BIOGEOGRAPHICAL AND ECOLOGICAL PREDICTORS OF DISJUNCTION IN THE TASMANIAN AND NEW ZEALAND FLORA

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by

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DECLARATION

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ABSTRACT

Long distance dispersal, the migration and establishment of propagules across large biogeographical barriers, has played a critical role in shaping the historical and current biogeography of the Southern Hemisphere flora. Vicariance, the physical separation and subsequent isolation and speciation of populations, alone cannot account for the geographic distribution of the plant lineages. The extant vascular flora of Tasmania and New Zealand provides insight into the process of long distance dispersal and its consequences. This thesis investigates the relative abundance, directional dispersal, and long distance dispersal-mediated traits of these species by considering the overall flora of these island masses, and in particular, the 293 species that occur in both landmasses (referred to herein as disjunct species). These disjunct species are likely to be all recent migrants, and therefore they can be used to infer the characteristics and processes involved in dispersal.

Analysis of within-species disjunctions showed a significant directional bias for immigration from Tasmania to New Zealand, rather than vice versa. Disjunct species that are common in both areas, defined here as ones that have widespread distributions of populations, were over-represented compared to species that were rare. This observation supports a direct association between relative abundance and frequency of dispersal. Furthermore, disjunct species were more common in their source area than in the sink area, highlighting the effect of source size on the degree of dispersal. However, the observed ecological range of disjunct species in the source area was not greater or less than the observed ecological range of these species in the sink area, although disjunct species were likely to have wider ranges than nondisjunct species. No evidence was found to indicate that ecological release was an influence on establishment due to the under-representation of disjunct species common in the sink area.

Herbaceous species were more likely to be disjunct than woody species in New Zealand and Tasmania. High proportions of disjunct species inhabited freshwater aquatic, salt marsh and estuaries, coastal areas, and bogs and wet peats while low

proportions were in forests (including open), grasslands, and heaths. Disjunct species were more likely to have specialist features for wind dispersal and external transport on vertebrates, but less likely to have fleshy fruits. Despite these features, small disseminules were over-represented. Dioecy was significantly under-represented in disjunct species. Groups with high frequencies of disjunct species include ferns and the angiosperm families Caryophyllaceae, Chenopodiaceae, Cyperaceae, and Juncaceae. The under-representation of disjunct species that are more common in the sink area than the source implies that there is no evidence that ecological release was an influence on establishment.

The within-species disjunctions of Tasmania and New Zealand reinforce the shifting acceptance of long distance dispersal in the Southern Hemisphere and the relevance of relative abundance in evaluating the frequency of dispersal and ecological patterns. The results argue for a comparative evaluation of other island disjunctions.

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CHAPTER 1: GENERAL INTRODUCTION

Historical biogeography examines the impact of long-term processes, such as evolution or tectonics, on the distributional patterns of living organisms (Cox & Moore, 1993). Various theories, hypotheses, and models have been proposed how these processes underpin historical biogeography. Four main spatial-temporal processes are generally accepted as driving the geographical distribution of organisms (Crisci, 2002): extinction, evolution, vicariance, and long distance dispersal.

Although extinction is unanimously accepted as the demise and end of all representatives of a local population or a species and evolution receives an almost equal acceptance, vicariance and dispersal are controversial, competing explanations. Through time, biogeographers have attributed very different levels of relative importance to vicariance and dispersal. Vicariance dominated studies of historical biogeography until the late 1990s. In vicariance, a population of a widespread organism is split into several two or more populations by insurmountable barriers to dispersal or gene flow (biogeographic barriers), causing disjunctions (species or clades that occur on either side of the barrier). Because the timing of the barrier's appearance coincides with the disjunction, the age of the disjunction cannot be older or younger than the barrier. The processes of allopatric speciation ensure that vicariance is often followed by speciation. Thus, the classical vicariance paradigm presents the speciation of a widespread ancestral organism in response to successive geological upheavals of its distribution range (Raven & Axelrod, 1972; Nelson & Platnick, 1981; Humphries & Parenti, 1999). This speciation dovetails with the process of adaptive radiation where different niches encourage the diversification of one species into multiple species. The development of cladistic biogeography in the 1970s and 1980s (Nelson & Platnick, 1981) created an intellectual framework for understanding origins of biota and plate tectonic models that provide a mechanism for creation of vicariant disjunctions on intercontinental scales. As a result, vicariance defined historical biogeography for decades, but is not without its detractors who argue that timing of these upheavals does not always synchronize with the formation of

the disjunction, and attributing an organism's distribution entirely to vicariance is simplistic.

