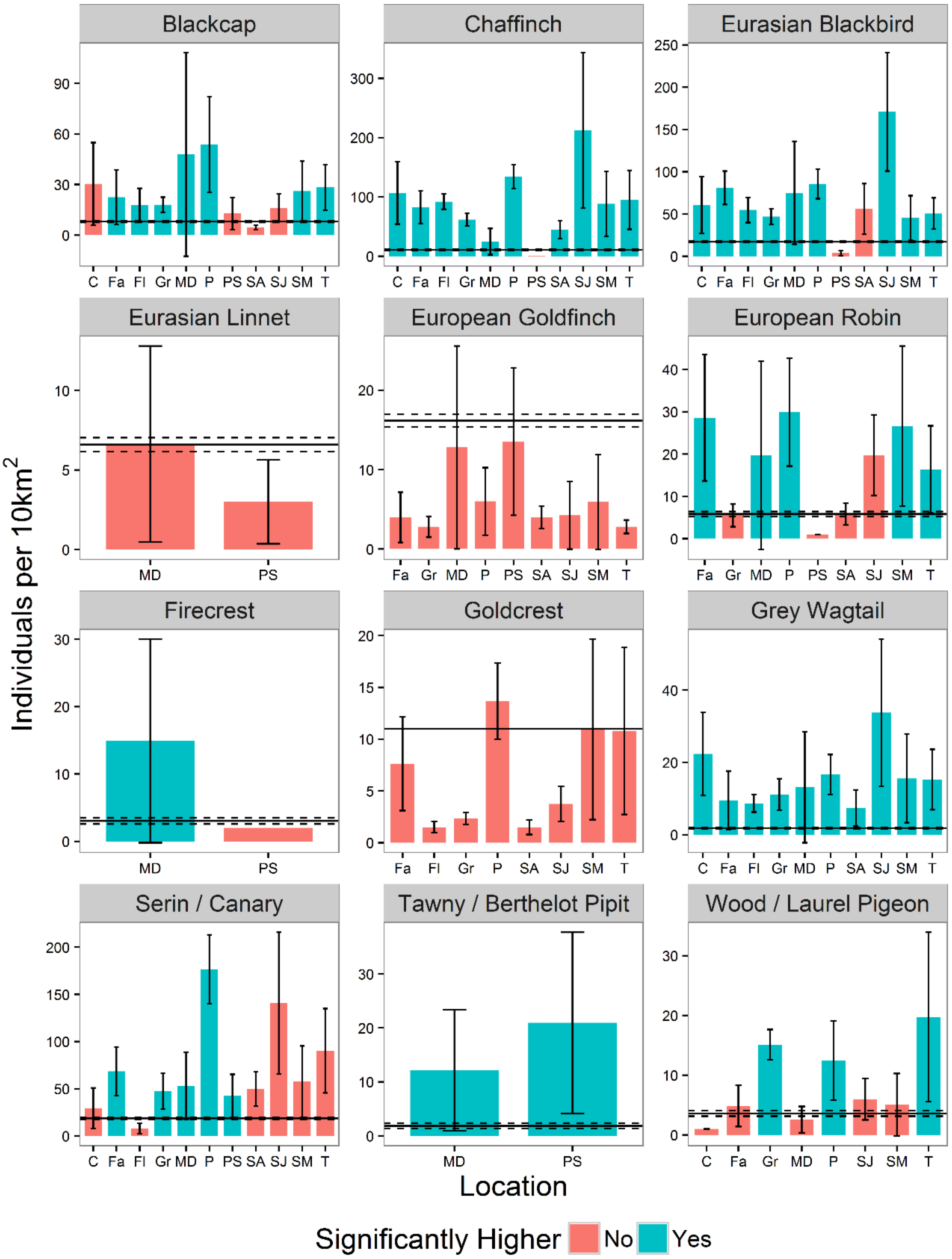

Figure 4.3: Average abundance (12 species - mean individuals per km^2 ± SD) across the Azores and Madeira. Significant differences were shown across sites for each species (Kruskal-Wallis, $P<0.001$). Significantly higher abundance than mainland counterpart is shown in blue (Pairwise Wilcoxon tests - $p<0.05$). Mainland abundance = black line, 95% confidence interval = black dotted line. Site codes: C = Corvo, Fa = Faial, Fl = Flores, Gr = Graciosa, MD = Madeira, P = Pico, PS = Porto Santo, PC = Portugal Continental, SA = Santa Maria, SJ = Sao Jorge, SM = Sao Miguel, T = Terceira.

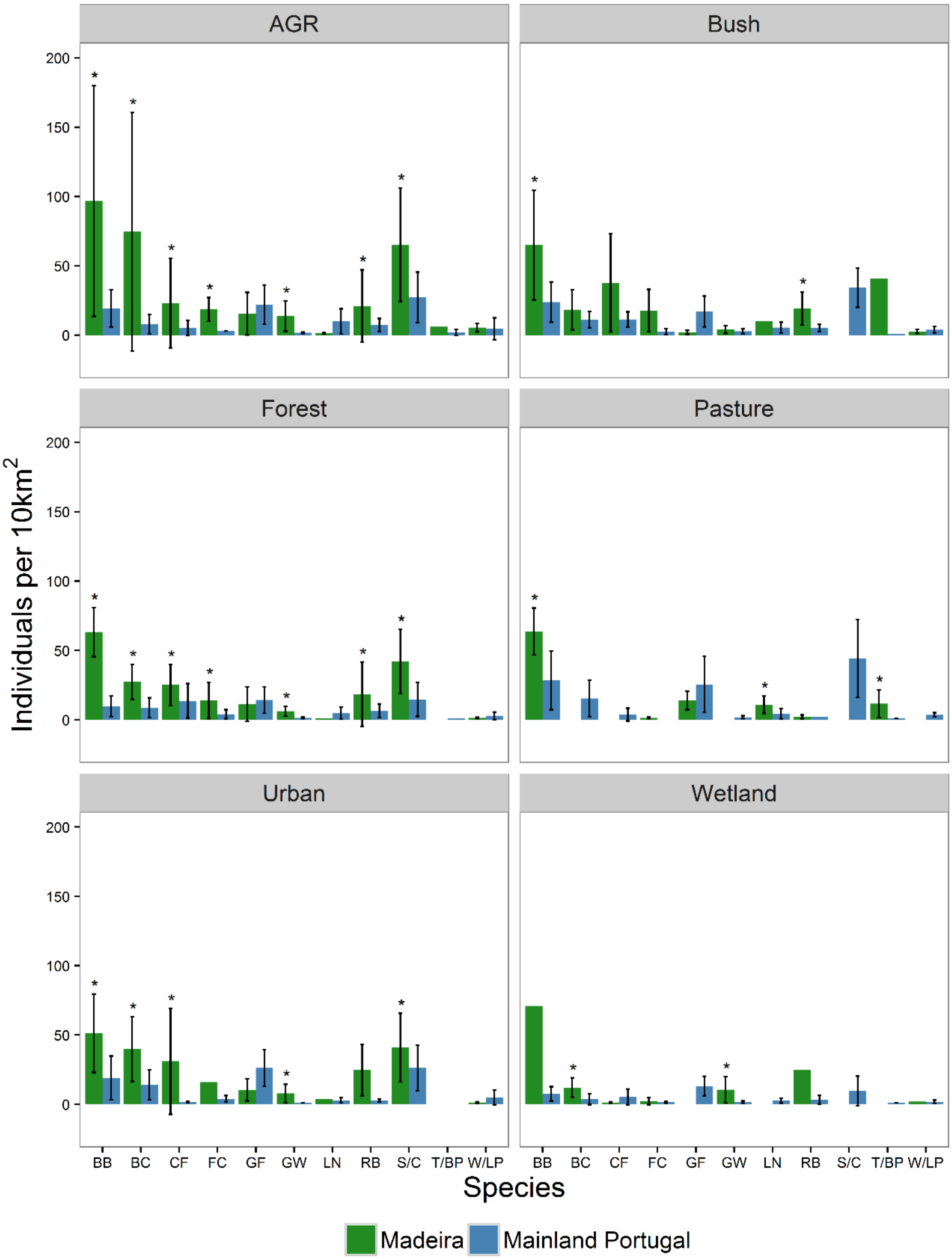

Figure 4.4: Average abundance across mainland Portugal and Madeira split by dominant habitat type (11 species – mean individuals per km^2 ± SD). Significantly higher abundance than mainland counterparts is shown by an * (Wilcoxon test - $p<0.05$). Site codes: MD = Madeira, PC = Portugal Continental. Species codes: BC = Blackcap, CF = Chaffinch, BB = Blackbird, LN = Linnet, GF = Goldfinch, FC = Firecrest, GW = Grey Wagtail, RB = Robin, S/C = Serin / Canary, T/BP = Tawny / Berthelot's Pipit, W/LP = Wood / Laurel Pigeon.

4.3.2 Taxon cycle ranks (Madeira and Azores)

Across Madeira and the Azores, no significant difference was observed in the percentage of points where a species was present (distribution) between taxon cycle rank (Kruskal-Wallis, $X^2 = 5.71$, df = 3, P = 0.13. Figure 4.5A) or stage (Wilcoxon signed-rank, W = 1044.5, p = 0.72. Figure 4.5B). However, a higher median percentage of points where a species was present was observed in the early stage species compared to the later stage species across Madeira and the Azores (Figure 4.5A and B). A significant difference in percent change compared to mainland counterparts was found between taxon cycle rank (Kruskal-Wallis, $X^2 = 8.38$, df = 3, P = 0.04. Figure 4.5C) and stage (Wilcoxon signed-rank, W = 756, p = 0.01. Figure 4.5D). The highest increase was observed in the later stage species, specifically those in stage 3 (Figure 4.5C and 4.5D), the lowest percentage increase was shown in species placed in rank 4.

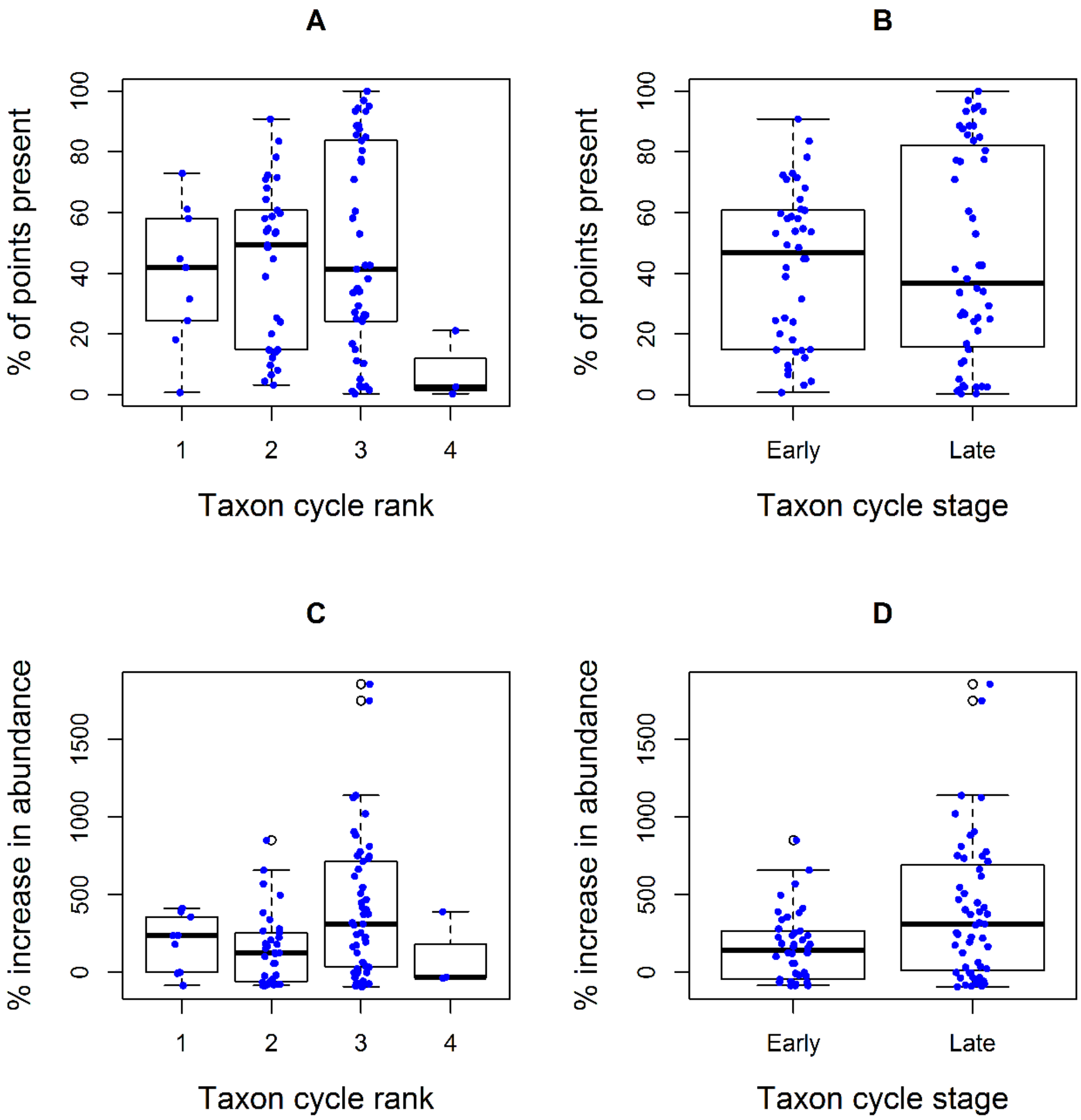

Figure 4.5: Distribution and abundance of species across the Azores and Madeira across taxon cycle rank (1-4) and stage (Early and Late). A). Percentage of points present across taxon cycle rank and B). Stage. Both A and B not significant ($P > 0.05$) C). Percent increase in abundance from mainland counterpart across taxon cycle rank and D). Stage. Both C (Kruskal-Wallis, $X^2 = 8.38$, df = 3, $P = 0.04$) and D (Wilcoxon signed-rank, $W = 756$, $p = 0.01$) showed a significant difference between ranks and stage respectively.