In the last decade or so, acceptance of mounting evidence for transoceanic dispersal has resurrected long distance dispersal as a major process in the assembly of floras (De Queiroz, 2005). In long distance dispersal, individuals of the widespread organism are capable of crossing the existing barrier (albeit rarely), forming disjunct distributions. If sufficiently isolated from the original population, the disjunct population may evolve into a different species in much the same way as vicariance can be associated with speciation. Darwin (1859) saw long distance dispersal as formative in colonization of oceanic islands, but the omnipresence of dispersal, local and long distance, made it less testable than vicariance. Proponents of the long distance dispersal process were vindicated with evidence that this process had a contributing role in biotic distributions previous considered products of vicariance (Setoguchi *et al.*, 1998; Swenson *et al.*, 2001a; Swenson *et al.*, 2001b; Cook & Crisp, 2005; Knapp *et al.*, 2005).

Effective dispersal (i.e. movement of propagules to another place, followed by successful establishment of a new population or contribution to the local gene pool) is fundamental to understanding biogeography. While localised or short-distance dispersal has been well studied (Ribbens *et al.*, 1994; Clark *et al.*, 1998; Clark *et al.*, 1999; Nathan & Muller-Landau, 2000), long distance dispersal (movement and establishment across substantial inhospitable barriers, like oceans) has not received adequate attention and is therefore less understood. The significance of long distance dispersal cannot be underestimated when considering diverse facets of plant biology, including population dynamics and evolution, biological invasions, and ecological dynamics and evolution (Harper, 1977; Sauer, 1988; Hengevevld, 1989; Hanski & Gilpin, 1997; Hovestadt *et al.*, 1999). Furthermore, strong evidence suggests that long distance dispersal is formative in the development of both island and continental biotas (Pole, 1994; Hurr *et al.*, 1999; Jordan, 2001; Muñoz *et al.*, 2004; De Queiroz, 2005; Sanmartín *et al.*, 2007).

Indeed, the ability of an organism to disperse effectively is frequently cited as a major factor determining relative abundance and has been implicated as an explanation for geographic distribution in terrestrial and marine systems (Hanski *et al.*, 1993; Brown *et al.*, 1996; Gaston, 2003). The probability of dispersal can be considered as the cumulative effect of three factors: (1) the number of disseminules produced (i.e. the size of the source); (2) the likelihood of a viable disseminule being carried from the source to the sink, which is dependent on the morphological dispersal traits, the probability of non-standard mechanisms, transport vectors, such as wind patterns, ocean currents, and migrant birds, the time taken to move from source to sink areas, and the time that the disseminule remains viable; (3) the likelihood of the disseminule establishing and expanding the gene pool, which is dictated by the availability of suitable habitat, and variables within the mating system (i.e. sink factors);

BIOGEOGRAPHY OF SOUTHERN HEMISPHERE FLORA

Plant biogeography in the Southern Hemisphere flora has attracted considerable attention (Setoguchi *et al.*, 1998; Muñoz *et al.*, 2004; Sanmartín & Ronquist, 2004; Sytsma *et al.*, 2004; Sanmartín *et al.*, 2007). The disjunct distributions in the Southern Hemisphere have long challenged biogeographers ever since Hooker (1855) first observed the floras of Tasmania, southern South America, New Zealand and the sub-Antarctic islands. Much speculation has been directed towards origins of these disjunctions (Wegener, 1912; Good, 1927; Koch, 1931; Camp, 1947; Good, 1951; Camp, 1952; Burbidge, 1960; Steenis, 1962; Good, 1964; Raven & Axelrod, 1974). Vicariance from Gondwanaland became the prevailing model in the late 20th century (Pole, 1994; De Queiroz, 2005; McGlone, 2005). However, recently, molecular studies, especially ones using molecular dating methods, have provided evidence for the prevalence of more recent long distance dispersal of Southern Hemisphere plants (Winkworth *et al.*, 1999; Winkworth *et al.*, 2002; De Queiroz, 2005; McGlone, 2005). In these studies, vicariance cannot adequately explain the divergence dates of the plant lineages (Wagstaff & Garnock-Jones, 1998; Hurr *et al.*, 1999; Lockhart *et al.*, 2001; Swenson *et al.*, 2001a; Von Hagen & Kadereit, 2001; Heenan *et al.*, 2002;

Perrie & Brownsey, 2005; Barker *et al.*, 2007; Perrie *et al.*, 2007). Even lineages considered the product of Gondwanan origins, such as *Nothofagus* (Swenson *et al.*, 2001a), appear to have undergone long distance dispersal, although there are still a few plant distributions, such as *Agathis* (Stöckler *et al.*, 2002; Knapp *et al.*, 2007), attributed strictly to vicariance. Therefore, the Southern Hemisphere flora may owe their current distribution to some complex combination of vicariance and long distance dispersal.

Among Southern Hemisphere systems, the floristic links between Tasmania and New Zealand have provided an ideal system for the study of historical biogeography. The claim that ―The current New Zealand flora is therefore best characterised as a specialized cool temperate subset of the Australian flora" (McGlone *et al.*, 2001) encapsulates the keystone motive behind floristic comparisons in New Zealand and Tasmania. Tasmania carries a ―specialised cool temperate subset of the Australian flora" (McGlone *et al.*, 2001) and shows climatic parallels with New Zealand, which falls in a similar latitudinal range, and is under the influence of the same strong westerly systems results in broadly similar vegetation types and habitats in the two regions.

Despite these similarities, some significant differences between Tasmania and New Zealand exist. Because Tasmania, like the mainland Australia, is subject to north to northwesterly winds, high temperatures and low humidity during summer (Foley, 1947), it is fire-prone. In response, members of the Tasmanian flora have evolved survival adaptations called vital attributes (Noble & Slatyer, 1981). The incidence of fire shapes the vegetation by creating disclimax scenarios where a stable ecological stage supplants the normal climax. These scenarios have given eucalypts and other trees within sclerophyll forests a competitive advantage in establishing new areas. Given its former geological link with mainland Australia, Tasmania also boasts a higher diversity of sclerophyllous species than New Zealand. Although it is positioned within the domain of mid-latitude winds, westerlies (Wardle, 1991), New Zealand lacks the continental influence of the mainland Australia on its climate and vegetation types. The incidence of fire is lower, thus the New Zealand flora lacks the vital attributes of the Tasmanian flora.

These attributes associated with species persistence in a fire-prone environment encompass vegetative resprouting (epicormic buds and lignotubers), and post-fire seed recruitment following disturbance. An exception is *Leptospermum scoparium* J.R. Forst. & G. Forst., a woody Myrtaceae for which seed germination is enhanced by fire (Stephens *et al.*, 2005). The sclerophyllous species that define Australian flora are noticeably absent or less diverse in New Zealand. Instead, New Zealand has a better representation of subtropical taxa in the lowland rainforests (Dawson, 1986). However, these differences do not preclude Tasmania and New Zealand as strong candidates for examining the dynamics of transoceanic dispersal.

Geology has long accounted for the biotic distributions of Tasmania and New Zealand. Separated by what is now East Antarctica, Tasmania and New Zealand were both part of Gondwana during the Jurassic and Early Cretaceous (McLoughlin 2001). New Zealand broke away from the supercontinent in the Late Cretaceous approximately 80 million years ago, and moved northwards. Although Tasmania and rest of Australia begin to rift away as early as the Jurassic, they remained physically close to Antarctica up to the mid Cenozoic, only breaking free 34 million years ago (McLoughlin 2001). During the 1990s and 1980s, scientists maintained the notion of ―Gondwanan‖ ancestry for New Zealand plants and animals, but recent work has suggested otherwise that long distance dispersal had an influential role in the assembly of New Zealand biota (Pole 1994; McLoughlin 2001; McGlone 2005).

Dispersal from Australia to New Zealand is a recurring pattern in molecular studies (Wagstaff & Garnock-Jones, 1998; Wagstaff *et al.*, 1999; Wagstaff & Wege, 2002; Ford *et al.*, 2007) that is largely congruent with the dominant West Wind Drift (Raven, 1973; Winkworth *et al.*, 2002; Muñoz *et al.*, 2004; Sanmartín *et al.*, 2007). In addition, there is evidence for some dispersal from Australia to New Zealand (Wagstaff & Garnock-Jones, 2000; Lockhart *et al.*, 2001; Wagstaff & Breitwieser, 2002; Wanntorp & Wanntorp, 2003). By no means are Australia and New Zealand the only land masses involved in reciprocal long distance dispersal since movements between New Zealand to Papua New Guinea, New

Zealand to South America, and New Zealand to Rapa have been revealed (Wagstaff *et al.*, 2002). What is remarkable is how a single long distance dispersal event can account for the proliferation and establishment of certain plant groups, especially those in New Zealand (Wagstaff & Garnock-Jones, 1998; Winkworth *et al.*, 1999; Perrie *et al.*, 2003; Meudt & Simpson, 2006).

WITHIN-SPECIES DISJUNCTIONS IN NEW ZEALAND AND AUSTRALIA

Within-species disjunctions between New Zealand and Australia occur in plant species ranging from ferns and fern allies to angiosperm woody shrubs. These disjunctions have yet to be accorded their full potential in historical biogeography, although they are utilised in studies of species richness, fossil records, and climatic and geological history. Endemic species (species confined to a specific geographical area) have been compared with disjunct species across the levels of taxon and habitat. Low rates of endemism within certain plant groups, such as ferns and orchids (McGlone *et al.*, 2001), and habitat types, like forests (Pole, 1994), have been interpreted as indicating high rates of recent disjunctions by long distance dispersal. However, low evolutionary rates can also result in low rates of endemism. Connecting disjunctions with fossil records has helped reconcile these limitations of the latter. Macphail (1997) compared ancient and modern disjunctions to argue that ancient lineages, even those of Gondwanan inheritance, may be just as susceptible to long distance dispersal as younger lineages.