4.3.3 Species distribution patterns across Macaronesia

Canary Islands, Azores, and Madeira.

No significant difference was found in total distribution (percentage of total occurrence in each island group occupied) when comparing across the taxon ranks or between early and later stage species (Figure 4.6 A-B, $P > 0.05$). However, species at higher ranks or in the late stage of the taxon cycle were distributed less widely, present in fewer quadrats across the three island chains (Figure 4.6). No significant difference was observed in the average percentage of quadrats occupied per island across the taxon ranks (Kruskal-Wallis, $X^2 = 5.04$, df = 3, P = 0.169) with the highest average island occupancy in rank 1 and 3 and the lowest in rank 4 (Figure 4.6 C and D).

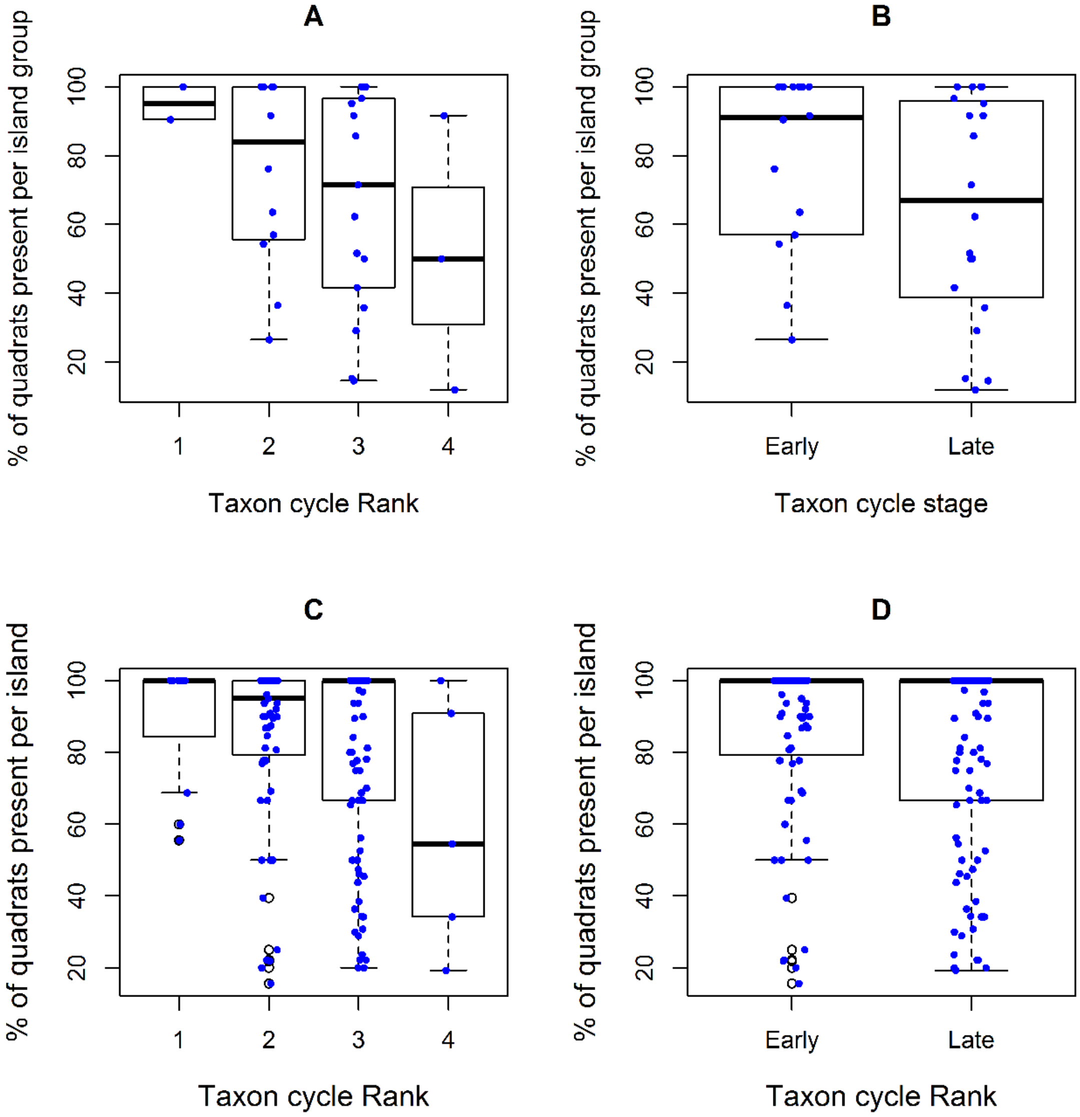

Figure 4.6: Species distribution across Azores, Madeira, and the Canary islands. Percentage of quadrats present per island chain separated by taxon cycle rank (A) and separated into early (rank 1 and 2) and late (rank 3 and 4) stage species (B). Percentage of each island present per taxon cycle rank (C) and stage (D).

4.3.4 Cape Verde Islands

No Significant difference was shown in distribution across the Cape Verde Islands between taxon cycle rank (Kruskal-Wallis, $X^2 = 4.8$, df = 3, P = 0.187) and early and late stage species (W = 144, p = 1) (Figure 4.7 A and B). However, the lowest distribution was shown in rank 4 species (Figure 4.7A). Little difference was shown between the stages in species distribution across the Cape Verde Islands (Early stage distribution, mean = 18.03, Median = 17.27; Late stage, mean = 18.29, median = 18.18) (Figure 4.7B).

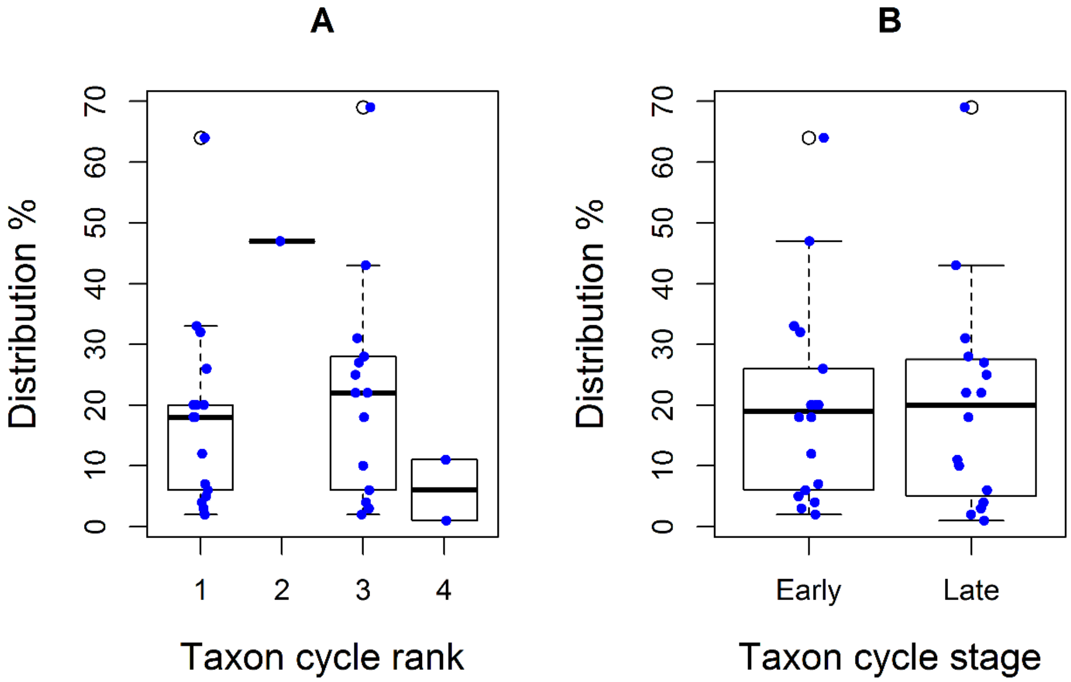

Figure 4.7: Distribution (Percentage of total 5x5km squares present across the Cape Verde Islands) between across taxon cycle rank (A) and early (Rank 1 and 2) and late (Rank 3 and 4) stage species (B).

4.3.5 Taxon cycle, genetic distance, and lineage age

A significant positive correlation was found between in genetic distance and taxon cycle rank (Spearman Rank Correlation, rho = 0.63, $p < 0.001$). A significant difference in genetic distance between species pairs (island and mainland population) was also shown across the 4 taxon cycle ranks for Madeira, Canary Islands, and the Azores (Kruskal-Wallis, $X^2 = 35.2$, df = 3, $p < 0.001$; Figure 4.8). A post-hoc test showed significant differences between each rank ($p < 0.05$), with median genetic distance increasing through the ranks (Median; 1 = 0.0003, 2 = 0.002, 3 = 0.026, 4 = 0.052).

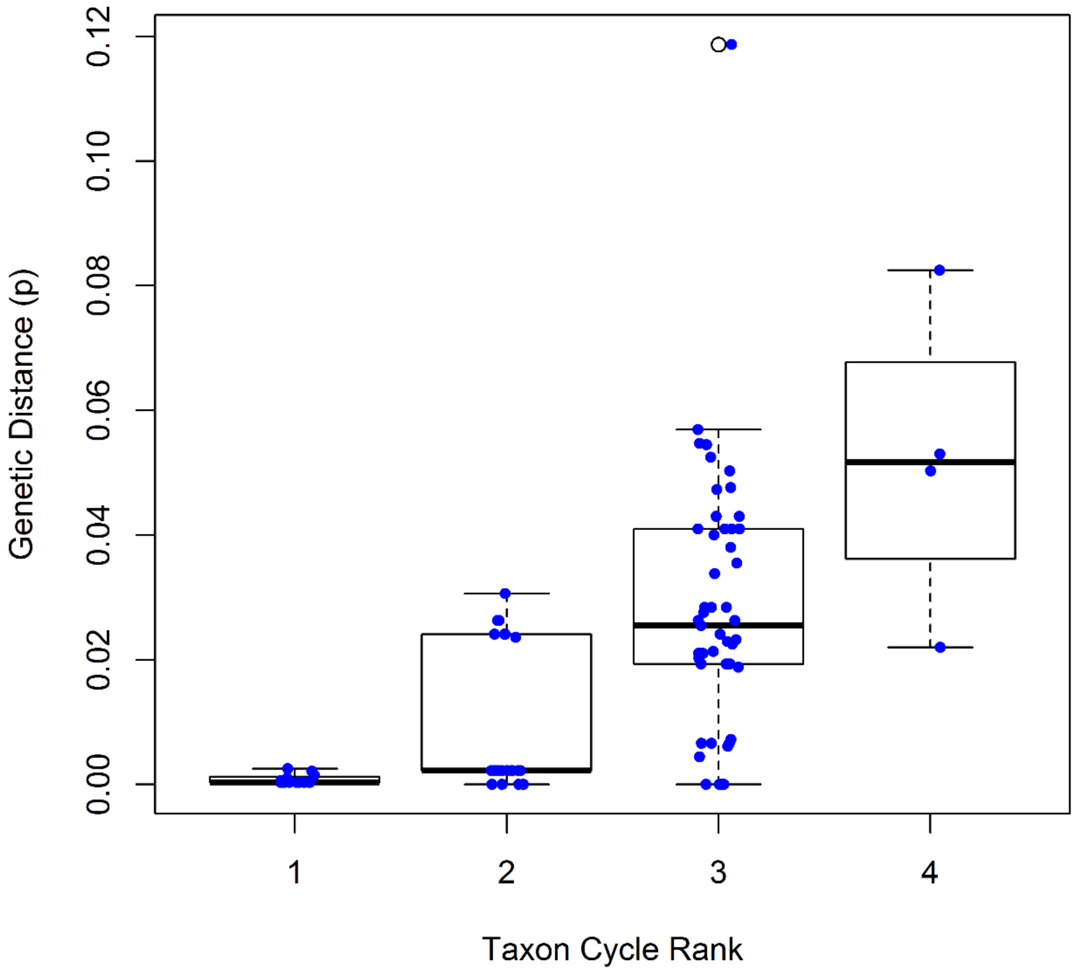

Figure 4.8: Genetic distance (p-distance between each species pair per island) between the predicted taxon cycle ranks.