The within-species disjunctions between Australia and New Zealand are invaluable for biogeography because the long isolation of these land masses, and combined with the broad similarity of the environments between the two regions this means that the incidence of these disjunctions can be capitalised as a proxy to estimate the relative rates of long distance dispersal. This proxy assignment is possible because these disjunctions can be confidently attributed to long distance dispersal. A vicariant history, the alternative view, seems implausible for within-

species disjunctions between New Zealand and Australia when geological, morphological, and phylogenetic histories are closely considered. Jordan (2001) explained that there has been no land connection between Tasmania and New Zealand for at least 50 million years (Wilford & Brown, 1994; Jordan, 2001; Ladiges & Cantrill, 2007), meaning that any vicariant within-species disjunctions would imply either morphological stasis in two genetically isolated populations for at least this period or remarkable convergent morphology. The former is particularly unlikely considering that although New Zealand and Tasmania have many current environmental similarities, the histories of the regions are highly divergent (Reid *et al.*, 1999; Lee *et al.*, 2001). Although Jordan (2001) cited the remarkable identical leaves of extinct and extant species in fossilized sediments these fossils are much younger than the last land connection between New Zealand and Australia. Jordan (2001) considered these examples as exceptions rather than the rule, and postulated that there may have been differences in morphological traits not observable on fossils (i.e. that although the fossils may have resembled the comparable organs on the modern relatives, the plants may have differentiated in other organs). Additional evidence have come from molecular studies of trans-Tasman within-species disjunctions that invoked long distance dispersal as an explanation for disjunctions appear to be much too recent to be vicariant (Setoguchi *et al.*, 1998; Smissen *et al.*, 2003; Smissen *et al.*, 2004). Ladiges and Cantrill (2007) urged a conservative interpretation of these studies.

The use of the frequency of within–species disjunctions as a proxy for the probability of dispersal within floras depends on the assumption that the disjunctions occur on the same temporal scale. This assumption would be satisfied if rates of speciation were equal among groups. This assumption is highly unlikely to be satisfied because rates of evolution vary markedly among taxonomic groups (Britten, 1986; Bousquet *et al.*, 1992) and among life forms (Donoghue, 2005; Edwards & Donoghue, 2006). However, the proxy will also hold true if the variation in rates of speciation is randomly organised with regard to the traits considered. This study depends on this latter assumption. Given that the criteria and assumptions are reasonably fulfilled, the within-species disjunctions in New

Zealand and Tasmania can serve as the foundation upon which the long distance dispersal model can be explored.

Care must be taken in utilising within-species disjunctions in biogeographical studies since not all disjunct species are equal. One limitation of these disjunctions may be their uncertain taxonomic status when disjunct species having significant prowess as transoceanic dispersers are investigated. For instance, *Dodonaea viscosa* is native in all the continents except Antarctica, with a distribution from 44°S (South Island, New Zealand) to 33°N (California and Arizona, North America) (West, 1984; Harrington & Gadek, 2009), while *Sicyos australis* occurs not only in Australia, but also Pacific islands and coastal North and South America. The virtually pan-global distribution of these transoceanic dispersers does present taxonomic conundrums since these dispersers are notoriously polymorphic and variants are tenuously recognised by either varietal or subspecies level rather than separate species. *Myriophyllum* exemplifies a case where one disjunct species was recognized as five separate species, which are nonetheless closely related and owe their distribution to long distance dispersal (Hill & Orchard, 1999). Local populations of disjunct species undergoing incipient speciation can be equally problematic. *Euphrasia*, a disjunct genus common in New Zealand and Tasmania, can have highly variable local populations that are difficult to accommodate taxonomically (Barker, 1982; Heads, 1994). Sometimes the comparisons on the species level between New Zealand and Tasmanian plants have been invalidated, as the example of *Coprosma pumila*, which was once thought to range from Australia to Tasmania, New Zealand and subantarctic islands, proved to be a Tasmanian endemic (Orchard, 1987; Orchard, 1987). In contrast, some disjunct congeners have, after careful taxonomic consideration, been established as being conspecific. For instance, *Montitega dealbata* was previously considered as one New Zealand species (*Cyathodes pumila*) and one Australian species (*Cyathodes dealbata*) (Albrecht *et al.*, 2010). These taxonomic challenges again introduce the ever-contentious issue of delimiting species and reconciling the species concept with historical biogeography. To date, the routine practice has been the treatment of species as fundamental units of analysis.

RESEARCH AIMS

This work considers the hypotheses described in subsequent chapters by estimating and comparing the frequency of disjunct species in New Zealand and Tasmania based on relative abundance and direction of dispersal under the assumption that these within-species- disjunctions are the product of long distance dispersal rather than vicariance.