To evaluate the relationship between species abundance and distribution and the time since divergence (measured using genetic distance), a number of alternative models were tested (Table 4.1). There were two measures of distribution (% of quadrats occupied and % of points present) and two measures of species abundance (Individuals per 10km^2 and % increase from mainland abundance), the GAM models with cubic splines provided the best fit and highest level variance or deviance explained (Table 4.1). These models identified non-linear trends in genetic distance or divergence time in relation to abundance and distribution, with an initial increase in both distribution (Figure 4.9: A and B) and abundance (Figure 4.9: C and D) with an increased in genetic distance, which is then followed by a decline for all variables with increasing genetic distance.

Table 4.1: Model evaluation for the prediction of species abundance and distribution using genetic distance (p-distance) between species pairs as a measure of lineage age. R^2 and pseudo R^2 calculated for regression and GLM, deviance explained calculated for GAM models.

Term	Model Type	AICc	R^2 (Deviance explained)	Significant
Distribution (%) ~ Genetic distance (p) (n= 89)	**Linear regression**	**829.71**	**0.162**	**<0.001**
	GLM (with quadratic function)	831.66	0.174	<0.001 0.624
	GAM (default isotropic smoother)	831.71	0.162 (17.1)	<0.001
	GAM (Cubic regression splines)	**832.94**	**0.181 (21.5)**	**<0.001**
Points present (%) ~ Genetic distance (p) (n=44)	Linear regression	425.70	0.000	0.535
	GLM (with quadratic function)	421.09	0.156	0.707 0.011
	GAM (default isotropic smoother)	417.36	0.268 (33.2)	0.006
	GAM (Cubic regression splines)	**413.40**	**0.334 (39.4)**	**<0.001**
Species abundance ~ Genetic distance (p) (n=44)	Linear regression	465.67	0.048	0.082
	GLM (with quadratic function)	555.12	0.308	0.631 <0.001
	GAM (default isotropic smoother)	448.26	0.440 (48.8)	<0.001
	GAM (Cubic regression splines)	**446.40**	**0.466 (51.4)**	**<0.001**
Increase in abundance from mainland (%) ~ Genetic distance (p) (n=44)	Linear regression	648.55	0.139	0.008
	GLM (with quadratic function)	642.85	0.300	0.009 0.006
	GAM (default isotropic smoother)	644.77	0.269 (30.5)	0.002
	GAM (Cubic regression splines)	**642.11**	**0.351 (40.8)**	**<0.001**

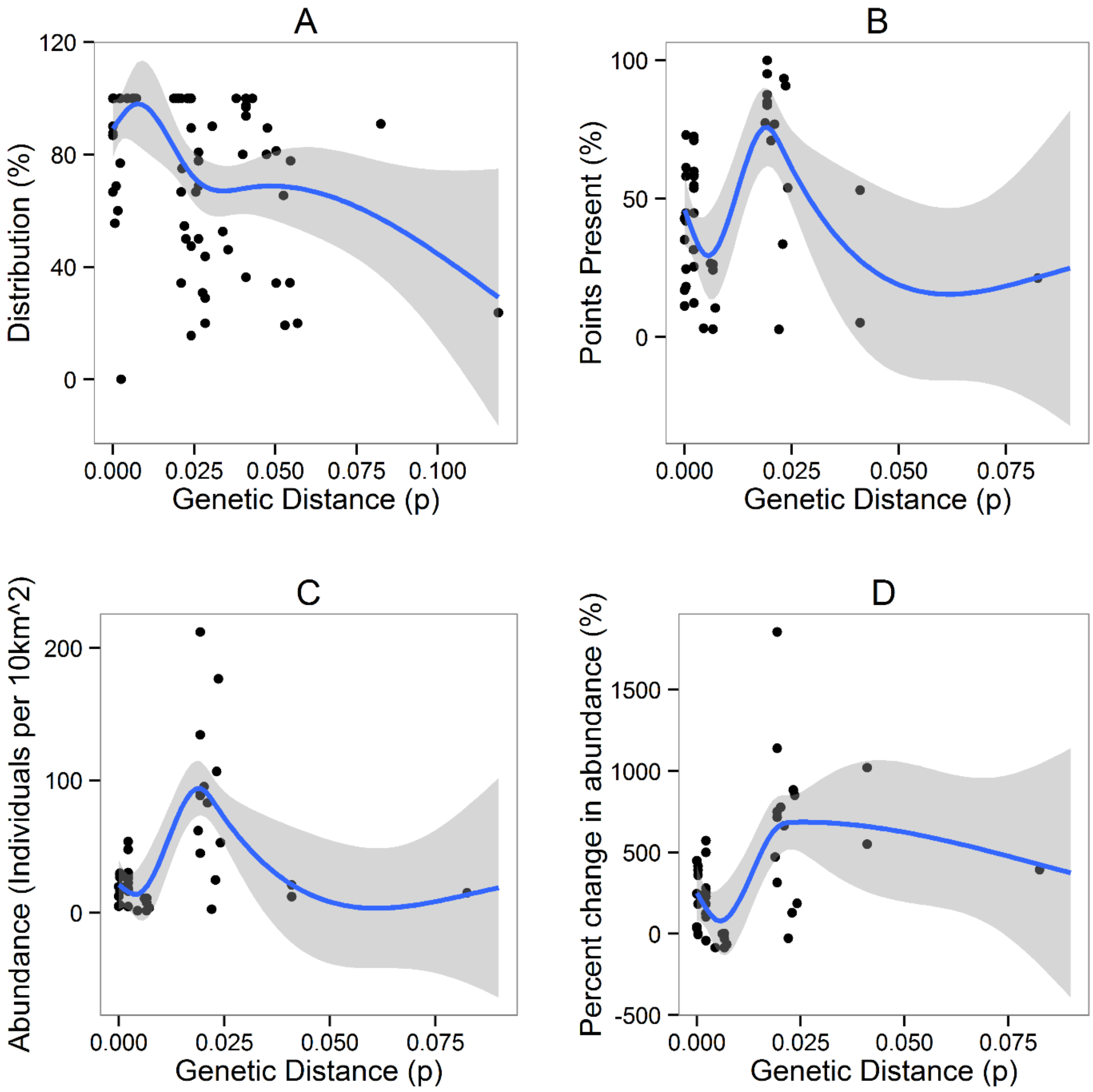

Figure 4.9: Plots of the GAM relationship between genetic distance and species distribution (A and B) and abundance (C and D).

4.4 Discussion

4.4.1 Relationship between species age and their distribution and abundance

A significant non-linear relationship between species arrival time (genetic distance), distribution, and abundance was found in the birds across the Atlantic islands. Models for both distribution and abundance show a complex, consistent pattern of increase then decrease with lineage age (genetic distance; prediction Figure 4.1C). This is consistent with predictions for the taxon cycle (Wilson, 1961; Ricklefs and Cox 1972; 1978) and is similar to recent studies that have also found a relationship between lineage age, and distribution and abundance, in the form of expansion and contraction cycles (Ricklefs and Bermingham, 1999; Jonsson *et al.,* 2014). The increase in species abundance compared to mainland species also suggests an increase with age followed by a decrease. This is consistent with expectations under ecological release with higher island abundances due to density compensation (MacArthur *et al.,* 1972) and the taxon cycle hypothesis with a decline in overall abundance with lineage age (Ricklefs and Bermingham, 1999). This study provides the first test and evidence of the taxon cycle across Macaronesia using modern approaches. For all models shown in figure 4.9, there is likely to be an effect from the few species with high genetic differences. These were not excluded from the analysis as they are not anomalies but represent older island species that would be expected to be in the late stages of the taxon cycle.

4.4.2 Taxon cycle rank

Species were placed in four taxon cycle ranks based on their taxonomic status, ranging from recent colonists to island endemics (similar to Carrascal *et al.,* 2008; Economo and Sarnat, 2012; Carstensen *et al.,* 2013). This study found a linear increase in genetic distance from ranks 1-4, consistent with assumptions underlying the taxon cycle hypothesis. Ricklefs and Bermingham (1999) found a similar correlation between genetic distance and taxon cycle rank. These ranks were then used to identify differences in distribution and abundance across the different taxon cycle stages (as proposed by Wilson, 1961; Ricklefs and Cox 1972; 1978). Across three island groups (Madeira, Azores, and Canary Islands), species were found less frequently with a smaller proportion of the island occupied, and lower presence at point counts at the later stages of the taxon cycle ranks. The highest species abundance were found in species at the early stages of the taxon cycle. However, the largest average increase in abundance compared to the mainland counterparts was shown in the 3 rank followed by a decrease compared to the mainland in rank 4 species. Overall, the pattern observed for species distribution and abundance in relation to taxon cycle ranks provides some support for previous studies and provides the first test and evidence for the presence of the taxon cycle across Macaronesia using modern tools (Ricklefs and Bermingham, 1999; 2002; Ricklefs and Cox, 1972; 1978; Economo and Sarnat, 2012; Johnson *et al.,* 2014). Evidence for the presence of the taxon cycle across Macaronesia suggest that cycles of expansion and contraction and associated microevolutionary changes may have played a role in shaping the distribution and abundance of bird fauna of Macaronesia. An initial increase and then decrease in distribution in stage 4 was also observed in Cape Verde species across taxon cycle rank, which is consistent with taxon cycle predictions (Ricklefs and Cox, 1972; 1978), although this difference was not observed when the early stage (rank 1 and 2) and late stage (rank 3 and 4) species were grouped. The Cape Verde aspect of this study provides mixed support for the taxon cycle and would benefit from genetic data to provide support for the taxon cycle rank and add a temporal scale to this area of the study. Ricklefs and Bermingham (2002) acknowledge that the island size, distance between islands, and distance to the mainland, may effect patterns in species distribution needed to recognise the phases of the taxon cycle. A closer examination of each islands environmental characteristics, species composition, and interactions between the two in relation to how well each island group fit the taxon cycle hypothesis, would be an interesting extension of the current study (Steinbauer, 2017).

4.4.3 Ecological release - Density compensation

Across the study, 52 species comparisons out of 94 demonstrated significantly higher abundances on islands compared to mainland counterparts. Nine of the twelve species studied were found at significantly higher abundances on at least one island in the Azores and Madeira compared to mainland. This is consistent with predictions for ecological release and is similar to previous empirical results for island bird fauna (i.e., density compensation, see MacArthur *et al.,* 1972). In contrast, there were 42 instances of non-significant differences with 15 occasions with higher abundance and 27 with lower abundance on islands compared to the mainland population.