In addition, the work seeks to test and compare the frequency of dispersal traits in the New Zealand and Tasmania. If the New Zealand flora is largely the product of long distance dispersal, then the disjunct flora is typical in terms of the dispersal traits. In contrast, the disjunct flora in Tasmania is atypical because Tasmania and mainland Australia is the source of most migrants to New Zealand, and Gondwanan inheritance has influenced largely their floristic composition.

These aims delineate the subsequent structure of the dissertation. Chapter 2 analyses the relationship between relative abundance and the frequency and direction of dispersal in within-species disjunctions in New Zealand and Tasmania. By considering the flora of these islands in its entirety (including within-species disjunctions), Chapter 3 investigates the influence of dispersal traits. Chapter 4 summarises and discusses the findings, which are fitted within the overall context of the Southern Hemisphere biogeography.

CHAPTER 2: THE EFFECT OF RELATIVE ABUNDANCE ON DISJUNCT VASCULAR SPECIES OF NEW ZEALAND AND TASMANIA

INTRODUCTION

Abundance, the density and distribution of individuals within an area or community at a given time, can reflect an organism's reproductive rate and subsequent establishment in a geographical region. An organism may boast a prolific reproductive rate that ensures a higher probability of its disseminules being dispersed, but its measure of ecological success comes from the frequency of those disseminules exploiting and forming additional populations on virgin territory. Except for those having largely vicariant origins, disjunct species typify such dispersible organisms because they have traversed barriers to form self-reproducing immigrant populations. The flow between separate landmasses does not need to be regular since rare or infrequent long distance dispersal events can be more significant than successive local dispersal events over a long period (see Chapter 1). Thus, the relative abundance of organisms that show intra-specific disjunctions can provide evidence on the frequency and direction of the dispersals in the long distance dispersal model. As a result, examining the disjunctions between New Zealand and Tasmania will help close the conceptual gap of relative abundance and island biogeography.

It has been long recognised that dispersal and relative abundance may be positively correlated. If disjunctions are less frequent for uncommon species than common species, it provides evidence that the degree of dispersal is related to relative abundance. There are several reasons to expect this and these alternatives explanations raise testable hypotheses as summarised in Table 1.

Firstly, given the theory established in Chapter 1, source size should be expected to influence the frequency of dispersal by affecting the number of disseminules. All other things being equal, large sources will produce more disseminules than small ones, and therefore have higher probabilities of dispersal. Consequently, species that are rare in the source would be under-represented in the dispersed flora.

Table 1 Hypotheses examined in the relative abundance-disjunction relationship in New Zealand and Tasmania. Note that hypotheses 2 and 3 do not necessarily provide mutually exclusive predictions.

HYPOTHESIS	PREDICTION
1. Relative abundance is related to dispersal frequency	Over-representation of common species in the disjunct flora
2. Source size affects probability of dispersal, by providing more disseminules	Disjunct species are more common in the source area than in the sink
3. Immigrant species have not expanded to their full potential range within the sink	Disjunct species are rarer in the sink area than the source area; and On average, observed ecological range of disjunct species in the source area should be greater than the observed range of these species in the sink area
4. Species that arrive are successful due to ecological release	Disjunct species are more common in the sink area than source area; and The observed habitat range of disjunct species in the source area is less than their apparent ecological range in the sink area.
5. Species with broad ecological tolerance ranges (ecological niche breadth) are more likely to disperse because of greater habitat availability in the sink area	Over-representation of common species and under-representation of rare species in both source and sink; and Apparent ecological range of common species in the source area is greater than that of rare species in the source area

Secondly, species may not have realised their full potential in the sink, increasing the likelihood of disjunct species being rarer in the sink area than the source area, and that the ecological range of the species may be similarly smaller in the sink than the source.

Thirdly, ecological release in which a species increases its habitat and resource range in areas of less interspecific competition (Van Valen, 1965; Schoener, 1989; Bolnick *et al.*, 2010) may result in an impact on the relative abundance of disjunct species. This release would be expected to promote the success of species in the sink area, both in terms of abundance and ecological range, through processes that

are analogous to the well documented expansion of weed species (Di Castri *et al.*, 1990; Groves & Di Castri, 1991; Ramakrisnan, 1991). Under this scenario, disjunct species can become more common in the sink area than the source area.

A fourth relationship between relative abundance of dispersal is that species with wide ecological ranges may be more likely to be dispersed. The underlying logic behind this is that species with wide ecological ranges may be more likely to find areas of suitable habitat in the sink area. Given the other factors affecting the abundance of species in the sink (as described above), this is best tested by considering the ecological range of common disjunct species in the source area - these should be greater than those of uncommon disjunct species in the source area. This evidence may be reinforced if common species were over-represented in both source and sink, and uncommon species being under-represented in both areas.