Positive density compensation has been demonstrated in a number of taxa (Birds: MacArthur *et al.,* 1972; Primates: Peres and Dolman, 2000; Lizards: Case, 1975; Herpetofauna: Rodda and Dean-Bradley, 2002; Microbial wood-webs: McGrady-Steed & Morin; 2000). However, not all species across studies have identified higher island densities compared to mainland populations (e.g., George, 1987; Vassello and Rice, 1982). Likewise, three species were found with similar abundance on islands compared to mainland Portugal (Linnet, Goldcrest, and Goldfinch). Two of the species that were not higher in abundance on island across Macaronesia had a congeneric species within its island range, which may have limited their response to the novel island ecosystem.

However, there are many factors that may affect population density, which could override the effect of low species number on islands or mask the presence of density compensation (Wright, 1980). It has been suggested that the pattern of ecological release could be incorporated into other evolutionary processes, such as the taxon cycle, where species undergo phases of expansion and contraction over time (Wilson, 1961; Ricklefs and Bermingham, 2002), complicating a clear expectation for every species pair in all circumstances.

Previous mainland-island comparative studies have been criticised for various deficiencies including small sample size, inequitable variation in climate, habitat type, and species (Wright, 1980; McGready-Steed and Morin, 2000). In this study, these shortcomings were overcome through comparison of multiple island chains, including only comparable climates, habitat types, and species pairs (same or closely related species on the mainland and islands). Identifying a signal of the taxon cycle has previously been difficult to test empirically. However, advances in molecular and statistical tools and the availability of large datasets have improved our ability to investigate patterns in species distributions, diversity, and evolutionary processes (Economo and Sarnat, 2012).

Understanding the traits and conditions that support or inhibit ecological release could be beneficial to understanding the response of invasive species to novel environments (Ricklefs and Bermingham, 2002). Further research in this area could also identify the timing of species colonization in relation to each other and provide a quantification of possible interaction (pathogen and parasite transfer / switching) and interspecific competition, both currently and historically. Further models of both ecological release and the taxon cycle could also factor in island area, age, and distance to mainland and nearest island. The patterns of distribution and abundance of a species and associated traits as they pass through taxon cycle such as restricted distribution, low abundance and habitat specialism are also correlates of extinction risk supporting the importance of understanding the taxon cycle (Purvis *et al.,* 2000; O'Grady *et al.,* 2004).

4.4.4 Conclusion

The results from this paper provide some support for the presence of both ecological release and the taxon cycle across the Macaronesian bird communities. Higher abundances were observed for many of the species across the Azores and Madeira compared to their mainland counterparts, consistent with the density compensation element of the ecological release theory. Patterns of distribution and abundance across species rank and with species age identified in this paper were also consistent with expectations from the taxon cycle supporting the theory that taxon cycles may be important in shaping the distribution and abundance of insular taxa.

Chapter 5. Habitat association and population size of the Madeira Firecrest (*Regulus madeirensis*)

Abstract

The assessment and classification of species limits due to the development of new genetic and acoustic analysis tools to identify distinct taxonomic units is likely to result in an increase in threatened or endangered species with smaller ranges and populations sizes. Information is often lacking for such newly recognised species, yet such information is essential for conservation and management. This chapter provides an assessment of population size and habitat association in a newly recognised species, the Madeira Firecrest (*Regulus madeirensis*). Detailed distance sampling and ecological data were used in conjunction with Madeira bird atlas data for this study. The population size of the Madeira Firecrest was estimated to far exceed the threshold of the IUCN category 'vulnerable' (10,000 individuals) with an estimate of 96,700 individuals (95% CI: 66,383 and 169,454). The distribution and abundance of the Firecrest was strongly linked with the presence of laurel and heath forest on Madeira, with a significant percentage (79.7%) of the population found in these two habitat types. Much of the indigenous forest has been lost on Madeira, but remaining native forest habitat is now protected. The results of this study are discussed in the context of the conservation and management of the Madeira Firecrest.

5.1 Introduction

The loss of biodiversity due to anthropogenic causal factors is recognised as one of the predominant conservation issues of our time and it is estimated that the extinction rate of species is up to 1,000 times greater than that which is independent of human activities (Pimm *et al.,* 1995). A primary function of the IUCN Red List is to provide an evidential assessment of risk of extinction for species (IUCN, 2015), yet data deficiency and cryptic species present significant challenges to this approach. Thus, data limitation is recognized for a large proportion of species (Brooks *et al.,* 2006). Also, cryptic and recently recognised species constitute a special case since their conservation status may not be well understood and relevant data may be difficult to assemble or collect, yet cryptic species are thought to be common across a variety of taxa and geographical regions (Pfenniger & Schwenk, 2007). This contributes to a paradox, such that organisms which are the most rare and endangered tend to be the hardest to study because of their scarcity, and thus are less likely to be represented by data (Norris & Pain, 2002), particularly for island endemics (Kier *et al.,* 2009).

The recognition of new species is increasing rapidly with the development of new tools to identify distinct taxonomic units (Köhler *et al.,* 2005; Sangster, 2009). These tools (e.g. molecular genetics, acoustic analysis) have informed reinterpretation of species limits, leading to a larger number of less inclusive species units (Agapow *et al.,* 2004). This increase in biodiversity has been driven by the elevation of known subspecies to species level rather than new discoveries (Isaac *et al.,* 2004). The identification of such "taxonomic units for conservation", defined as a discrete population or populations comprised by a single species or variant thereof, has been recognised as conceptually and legally important in the context of conservation monitoring and management (Frankham *et al.,* 2010).

Taxa that are newly recognised as species present a special problem in conservation biology. For example, species with a wide geographical range might be considered separate subspecies or merely populations of the same species, as is common in groups lacking obvious morphological traits, such as in amphibians (Köhler *et al.*, 2005). These species can also be classified as cryptic (Bickford *et al.,* 2007). However, if a discrete population is newly recognised as a distinct species, there is immediate recognition that it is found in a smaller geographical range, and that the finite, global population size may or may not be known at all (Isaac *et al.,* 2004). A recent study of the endangered northern sportive lemur (*Lepilemur septentrionalis*) concluded that one of four previously described subspecies was a separate species in its own right; however, because of this designation, the new species had no legal protection, a restricted range, and small population size (Ravaoarimanana *et al.,* 2004). This phenomenon has occurred in diverse vertebrate taxa: including birds (Lohman *et al.*, 2010; Sangster, 2009), primates (Isaac *et al.,* 2004), and amphibians (Bickford *et al.,* 2007; Meegaskumbura *et al.,* 2002).

Taxonomic inflation, therefore, is likely to result in an increased number of threatened and endangered species as species' ranges and population size decline (Agapow *et al.,* 2004), resulting in a significant challenge for conservation management. To mitigate this challenge, one approach would be to manage ecological and anthropogenic factors that influence density and distribution patterns in these rare species (Agapow *et al.,* 2004). However, for many species there remain insufficient data for a scientifically informed conservation management plan and, as a consequence, species management and conservation may not be efficiently implemented (Kansky and Knight, 2014). The Madeira Firecrest (*Regulus madeirensis*) provides an example of a cryptic, polytypic, recently recognized island endemic (Clarke, 2006; Sangster *et al.*, 2005). The Madeira Firecrest has been treated as a separate species due to differences in morphology, vocal signals and genetic divergence (Päckert *et al.,* 2001, 2003; Sangster *et al.*, 2005) yet, while it is categorized as IUCN Least Concern, there is limited data on habitat association, population size, and susceptibility to disturbance for the Madeira Firecrest (del Hoyo *et al.,* 2006). Assessment of these factors is imperative to inform conservation management.

The aim of this paper is to conduct the first quantitative estimate of population size and habitat use of the Madeira Firecrest. Specifically, the objectives of this study were (1) Identify the spatial pattern of density to provide the first quantitative estimate of population size, (2) assess the influence of habitat disturbance on species presence and (3) identify habitat hotspots. The results will be discussed in relation to using this method to inform IUCN status designation for newly recognized, data deficient species and, specifically, in the context of management of the Madeira Firecrest.

5.2 Methods

5.2.1 Study area

Madeira is a volcanic island approximately 5.2 million years old located in the eastern Atlantic (Jones *et al.,* 1987) (Figure 1.1). Madeira has an area of 742km^2 with a maximum elevation of 1861m along a mountainous central ridge (Jones *et al.,* 1987). The island consists of a number of habitat types including agriculture, urban, coastal, heath, upland, indigenous forest, and exotic forest (Jones *et al.,* 1987*;* Oliveira *et al.,* 2004*)*. Indigenous forest on Madeira is the Laurisilva or laurel forest that once covered most of the island and is considered a relict forest type (Clarke, 2006; Jones, 1988; Oliveira *et al.,* 2004). Due to a combination of habitat loss, degradation, and fragmentation as a result of clearance for agriculture and cattle grazing, the laurel forest now covers around 15% or

16,000ha representing around 20% of Madeira's surface area (Fernandez-Palacios *et al.,* 2011; Marrero *et al.,* 2004).

5.2.2 Focal species

The Madeira Firecrest is one of six species in the genus *Regulus* (Hoyo *et al.,* 2006). Globally, all *Regulus* species are categorised as being of Least Concern status (IUCN, 2016). The Madeira Firecrest is locally common in some habitats on Madeira, and previous census estimates are >10,000 individuals (IUCN Red List, 2015; Oliveira *et al.,* 2004). However, the extent to which the endemic Madeira Firecrest population meets or exceeds this IUCN Least Concern threshold of 10,000 individuals is critical. The most recent population estimate is more than a decade old (Sangster *et al.,* 2005). Recent contraction of laurel forest, due to introduced *Eucalyptus* plantations, is noted as a particular point of conservation concern that could affect breeding success of Madeira Firecrest (Hoyo *et al.,* 2006). Finally, while the Madeira Firecrest is an endemic species, there is no specific management or conservation initiative devoted to the species (Oliveira *et al.,* 2004). Thus, there is a clear imperative for an updated estimate of population status for the Madeiran firecrest.

5.2.3 Data collection

Distance sampling

Data on Madeira were collected between March and June during the breeding season over a four week period in 2008, 2010, and 2011. Density data were collected using a point transect distance sampling method (Buckland *et al.,* 2001). A total of 55 point transects were conducted resulting in 584 census points. Transects locations were stratified to include all major habitats types on Madeira. The start point of each transect was chosen randomly (using a stopwatch). Habitat types sampled were categorised according to the predominant types occurring on Madeira laurel forest (*Laurus azorica* and *Ocotea foetens),* exotic forest (*Pinus pinaster* or *Eucalyptus globules*), mixed forest (mixture of exotic and indigenous tree species), agriculture, upland (high altitude regions not dominated by forest), residential (evidence of human presence), and coastal (Jones *et al.,* 1987; Oliveira *et al.,* 1999).

At each census point, the percentage cover of each habitat type was estimated and the dominant habitat type was recorded within a 30m radius of the point (Jones, 1988). Surveys were conducted between 07:00 and 11:30 to coincide with peak activity levels (Bibby *et al.,* 1999; Buckland *et al.,* 2008). However, surveys were not conducted during inclement weather. Point counts were positioned systematically at intervals of 200m and conducted over 4-minute periods. A minimum of 50 points per habitat type were sampled, consistent with the methods of Buckland *et al*. (2001) and Bibby *et al.* (1998). Where points were positioned along paths, roads, or watercourses, points were positioned 10-30m perpendicular to the transect to avoid edge effects (Lee and Marsden, 2008). Birds in flight were ignored unless their original position (i.e. the point of alighting) could be identified. However, birds disturbed or flushed before the counts were recorded as present. Point counts were conducted immediately after arrival, as the use of a settling down period has been identified as having a detrimental effect on the number of contacts. Distances to each contact were measured using a range finder (Bushnell Yardage Pro) and the method of contact recorded by sight (Si) or sound (So). The contacts identified by sound were placed in distance bands if an accurate distance could not be taken due to the likelihood of error in the estimation. The bands used were 0-10, 11-30, 31-100, and >100m. In addition, the position of the contact observed within the canopy was also noted (Ground, Low, Mid, and High). The presence of disturbance was also noted in the laurel and heath forest with the occurrence of exotic forest species (Pine / Eucalyptus) or agriculture exceeding 10% at each point used as an indication of anthropogenic disturbance.