Additional hypotheses can be raised, but these are not testable based on the current data. However, they may be tested using chronologically controlled evidence such as fossil record or molecular dating. Thus, species with limited dispersal ability may be less common because they are less likely to colonize and distribute propagules to distant sites (Wellington & Victor, 1989; Gutiérrez & Menéndez, 1997; Kunin & Gaston, 1997; Thompson *et al.*, 1999; Latimer *et al.*, 2005; Urban *et al.*, 2008). Also, poorly dispersed species may be expected to expand to reach their full potential geographic range more slowly than well dispersed species. Furthermore, poorly dispersed species are predicted to undergo more isolation and lower gene exchange between populations, therefore the probability of speciation increases (Shuto, 1974; Hansen, 1980; Jablonski, 1986; Palumbi, 1992). Species restricted or rare in their ranges may be the product of natural selection for limited dispersal if high dispersal is not advantageous (Gutiérrez & Menéndez, 1997; Thompson *et al.*, 1999; Gaston, 2003).

Although the relationship between relative abundance and dispersal is clearly complex, the discussion above shows that relative abundance has a potential to be used to create an estimable and reasonable structure for comprehending the

phenomenon of long distance dispersal between New Zealand and Tasmania. In dealing with these concepts, however, it is important to remember that relative abundance can vary markedly through time. In particular, the dispersal event that led to the within species disjunction may be old. The exact age of any of the within-species disjunction is at present unclear, but given estimated rates of speciation in the order of millions of years (Magallon & Sanderson, 2001), major environmental changes are since the time of dispersal for many of these species. In other words, environmental change may have decoupled the relationship between relative abundance and dispersal. However, assuming that this decoupling results in random patterns, significant relationships matching the predictions would provide evidence for the hypotheses.

This chapter presents a comparative study of the relative abundance of within-species disjunctions and that of the non-disjunct indigenous species in the New Zealand and Tasmania vascular flora. Relative abundance is treated here as a cumulative unit for the hypothetical number of dispersal events and post-dispersal survival and success (even when conditions are influenced by human intervention). In addition, the direction of dispersal was compiled from literature and compared for the within-species disjunctions in correlation to their relative abundance. In particular, to test the aforementioned hypotheses, the specific predictions described in Table 1 will be tested. Several of these predictions rely on a grasp of the species ecological range, and because an objective and uniform assessment of the species ecological range is difficult to produce, the altitudinal zone will serve as the proxy.

MATERIAL AND METHODS

This work is based on data compiled from the vascular plant species currently recognised as indigenous to Tasmania (Curtis, 1963; Curtis, 1967; Curtis, 1975, 1979; Curtis & Morris, 1994; Buchanan, 2009) and New Zealand (Allan, 1961; Moore & Edgar, 1970). The following characteristics were scored for each species in Tasmania and New Zealand.

Group: Species were categorised according to major taxonomic group: conifers, dicots, monocots, ferns.

Family: Families were based on Angiosperm Phylogeny Group (2003).

Altitudinal Zone: Species were categorised into major altitudinal zones: coastal, lowland, montane, subalpine/alpine (Wardle, 1991; Reid *et al.*, 1999). Species that occurred in both Tasmania and New Zealand were given separate scores for each region. Altitudinal zone can be a measure of a species' ecological range. If immigrant species are predicted to be more ecologically versatile, then they should occupy more altitudinal zones than being constrained within one. The data were collated from various sources (Allan, 1961; Curtis, 1963; Curtis, 1967; Moore & Edgar, 1970; Curtis, 1975, 1979; Salmon, 1985; Johnson & Brooke, 1989; Wardle, 1991; Curtis & Morris, 1994; Mark & Adams, 1995; Williams & Potts, 1996; Kirkpatrick, 1997; Reid *et al.*, 1999; Bayly & Kellow, 2006; Burrows, 2008, 2009).

Coastal: Species were classified as coastal if they occurred in areas within a few kilometres of the sea and influenced by marine processes, such as prevailing on-shore winds, salt deposition, salt or brackish water, and sand movement. With temperatures moderated by water bodies, the coastal areas in New Zealand and Tasmania include wetlands (lagoons, swamps, and estuaries) and sand dunes sparsely vegetated to heathlands and neighboring woodlands usually (Wardle, 1991; Reid *et al.*, 1999). Coastal forests are lower in stature than inland forests due to exposed conditions.

Lowland: Species were placed in the lowland category if the habitats indicated in the references above were free of maritime influences, although some did have both coastal and lowland distributions. Although there is some overlap with coastal vegetation, the key discriminating feature is that they are not regularly subject to the saline conditions of the coastal areas, the lowland areas cover a broader range of habitats encompassing wetlands, moorlands, grasslands, and most importantly forests (Wardle, 1991; Reid *et al.*, 1999). Dry and wet sclerophyll forests form extensive communities in Tasmanian lowland areas,

although the distinction between dry and wet sclerophyll forests is based on increasing water availability and heights of woody plants (Reid *et al.*, 1999). Tussock grasslands and fernlands occupy the lowland plains of New Zealand, although broadleaf conifer and *Nothofagus* forests can be found as well (Wardle, 1991). One principal difference between the lowland forests of New Zealand and Tasmania is that conifers are found in the former, but generally missing in the latter.

Montane: Species were classified as montane if they inhabited the highland areas below the subalpine zone. Generally, the montane zone has colder temperatures and higher precipitation than the lowland zone. *Nothofagus* rainforests loosely characterize the montane zones in New Zealand and Tasmania. Lianes, vascular epiphytes, *Weinmannia racemosa*, and *Nothofagus fusca* delineate the upper limit of the montane zone in New Zealand (Wardle, 1991). However, given its overlapping range in the subalpine and alpine regions of Tasmania, the tree line is poorly defined.

*Subalpine***:** Species were deemed subalpine if they inhabited coniferous – hardwood or beech forests and shrublands in New Zealand and Tasmania before giving away to microshrubs and bolster plants (tussock grasslands in New Zealand) (Wardle, 1991; Mark & Adams, 1995; Reid *et al.*, 1999). Although the subalpine zone in New Zealand is defined as penalpine, meaning a zone lacking otherwise dominant subalpine trees, but having scrub and tussock-herbland (Wardle, 1991), subalpine here applies to forest and tall scrub below the tree-line for easier categorization.

The subalpine-alpine boundary is not obvious, and references sometimes do not make the distinction clear, preferring instead to combine the subalpine and alpine zones together (Mark & Adams, 1995; Kirkpatrick, 1997; Reid *et al.*, 1999).

*Alpine***:** Species were defined as alpine if they occurred above the tree line (Mark & Adams, 1995; Kirkpatrick, 1997). In Tasmania, the climatic tree line is variable, ranging from approximately 800 m above sea level in southwest Tasmania to over 1400 m above sea level in northeast (Kirkpatrick, 1997). In New

Zealand, the tree lines range from 500 m in the far South Island to 1,500 m in the northern parts of the North Island (Wardle, 1991).

Alpine species display patterns of endemism and disjunction that can signify biogeographical histories. McGlone *et al.* (2001) discovered that only 35% of the alpine specialists were capable of long distance dispersal in contrast to 65% of the nonspecialists. They concluded that alpine specialists were less capable of bridging regions of unsuitable habitat through long distance dispersal.

Width of altitudinal zone: Species were defined as having a narrow altitudinal zone in one or other region if they were restricted to only altitudinal zone in that region. Other species were defined as having a broad altitudinal zone. This differentiation was used as a proxy for breadth of realized ecological niche.

Abundance: two levels: ―Uncommon" includes all species that have been identified as being extinct, rare, endangered or vulnerable by Kirkpatrick *et al.* (1991) and Molloy *et al.* (2002) or Uncommon by Kirkpatrick *et al.* (1991) and de Lange *et al.* (2009); ―Common" represents all other species.

Direction of Dispersal: Species showing within species disjunctions were categorised according to inferred direction of dispersal: Australia (Tasmania) to New Zealand; New Zealand to Australia (Tasmania); unknown. The direction of dispersal was inferred from the published phylogenetic reconstruction and molecular dating, especially sequence divergence and divergence times (i.e. vicariance is unlikely to account for recent divergence dates) for New Zealand and Australian groups, within the relevant papers. Appendix 1 contains a list of the disjunct species, with inferred direction and source of evidence for directionality.

STATISTICAL ANALYSES

The data were organised in MS Excel 2003 worksheets, and the analyses were performed on MS Excel 2003's PivotTable and PivotChart Report. Differences in the incidence of disjunction, habitat, and relative abundance were established

using the chi-test for independence in 2 x 2 contingency tables. The tables were used to test for interactions among the variables.

RESULTS

Relative abundance of disjunct and non-disjunct species

293 species of vascular plants are recognized as disjunct in Tasmania and New Zealand (Appendix 1). This number represents 17.2% of the Tasmanian flora (1691 species) and 14.3% of the New Zealand flora (2083 species). In both New Zealand and Tasmania, disjunct species are significantly more likely to be common than non-disjunct species ($P<0.001$) (Table 2). 29% of disjunct New Zealand species are uncommon, whereas 43% of the non-disjunct New Zealand species fall within the same rarity category (Fig. 1). Similar frequencies were observed within the Tasmanian flora: only 30% of disjunct Tasmanian species were uncommon whereas 47% of the non-disjunct Tasmanian species were uncommon (Fig. 1). Thus, non-disjunct rare/uncommon species in New Zealand and Tasmania are over-represented by 4.5% and 6.0% respectively, whereas the disjunct rare/uncommon species in New Zealand and Tasmania were under-represented by 41% and 30% (Table 2).