Madeira breeding bird atlas

Data from a systematic survey of Madeira was provided by the Parque Natural da Madeira, conducted over three breeding seasons from 2009 – 2011 (Atlas das Aves do Arquipélago da Madeira, 2009). These data were used to identify trends in species presence and habitat use across Madeira and used in conjunction with finer scale density estimates for individual habitat types. The Madeira archipelago was surveyed within a grid system composed of 291 2km^2 quadrats, 181 on the main island Madeira. Each quadrat was surveyed at least once (Atlas das Aves do Arquipélago da Madeira, 2009). Each transect lasted 1-hour, split into six 10-minute increments and were walked at a constant speed (2.5-3km/hour) using a GPS and a stopwatch. During each of the 6 transect increments, the total number of individuals observed, habitat type (listed in

Appendix 1) and any indications of breeding were noted. These habitat types have been placed into the broader habitat types defined in the distance sampling survey for the purpose of this analysis (Habitat descriptions in appendix 1 were aligned to habitat description in the distance sampling survey). Surveys were conducted 3-hours after the first hour of sunrise and the three hours before the hour of sunset to coincide with peaks in bird activity (Bibby *et al.,* 1999).

5.2.4 Analysis

Density was estimated using Distance 6.2 (Thomas *et al.,* 2010). Distance analysis followed guidelines suggested by Buckland et al. (2001). Briefly, exploratory analysis was undertaken on the data prior to distance analysis. Histograms were created for each habitat type in order to identify the presence of errors, outliers and variation in detectability based on the method used (sight or sound). Outliers were removed (furthest 10%) and then contacts were placed into distance bands to fit detection curves. Detection curves, AIC, and Chi-squared goodness of fit test were used to determine the best model fit and series expansion to each habitat type. Density estimates are expressed as the number of individuals per km^2. A comparison of the detection functions applied to the Madeira Firecrest across habitat types using the AIC value, selected the hazard rate or the half normal model (Table 5.2). All statistical analysis was conducted using R 2.13.2 (R Development Core Team, 2011). An ANOVA was applied to compare density estimates across habitat types to determine habitat preference. A t-test was used to examine the effect of disturbance in indigenous forest.

Average relative abundance and the number of individual observed per quadrat and per km^2 were calculated using the broad-scale habitat sampling data, to identify any habitat associations across the broadest possible range of habitat types. The number of individuals per quadrat (or average where there were two visits) was used to calculate the average relative abundance of individuals across habitat types and analysed using a Chi-squared goodness of fit test. The number of quadrats occupied in each habitat type was used in conjunction with the density calculated for each habitat type to estimate the total population size. Chi-squared goodness of fit test was used to examine the partitioning of the population across habitat types.

The distribution of the Madeira Firecrest was investigated using the QGIS 1.7.3 (Quantum GIS Development Team 2011) in relation to habitat type and disturbance. Random forest (RF) classification with 10,000 classification tree was applied to rank and identify the most important habitat variables to predict Madeira Firecrest relative abundance (Liaw and Wiener, 2002). This method was chosen as it has been shown to have high classification and predictive accuracy and provides a method for determining variable importance (Cutler *et al.,* 2007).

5.3 Results

Contact frequency

Fine-scale contact frequency by habitat type is shown in Table 5.1. Laurel forest had the greatest number of contacts per point count (1.36), followed by mixed forest (1.21) and heath forest (0.81). Exotic forest (0.46) and agricultural (0.34) habitats yielded lower contact frequency per point count. No contacts were observed in either coastal or urban habitats. A similar pattern was also observed in the broad-scale study (Appendix 2) with 100% of laurel forest, mixed forest, heath forest, and farmland (which has nearby forest) quadrats occupied by Madeira Firecrest, , in addition to 94.4% of exotic forest quadrats.

Table 5.1. Fine and broad-scale survey data across habitat types.

Habitat	Points	Contacts	Quadrat Occupancy Visit 1	Quadrat Occupancy Visit 2	Total Quadrats surveyed	Total Quadrat occupancy
Laurel forest	193	263	13	18	19	19
Heath Forest	68	55	14	8	13	13
Exotic Forest	72	33	30	27	36	34
Mixed Forest	19	23	7	7	7	7
Upland	98	51	13	10	20	13
Coastal	70	0	2	0	10	3
Agricultural	62	21	33	31	68	43
Urban	58	0	0	0	8	0
Total	640	446	112	101	181	132

Quadrat Occupancy = number of quadrats occupied per habitat by the Madeira Firecrest.

The Madeira Firecrest density estimates (Individuals per km^2 or I/km^2), calculated for each habitat type are shown in Table 5.2. The highest density was observed in laurel forest (898.83 I/km^2), followed by heath forest (169.06 I/km^2) (Figure 5.1). The preference of the Madeira Firecrest to particular habitat types (laurel and heath forest) was shown to be significant using an ANOVA ($F = 3.71$, $df = 7$, $P < 0.001$). A comparison of Madeira Firecrest densities observed in pristine laurel forest and disturbed laurel forest failed to identify a significant difference ($t = 0.88$, $df = 2$, $P = 0.4$), although higher Madeira Firecrest densities were observed in the disturbed laurel (606.11 ± 79.55 and 495.19 ± 99.00 individuals per km^2). Relative abundance calculated from the broad-scale study (Appendix 2) highlights greater relative Madeira Firecrest abundance in laurel forest (31.4) (Figure 5.2) followed by exotic forest (24.3) and in contrast to the finer-scale study, in human dominated agriculture or rural areas (13.8). In terms of relative abundance, heath forest supported a smaller proportion of the Madeira Firecrests observed in the broad-scale study (7.7). However, as 100% of all quadrats dominated by heath were occupied, this low relative abundance is likely a result of lower survey effort in this habitat (Table 5.1). Preference for a particular set of forested habitats exhibited in the finer scale study was also shown to be significant relative to an equal distribution in the broad scale study ($\chi^2 = 224.28$, df = 15, $P < 0.001$).

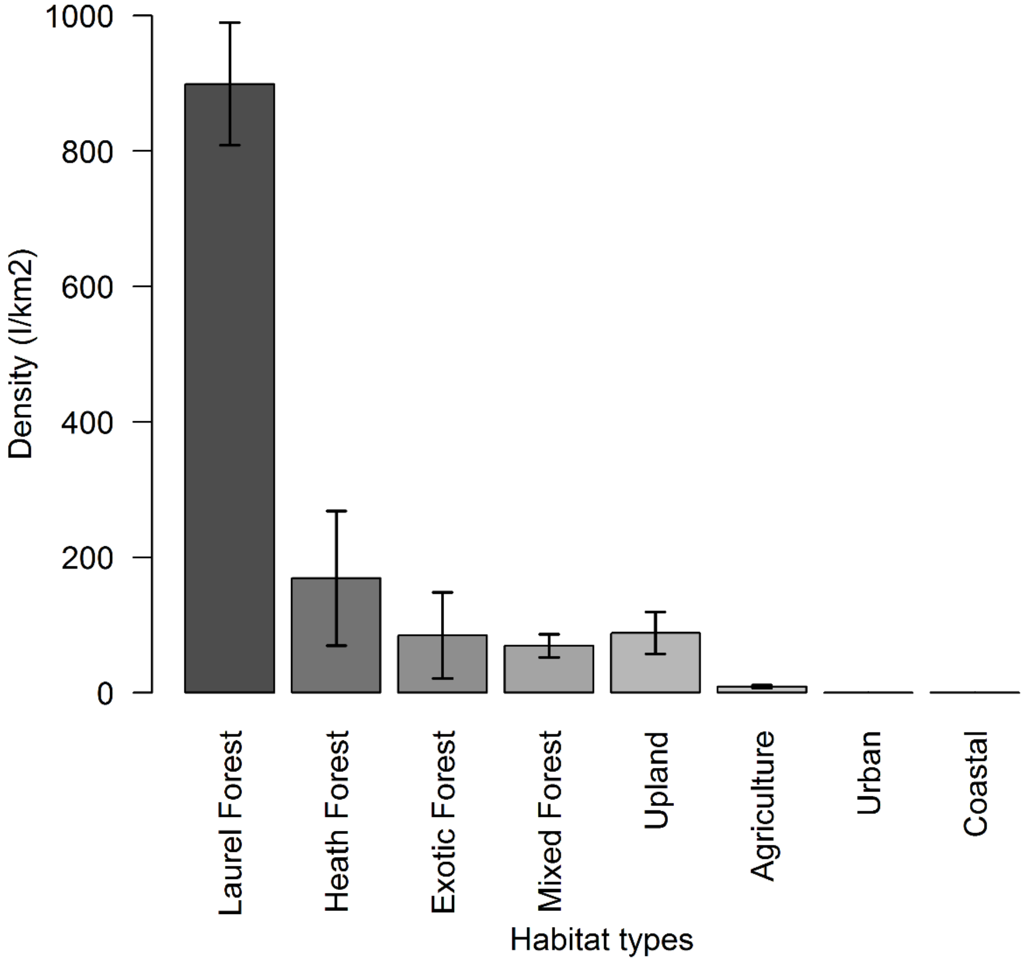

Figure 5.1. Density estimates (individuals per km^2 ± SE) of the Madeira Firecrest derived from distance sampling across 8 habitat types on Madeira.

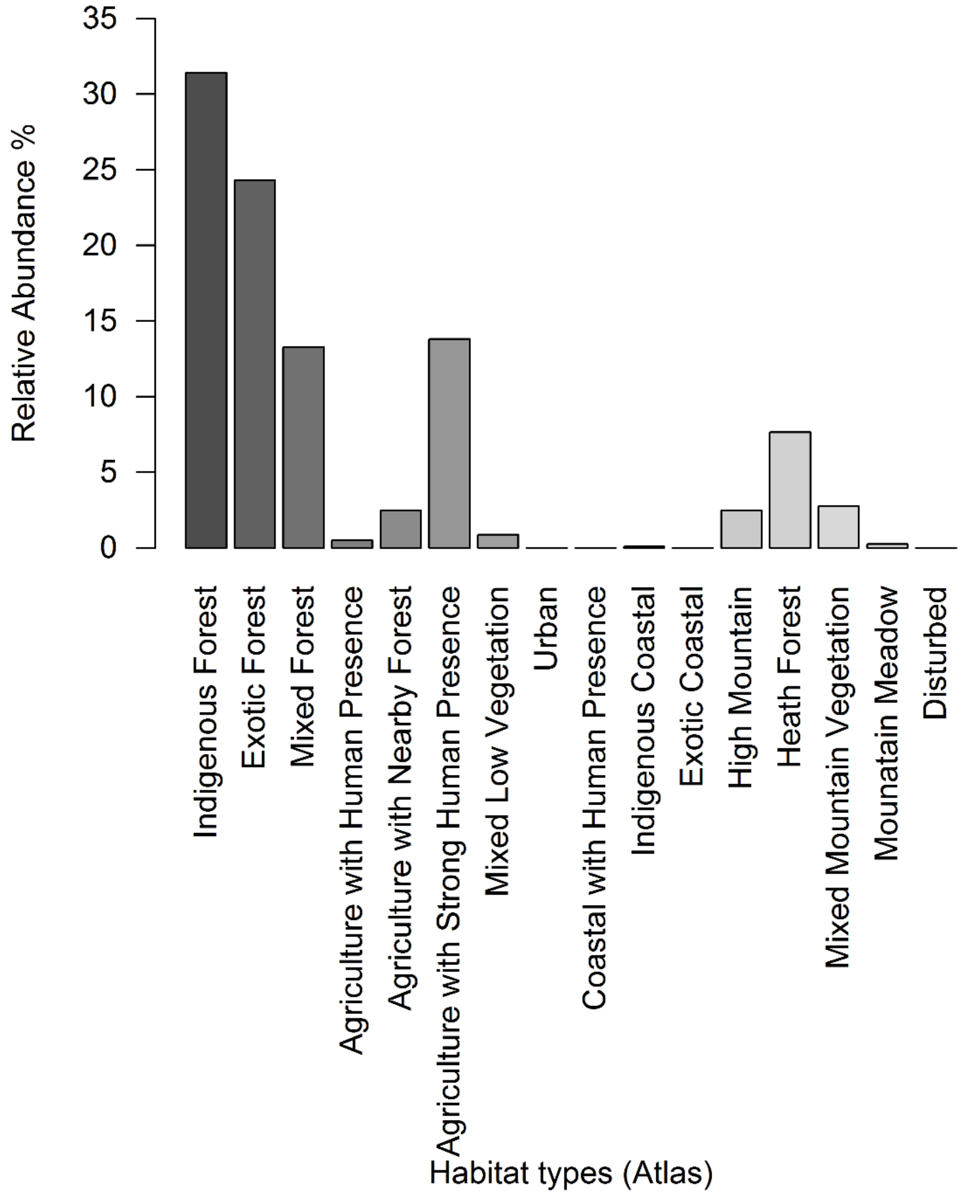

Figure 5.2. Relative abundance of the Madeira Firecrest across the 16 fine scale habitat types defined by the Madeiran natural park.

Table 5.2. Madeira Firecrest density estimates (Individuals per km2) across habitat types on Madeira.

Habitat	Model	AIC	Density	SE	95% LCL	95% UCL
Laurel forest	Hazard-rate	626.55	898.83	90.56	737.51	1095.40
Heath Forest	Hazard-rate	100.31	169.06	99.38	56.72	503.96
Exotic Forest	Hazard-rate	136.39	84.71	63.74	21.59	332.32
Mixed Forest	Half-normal	61.90	69.42	16.89	42.60	113.13
Upland	Hazard-rate	107.90	88.30	30.94	44.60	174.82
Coastal	-	-	0	-	-	-
Agricultural	Half-normal	88.21	8.97	2.21	5.44	14.80
Urban	-	-	0	-	-	-

Listed model selected based on lowest AIC score (also listed), Lower and upper confidence limits also recorded to inform the range in possible population size

Madeira Firecrest population estimates are summarised in Table 5.3. Consensus population size is estimated at 96,700 individuals (95% CI: 66,383 and 169,454). The population is not evenly distributed across habitat types ($\chi^2 = 308978.9$, df = 7, $P < 0.001$), with the largest density occurring in laurel forest (68311 individuals; 70.64%). Exotic forest holds 11.91% of the population, heath forest 9.09% and the other habitats containing lower amounts.

Table 5.3. Madeira Firecrest population size and contribution from each habitat type.

Habitat	Visit 1 estimate (range)	Visit 2 Population size (range)	Total Population size (range)
Laurel forest	46739	64716	68311
	(38351 - 56960)	(53101 – 78869)	(56051– 83250)
Heath Forest	9467	5410	8791
	(3176 – 28222)	(1815 – 16127)	(2949 – 26206)
Exotic Forest	10165	9148	11520
	(2591 – 39878)	(2332 – 35890)	(2937 – 45195)
Mixed Forest	1944	1945	1944
	(1193 – 3168)	(1193 – 3168)	(1193 – 3168)
Upland	4592	3532	4592
	(2319 – 9091)	(1784 – 6993)	(2319 – 9091)
Coastal	0	0	0
Agricultural	1184	1112	1542
	(717 – 1953)	(674 – 1835)	(935 – 2545)
Urban	0	0	0
Total Population	74090	85862	96700
	(48347 – 139272)	(60898 – 142881)	(66383 – 169454)

Population size calculated over the two visits with an average taken. Lower and upper population estimates are noted in parenthesis and are based on lower and upper 95% confidence limits of the densities (I/km2) calculated.

The distribution and relative abundance of the Madeira Firecrest, in relation to the degree of habitat disturbance, indicates a preference for relatively undisturbed habitat (Figure 5.3). The highest relative abundances were observed in laurel, heath, and mixed forest and an absence of the species in disturbed habitats (Figure 5.3). The distribution of the Madeira Firecrest is also concentrated in Central and Northern areas of the island.

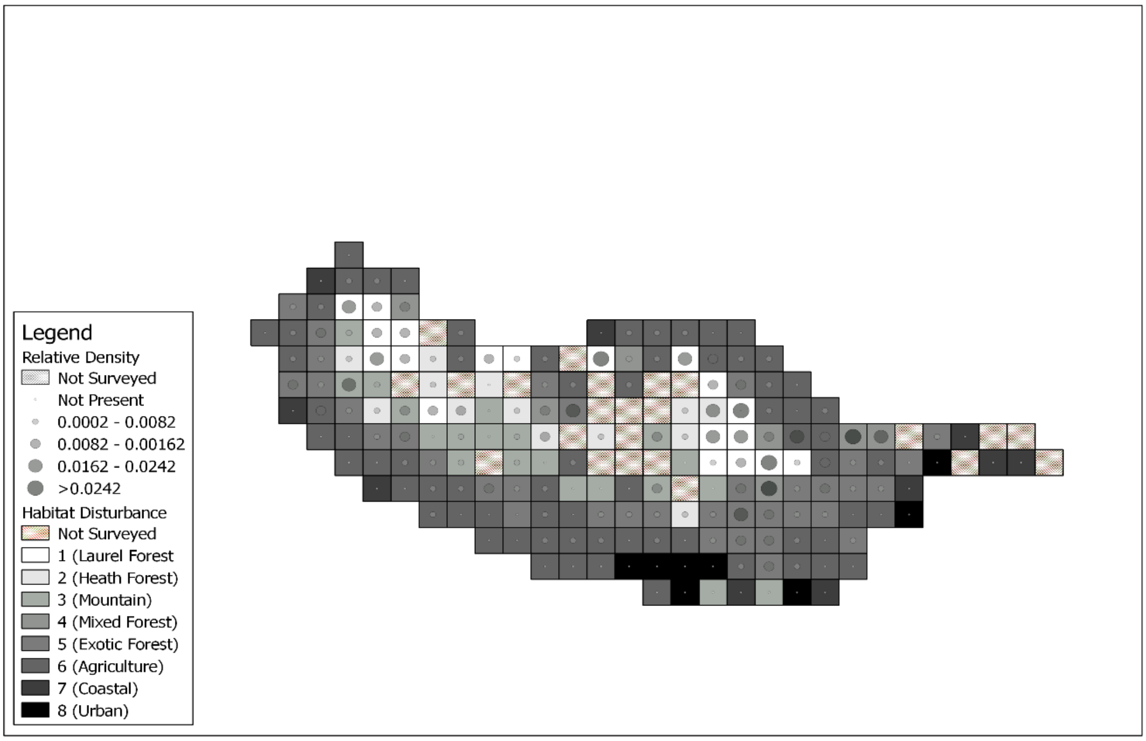

Figure 5.3. Map of the relationship between habitat disturbance and the distribution of the Madeira Firecrest.

A random forest (RF) classification technique was applied to identify important variables to predict relative abundance (Liaw and Wiener, 2002). According to the RF classification, 46.9% of the data variance was explained and the two most important variables in predicting the relative abundance of the species was the proportion of laurel forest habitat and the proportion of mixed forest habitats (Figure 5.4). These results are consistent with the higher density estimates observed in laurel forest and the importance of undisturbed habitat in distribution of the Madeira Firecrest across Madeira.

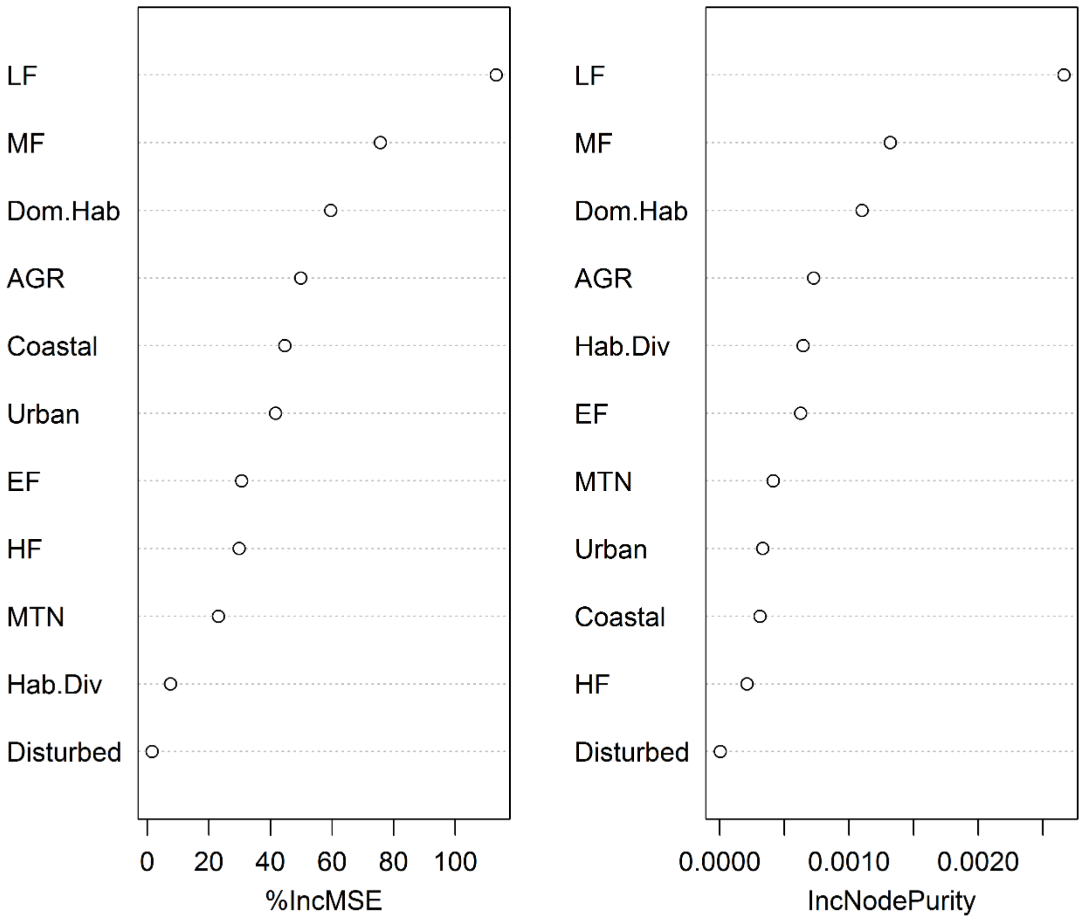

Figure 5.4. Variable importance plots from random forest (RF) to predict the relative abundance of the Madeira Firecrest (*Regulus madeirensis*) represented by IncMSE(%) = Increase in mean Square Error when variable is permuted, and IncNodePurity = Increase in Node Purity. LF= Laurel Forest, MF = Mixed Forest, Dom.Hab = Dominant Habitat, AGR = Agriculture, EF = Exotic Forest, HF= Health Forest, MTN = Mountainous areas, Hab.Div = Habitat Diversity, Disturbed = Disturbed habitat.

5.4 Discussion

This chapter estimated the population size for the Madeira Firecrest at 96,700 individuals, which is consistent with the IUCN designation as Least Concern (IUCN, 2016). However, this estimated population size is at the lower end of the 100,000 – 199,999 individuals recently estimated by BirdLife International (2015). A significant proportion of the population is concentrated in the laurel and heath forest (79.73%), with the primary range being much smaller, approximately 20% of the island (Marrero *et al*., 2004; Fernandez-Palacios *et al.,* 2011). These remaining indigenous habitats are concentrated in the Northern and Central areas of Madeira (Oliveira *et al.,* 1999).

The spatial patterns in distribution and the abundance of the Madeira Firecrest are strongly linked with the presence of the indigenous forest type of laurel and heath forest. Both forest habitats show little or no evidence of anthropogenic disturbance (Figure 5.3). Both broad and fine scale studies also indicate that the Madeira Firecrest is able to utilise disturbed remnants of the indigenous forest on Madeira as observed by del Hoyo *et al.* (1996) and, to a lesser extent, the exotic forest. This study also confirms that the Madeira Firecrest utilizes a broad range of habitats on Madeira. However, density and abundance estimates from both broad and fine scale studies show much higher in abundance in laurel and heath forests than the other habitat types. Using random forests, the proportion of laurel forest was the most important variable in predicting relative abundance of the Madeira Firecrest.

In terms of conservation management, a large proportion of the Madeiran Firecrest population occurs within strict or partial nature reserves under the jurisdiction of the Madeiran Natural Park (Oliveira *et al.*, 2004; Oliveira and Heredia, 1995). The Madeiran Natural Park provides legal protection to laurel forest habitat. This habitat is considered a priority habitat under the EU Habitat Directive, as part of the Macaronesian laurel forest (Oliveira *et al.*, 2004; Oliveira and Heredia, 1995). These protective measures have halted the impact of habitat loss, degradation, and fragmentation that resulted in the native laurel forests present cover (Oliveira *et al.,* 1999). In addition, the laurel forest also is important to the successful programme of conservation management for the endemic Madeira Laurel Pigeon (*Columba trocaz*; Oliveira and Heredia, 1995), which has likely imparted indirect benefit to the status of the Madeira Firecrest.

Chapter 6. Discussion

6.1 Possible sources of bias

To limit the effect of bias caused by differences in scale and methods across the different datasets used in this thesis, each dataset was analysed separately in most chapters to test individual questions and hypotheses or to test the taxon cycle and ecological release at different scales or on different island chains (see methods: Chapters 2-5). Where data have been combined, such as testing for the relationship between genetic distance and species distribution (Chapter 4) across Madeira, the Azores and the Canary Islands, both sets of presence and absence data were collected by volunteers and at the same scale (10km^2). Although combining the datasets may not control for the effect of inter-observer variability caused by multiple recorders, the methods of multiple observers across survey area and through time is consistent across both bird atlas projects. For the assessment of population size of the Madeiran Firecrest, data from the Madeiran bird atlas project and data collected using point counts and distance sampling were used together. The datasets were not compared, but the presence and absence across the island and dominant habitats were used in conjunction with density estimates to provide an estimate of the newly recognised species population size. The presence absence data for Madeira was collected by Parque Natural da Madeira by a small group of staff reducing the effect of observer bias. Sites were visited multiple times over the study reducing the possibility of missing a species presence.

6.2 Use of ‘citizen science’ data

A critical aspect of this PhD and most studies into species evolution, extinction, conservation and management is knowledge of species diversity, abundance, and distribution across large areas (Lepczyk, 2005). However, the resources for the collection of the data needed to answer questions in these areas is insufficient. Citizen science, such as bird atlas and breeding bird surveys, provides the opportunity to collect the data that would otherwise be impossible due to time and resource constraints (Tulloch *et al.,* 2013). There is however, bias associated with citizen science programmes such as observer bias and differences in scale, there are also trade-offs between quality and quantity of the data collected (Tulloch *et al.,* 2013). There is a need for more research into the impact of the bias associated with citizen science programs and a focus on data quality (Tulloch *et al.,* 2013; Dickinson *et al.,* 2010). The reliability and bias of volunteer projects associated with ad hoc and convenience sampling or surveys designed to be attractive to volunteers compared to more structured surveys and atlases has been questioned. However, others have suggested that with appropriate statistical and analytical tools bias in both types of survey can be minimised making them more robust (Szabo *et al.,* 2012).

Despite criticisms of citizen science data, no data set is perfect. A recent comparative study has successfully used citizen science to produce robust results that are similar to data collected from professionals (Szabo *et al.,* 2012). The use of citizen science is increasing, and may be the only practical method to collect data at geographic scales needed to inform conservation and management (Dickinson *et al.,* 2010) and in this PhD, identify large scale patterns in species abundance and distribution to test evolutionary theories such as the taxon cycle.

6.3 Chapter key findings

This thesis aimed to investigate evidence for ecological release and the taxon cycle across the Macaronesian islands. Predictions associated with ecological release and the taxon cycle were tested across multiple islands and species pairs, using spatial, genetic, morphological, and ecological data. This concluding chapter will summarise key findings, outline the importance and impact of the work, and identify further research motivated by the key findings.

In Chapter 2, point transects and distance sampling were used to study the response of six species to the species-poor environment of Madeira. Two components of the ecological release hypothesis, density compensation and niche expansion, were investigated using a mainland-island comparison. The study used comparable habitats and the same species or sister taxa when comparing Madeira and mainland Portugal populations. This chapter also used published density estimates to identify if trends in density compensation were consistent across multiple studies and European islands.

Key findings:

1. Five of the six focal species were found at higher densities compared to their mainland counterpart, three of which were significantly higher in density, in the indigenous laurel forest on Madeira.
2. Lower species richness and diversity across the island habitats.
3. Three species (*Fringilla*, *Regulus, Pyrrhula* species) were consistently higher in density on islands across this study using empirical and published data.
4. Five of the six focal species had a broader niche on Madeira than the mainland.

The ecological release hypothesis predicts that island species should exhibit density compensation and niche expansion as a consequence of reduced interspecific competition and predation in island ecosystems (Feinsinger and Swarm, 1982; Losos and Queiroz, 1997). The results in this chapter are consistent with ecological release for indigenous laurel forest on Madeira. Thus, this study constitutes some empirical evidence for density compensation and niche expansion, while addressing previous shortcomings in methodology and is consistent with previous studies (MacArthur *et al.,* 1972; Ricklefs and Cox, 1972; Terborgh and Faaborg, 1973).

Chapter 3 used a large, comprehensive dataset on abundance, habitat use, and distribution of bird fauna for the Madeiran Archipelago, with morphological and genetic data, to test predictions arising from taxon cycle theory. The aim of this chapter was to determine whether patterns in species abundance, distribution, and niche width on Madeira relate to species taxonomic status, morphological and genetic differentiation, and proposed taxon cycle rankings.

Key findings:

1. A significant increase in genetic distance with increasing taxon cycle rank and between early stage (recent colonists) and late stage species (endemic sub-species and species).
2. Genetic distance was negatively correlated with species distribution, number of habitats occupied, niche width and exotic forest and disturbed habitat abundance.

3. Species in the latter stages of the taxon cycle were significantly more abundant in laurel, exotic and undisturbed forest habitats, and had higher niche breadth.
4. Latter stage species (rank 4) were absent from some coastal areas, and had higher abundance in interior habitats, while early stage (rank 1 and 2) species were present widely across the archipelago.

The results from the chapter provide the first evidence for the taxon cycle on Madeira using genetic distance and ecological data. The results from the genetic analysis provide a strong, critical test of a key taxon cycle assumption, corroborating previous work (Ricklefs and Bermingham, 1999). The negative correlations between genetic and morphological difference and species distribution, number of habitats occupied, niche width, exotic forest, and disturbed habitat abundance identified in this chapter are consistent with predictions from the taxon cycle. Older species over time are expected to become reduced and fragmented is distribution, shift from marginal and disturbed to interior and forested habitats and become more specialised (Wilson, 1961; Ricklefs and Cox, 1972; 1978; Ricklefs and Bermingham, 2002). Higher abundances in laurel forest of older species is also consistent with the taxon cycle theory, with previous studies identifying a movement to interior forest habitats and higher elevations with progression through the later stages of the taxon cycle (Wilson, 1961; Ricklefs and Cox, 1972; 1978; Ricklefs and Bermingham, 2002). The results from this study suggest that the taxon cycle may be important in shaping the distribution and abundance of the birds of Madeira.

In Chapter 4, distribution and abundance datasets were collated for the Azores, Madeira, Canary Islands, and the Cape Verde Islands, and published mitochondrial genetic data, to text key predictions from taxon cycle theory.

Key findings:

1. Nine of the twelve species were found at significantly higher abundance on islands relative to mainland counterparts.
2. A significant difference in genetic distance was demonstrated for species pairs for increasing taxon cycle rank.

3. Overall, late taxon cycle species had a smaller distribution and lower abundance than species at early stages of the taxon cycle ranks (across all four archipelagos).
4. A significant non-linear relationship between species age, and distribution and abundance, showing a bell-shaped curve was found, showing strong support for a key taxon cycle assumption.

The results from this chapter provide the first test and evidence for the taxon cycle across Macaronesia using modern approaches. Patterns of distribution and abundance across species rank and with species age identified in this study were consistent with expectations from the taxon cycle supporting the theory that taxon cycles may be important in shaping the distribution and abundance of insular taxa across Macaronesia (Rickefs and Cox 1972; 1978).

In Chapter 5, ecological and distribution data were collated to conduct an assessment of population status and habitat association in a recently recognised, island endemic, the Madeiran Firecrest. This chapter used distance sampling and existing distribution data to conduct the first quantitative census estimate for the Madeira Firecrest, and identify the impact of habitat disturbance to inform species conservation management.

Key findings:

1. Population size of the Madeiran Firecrest was estimated to be 96,700 (95% CI: 66,383 – 169,454) individuals, exceeding the vulnerable population size threshold of 10,000 individuals set by the IUCN.
2. Distribution and abundance was linked with the laurel and heath forest. Association with laurel and health forest supported was by both the broad-scale and fine-scale study in this chapter.
3. Utilisation of disturbed indigenous forest exotic forest was marginal.
4. The largest proportion of the population was found within managed nature reserves.

This chapter, provides the first quantitative assessment of population size and habitat association for the Madeira Firecrest. These results update support for “Least Concern” classification (IUCN, 2016), but highlights the critical importance of native laurel and heath forest for the management of this species.

6.4 Ecological release

Understanding how species respond to novel and species-poor environments, such as islands, is important to our understanding of island biogeography and species invasions (Yoder *et al.,* 2010; Keane and Crawley, 2002). Island species, having undergone ecological release due to reduced competition and predation, are expected to exhibit density compensation and niche expansion (MacArthur *et al.,* 1972; MacArthur and Wilson, 2001). Release into vacant niches or under-utilised resources on islands (niche expansion) is also associated with morphological diversification and adaptive radiation (Losos and de Queiroz, 1997; Noseil and Reimchen, 2005; Yoder *et al.,* 2010).

Previous studies of ecological release have been criticised based on their experimental design with various deficiencies, including small sample size, and inequitable variation in climate, habitat type, and species (Wright, 1980; McGready-Steed and Morin, 2000). This thesis has addressed these limitations using comparisons over multiple islands to increase sample size across comparable habitats and climates. This study has also used the same or closely related species on the mainland for every focal species pair comparison. The results from chapters two and five suggest that some species across Macaronesia may have undergone ecological release in the form of density compensation and niche expansion. Evidence for density compensation was also identified at both fine and broad spatial scales. However, two species pairs studied showed no evidence of density compensation.

It is recognised that many factors can affect island population density, possibly reducing the putative effects of reduced competition or predation on islands (Wright, 1980; Wilson, 1961; Ricklefs and Bermingham, 2002). Patterns of ecological release in some species may be difficult to detect as island species are also predicted to pass through cycles of expansion and contraction in the form of the taxon cycle with episodes of speciation and adaptation to particular resources or microhabitat resulting in the evolution of smaller isolated populations, a likely precursor to adaptive radiation (Losos and Queiroz, 1997; Ricklefs and Bermingham, 2002; MacArthur and Wilson, 2001; Losos and Ricklefs, 2009). In addition, signals of ecological release may have been masked by anthropogenic effects such as habitat fragmentation or land use change such as the introduction of exotic species. The laurel forest studied in chapter 2 and 3 on Madeira is an undisturbed indigenous forest that once covered potentially up to 60 thousand hectares of Madeira (around 80% of surface area) prior to human colonization (AD 1420-1430) but now occupies about 25% of this potential range (15 thousand ha) due to forest clearing for cattle and agriculture (Fernandez-Palacios *et al.,* 2011). Results from chapter 2 focusing on the undisturbed laurel forest identified the presence of ecological release in the form of both density compensation and niche expansion suggesting that these results are a likely a response to the species poor conditions on Madeira and not a result of anthropogenic disturbance creating marginal and disturbed habitats.

6.5 Taxon cycle

The results from this thesis provide the first test and evidence for the taxon cycle across Macaronesia using modern approaches. Evidence in this thesis for the presence of the taxon cycle across Macaronesia suggest that cycles of expansion and contraction and associated microevolutionary changes may have played a role in shaping the distribution and abundance of bird fauna of Macaronesia. Understanding the pattern of species abundance, distribution and diversity are key to biogeography and conservation. Taxon cycle theory was proposed to explain species abundance and distribution through temporal expansion then contraction (Wilson, 1961; Economo and Sarnat, 2012). This framework is important in understanding microevolution of island taxa, but also can our expectation of biogeographical change in response to climate change and our understanding of natural and anthropogenic extinctions (Ricklefs and Bermingham, 2002; Economo and Sarnat, 2012). Studies that have examined the correlates of extinction risk have identified small population size, small range and redistricted distribution, endemism and specialism as the main predictors (Purvis *et al.,* 2000; O'Grady *et al.,* 2004). As species pass through the taxon cycle they are likely to exhibit traits such as restricted distribution, low abundance and habitat and niche specialism that make them susceptible to extinction.

6.5 Drivers of the taxon cycle

The mechanisms that drives a species movement through the taxon cycle are not well understood (Ricklefs and Bermingham, 2002). Wilson (1961) proposed competition as the main mechanism behind the taxon cycle, with the arrival of new colonists pushing earlier colonists through the cycle (Whittaker and Fernandez-Palacios, 2007). The results from this thesis indicate that across Macaronesia, in the presence of at least one congeneric species, species had a smaller island distribution (congeneric species present = 54%, absent = 80%) and smaller increase in abundance compared to their mainland counterpart when compared to species that had no congeneric species present (present = 93.9%, absent = 325.9%). These results suggest that the presence of possible competition may influence the abundance and distribution of the Macaronesian bird fauna.

Ricklefs and Cox (1972) suggested that counter-adaptation (or counterrevolution) and changes in the balance of co-evolution between birds, enemies and competitors was the main driver behind the taxon cycle (Ricklefs and Bermingham, 2002; Whittaker and Fernandez-Palacios, 2007). New colonists are expected to enter an expansion stage as a result of release from predation, pathogens and diseases. These species have a competitive advantage and put additional pressure on older colonists (Losos and Ricklefs, 2010). Over time the local fauna may adapt to use this new resource reducing the productivity and fitness of the colonist and causing the species to enter a contraction phase (Ricklefs and Bermingham, 2002). A recent study into the relationship between avian abundance and the prevalence of haemosporidian (malaria) parasites found a pattern and association that is consistent with expansion and contraction phases of the taxon cycle (Ricklefs *et al.,* 2016). This study supports previous work that has found twice the number of parasites species in native species compared to introduced or exotic species (Torchin *et al.,* 2003). Ricklefs et al. (2016) also identified negative effects of parasite load on host species abundance and identified an interaction between avian species who share pathogens, but at different relative abundances (apparent competition). Both studies provide support for the role of parasite co-evolution as a possible mechanism behind the taxon cycle.

6.6 Future work

This study has provided strong evidence of ecological release and the taxon cycle in the avifauna of Macaronesia. Further research is needed to investigate specific factors that may influence the strength of selection leading to ecological release. With increasing availability of large scale datasets of species distribution and biodiversity and published records and estimates, future research should look at global trends in island species abundance and niche width to investigate the factors influencing the presence and magnitude of ecological release. This research would not only benefit our understanding of insular species ecology but also conservation and the impact of invasive species. Research focused on newly introduced species would also provide the opportunity to observe how a new species fits into an island ecosystem (Santos *et al.,* 2016) and also investigate the early stages of ecological release and the taxon cycle.

The availability of large species distribution and biodiversity datasets and online databases of published genetic sequences have improved our ability to investigate patterns in species distributions, diversity, and evolutionary processes, prompting a renewed interest in testing historical theories that have been difficult to study empirically (Economo and Sarnat, 2012; Jonsson *et al.,* 2014). Future work should use this increasingly available data to continue to test for the presence of cycles of expansion and contraction in species distribution and abundance at a global scale.

Future work on the taxon cycle theory should also investigate the poorly understood driving mechanism behind the cycle and the factors that apparently prevent some species passing through the cycle. Despite difficulties in testing how ecological interactions such as competition, parasitism and predation influences island ecology and evolution, these factors are important (Whittaker and Fernandez-Palacios, 2007). Further work across Macaronesia could attempt to quantify the level of competition species are both currently under and have historically been exposed to by estimating colonization dates for all species. The level of competition could then be related to patterns in species abundance, distribution, niche width and proposed taxon rank to examine whether competition could be a possible driving mechanism. Host-parasite associations have also been proposed as a possible driving mechanism behind the taxon cycle, with some support (Torchin *et al.*, 2003; Ricklefs *et al.,* 2016). However, this is an area of research that requires further work to link phases of expansion and contraction with pathogen prevalence (Ricklefs *et al.,* 2016). Future work on Madeira and across Macaronesia could focus on assessing parasite and pathogen load in species at different stages of the taxon cycle. Older species in the latter stages of the cycle (Stage 3 and 4) should have a higher abundance of parasites compared to more recent colonists (stage 1 and 2). A future study could also examine the relationship between avian abundance, niche width and distribution and parasite abundance and diversity.

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Appendices

Appendix 1: Broad-scale habitat classifications in Madeira.

Atlas Habitat Type	Code	Description
Indigenous Forest	1	Dominated by indigenous laurel species (*Laurus azorica* and *Ocotea foetens*)
Exotic Forest	2	Dominated by exotic species (Pine *Pinus pinaster* and / or Eucalyptus *Eucalyptus globules)*
Mixed Forest	3	Without clear dominance of indigenous or exotic species
Agriculture with human presence	4	Agricultural area with active or recently abandoned human presence
Agriculture with nearby forest	5	Agriculture bordered by nearby forest
Agriculture with strong human presence (Rural)	6	Agriculture with strong human presence
Mountain - Mixed low vegetation	7	Mountain area with mixed low vegetation – no clear dominance of species
Urban	8	Strong human presence
Coastal with human presence	9	Habitats 4, 6 and 8 where the dominant element is located in close proximity to the sea / coastal zone
Indigenous Coastal Vegetation	10	Coastal zone dominated by Indigenous species and without human presence
Non-indigenous Coastal Vegetation	11	Coastal zone dominated by non-indigenous species and without human presence
Mountain Vegetation	12	High zones dominated by high altitude vegetation.
Heath Forest	13	Zones dominated by *Erica* species
Mixed-Mountain Vegetation	14	High zones not dominated by either exotic or high altitude vegetation
Mountain Meadow	15	High mountain region consisting of bare ground and herbaceous vegetation.
Disturbed Vegetation (Human Intervention	16	Areas where there is clear evidence of human disturbance (Fires, habitat disturbance)

Appendix 2: Information relevant to the analysis of the broad-scale Madeira Firecrest survey on Madeira and results of relative abundance and individuals per quadrat.

Habitat Type	No. Individuals	No. Quads	Relative Abundance (%)	Individuals per Quad
Indigenous Forest	530	19	31.44	27.89
Exotic Forest	410	36	24.32	12.06
Mixed Forest	224	7	13.29	32
Agriculture with human presence	8.5	2	0.50	4.25
Agriculture with nearby forest	42	5	2.49	8.4
Agriculture with strong human presence (Rural)	233	36	13.82	6.47
Mountain - Mixed low vegetation	15	1	0.89	15
Urban	0	0	0	0
Coastal with human presence	0	0	0	0
Indigenous Coastal Vegetation	1.5	3	0.09	0.5
Non-indigenous Coastal Vegetation	0	0	0	0
Mountain Vegetation	42	4	2.49	10.5
Heath Forest	129	13	7.65	9.92
Mixed-Mountain Vegetation	46.5	5	2.76	9.3
Mountain Meadow	4.5	1	0.27	4.5
Disturbed Vegetation (Human Intervention	0	0	0	0

Appendix 3: Source locations and number of sequences from Genbank for each species used in genetic analysis

Species	**Source**	**Location**	**Genbank Sequences (N)**
Anthus Berthelotii	Island	Canary island / Madeira	1
		Lanzarote / Gran Canaria	1
		El Hierro	1
		Lanzarotte / La Gomera	1
Anthus campestris	Mainland	Denmark / Sweden	2
Columba trocaz	Island	Madeira	4
Columba palumbus	Mainland	Spain	6
Columba palumbus azorica	Island	Azores	1
		Faial	2
		Pico	4
		Terceira	3
		Sao Miguel	1
Columba Bollii	Island	La Gomera	2
		La Palma	2
		Tenerife	2
Columba Junoniae	Island	Tenerife	2
Cyanistes caeruleus	Mainland	France	4
		Portugal	2
Cyanistes teneriffae ombriosus	Island	El Hierro	7
Cyanistes teneriffae denger	Island	Fuerteventura	7
		Lanzarote	5
Cyanistes teneriffae	Island	La Gomera	18
		Tenerife	14
		Gran Canaria	15

Erithacus rubecula	Mainland	Spain	3
		Portugal	9
	Island	Azores	2
		Faial	5
		Graciosa	5
		Madeira	10
		Pico	5
		La Palma	4
		Gran Canaria	13
		Tenerife	16
		La Gomera	9
		El Heirro	13
		Fuerteventura	2
		Sao Miguel	5
		Santa Maria	5
		Sao Jorge	5
		Terceira	5
Fringilla coelebs	Mainland	Spain	4
		Portugal	5
	Island	Madeira	5
		Corvo	5
		Faial	5
		El Heirro	2
		La Palma	7
		La Gomera	3
		Gran Canaria	4
		Tenerife	2
		Terceira	7
		Flores	5
		Graciosa	5
		Pico	5
		Sao Jorge	5

		Santa Maria	5
		Sao Miguel	5
Fringilla teydea	Island	Tenerife	4
Fringilla polatzeki	Island	Gran Canaria	6
Regulus ignicapillus	Mainland	France / Germany	4
Regulus madeirensis	Island	Madeira	14
Regulus regulus	Mainland	France / Austria / Germany / Portugal	7
	Island	Terceira	10
		Flores	6
		Sao Miguel	6
		Santa Maria	6
		Sao Jorge	5
		Pico	5
		Faial	4
Regulus teneriffae	Island	El Heirro	3
		La Gomera	12
		La Palma	3
		Tenerife	11
Sylvia atricapilla	Mainland	Portugal	2
	Island	Madeira	2
		Tenerife	3
		Azores	2
		El Heirro	1
		Gran Canaria	1
		La Gomera	3
		La Palma	2
Serinus serinus	Mainland	Spain	1
Serinus canaria	Island	Pico	14
		Madeira	40
		Tenerife	1
		Fuerteventura	1

	La Gomera	1
	Gran Canaria	1

Appendix 4: Cape Verde species list included in the analysis.

Common Name	**Scientific Name**
Barn Owl	*Tyto alba*
Bar-tailed Desert lark	*Ammomanes cintrurus*
Black Kite	*Milvus migrans*
Blackcap	*Sylvia atricapilla*
Black-crowned Finch-Lark	*Erompterix nigriceps*
Black-winged Stilt	*Himantopus himantopus*
Brown Booby	*Sula leucogaster*
Brown-necked Raven	*Corvus ruficollis*
Common Buzzard	*Buteo buteo*
Common Waxbill	*Estrilda astrild*
Cream-coloured Courser	*Cursorius cursor*
Cape Verde (swamp) Warbler	*Acrocephalus brevipennis*
Purple Heron	*Ardea purpurea*
Cape Verde Shearwater	*Calonectris edwardsii*
Cape Verde Swift	*Apus alexandri*
Egyptian Vulture	*Neophron percnopterus*
Grey-Headed Kingfisher	*Halcyon leucocephala*
Helmeted Guineafowl	*Numida meleagris*
Hoopoe Lark	*Alaemon alaudipes*
House Sparrow	*Passer domesticus*
Iago Sparrow	*Passer iagoensis*
Kentish Plover	*Charadrius alexandrinus*
Kestrel	*Falco tinnunculus*
Little Egret	*Egretta garzetta*
Cape Verde Shearwater	*Calonectris edwardsii*
Madeiran Storm Petrel	*Oceanodroma castro*
Magnificant Frigatebird	*Fregata magnificens*
Osprey	*Pandion haliaetus*
Quail	*Coturnix coturnix*
Raso lark	*Alauda razae*

Red-billed Tropicbird	*Phaethon aethereus*
Rock / Feral Pigeon	*Columba livia*
Spanish Sparrow	*Passer hispaniolensis*
Spectacled Warbler	*Sylvia conspicillata*

Appendix 5: Madeira species list and taxon cycle rank

Species	Rank
Anthus bertheloti	3
Accipiter nisus	2
Apus pallidus	1
Alectoris rufa	1
Apus unicolor	2
Bulweria bulwerii	1
Buteo buteo	3
Charadrius alexandrinus	1
Carduelis cannabina	3
Carduelis carduelis	2
Carduelis chloris	1
Coturnix coturnix	2
Calonectris diomedea	1
Columba livia	2
Carduelis spinus	1
Columba trocaz	4
Estrilda astrild	1
Erithacus rubecula	1
Fulica atra	1
Fringilla coelebs	3
Falco tinnunculus	2
Gallinula chloropus	1
Larus michahellis	2
Motacilla cinerea	3
Passer hispaniolensis	1
Psittacula krameri	1
Petronia petronia	2

Regulus madeirensis	4
Sylvia atricapilla	2
Serinus canaria	2
Sylvia conspicillata	2
Streptopelia decaocto	1
Sterna hirundo	1
Scolopax rusticola	1
Tyto alba	2
Turdus merula	2
Upupa epops	1