Table 2. Observed and expected numbers (disjunct and non-disjunct) of species according to their relative abundance within New Zealand and Tasmania. The number of indigenous vascular plant species in each flora is given (n). Results from the analysis of deviance are given (G, P)

	Class	Observed	Expected	% Difference	G
New Zealand n= 2079	Non-disjunct uncommon	777	741	+5%	20.50, P < 0.0001
	Non-Disjunct Common	1013	1048	-3%	
	Disjunct uncommon	86	121	-41%	
	Disjunct Common	207	172	+17%	
Tasmania n= 1691	Non-disjunct uncommon	657	617	+6%	26.52, P<0.0001
	Non-disjunct common	743	783	-5%	
	Disjunct uncommon	89	128	-44%	
	Disjunct Common	203	163	+20%	

Note: One disjunct species in Tasmania was excluded due to a lack of information regarding relative abundance.
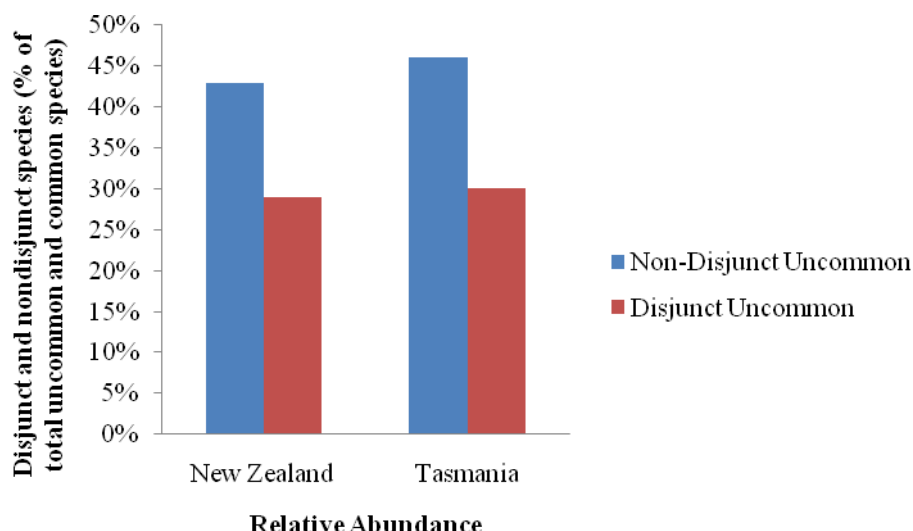
Fig. 1. Incidence of trans-Tasman disjunction in uncommon/rare species compared to common species. These are expressed as proportions of all uncommon/rare species and common species (respectively) in New Zealand and Tasmania.

There was a strong bias among disjunct species in the direction of dispersal, with species inferred as having migrated from Tasmania to New Zealand being approximately 19 times the number of species having migrated in the opposite direction (Fig. 2). This difference was very highly significant (χ^2 =147; *P* << 0.001; test based on expected values of equal numbers of dispersals in each direction). However, for ~38% of the species (many of these being ferns) the direction of migration was ambiguous. These species were excluded from the analyses of source-sink relationships. It is assumed that their exclusion does not bias the inferences.

Relative abundance in disjunct species in relation to dispersal direction

The disjunct species for which dispersal direction could be inferred revealed differences in relative abundances between the sink and source regions. 12% of these species (21 altogether) were uncommon in both sink and source regions (Fig. 3, Table 3).
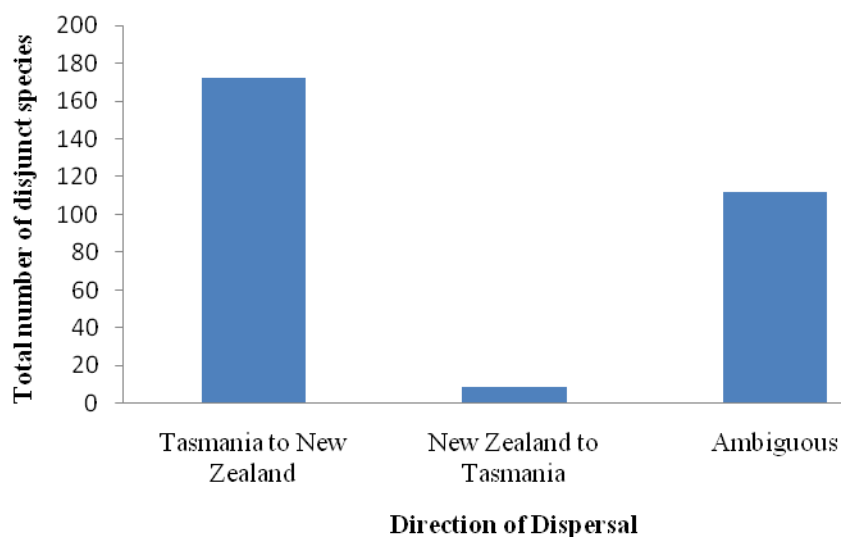
Fig. 2. Total number of disjunct species categorised by the direction of dispersal.
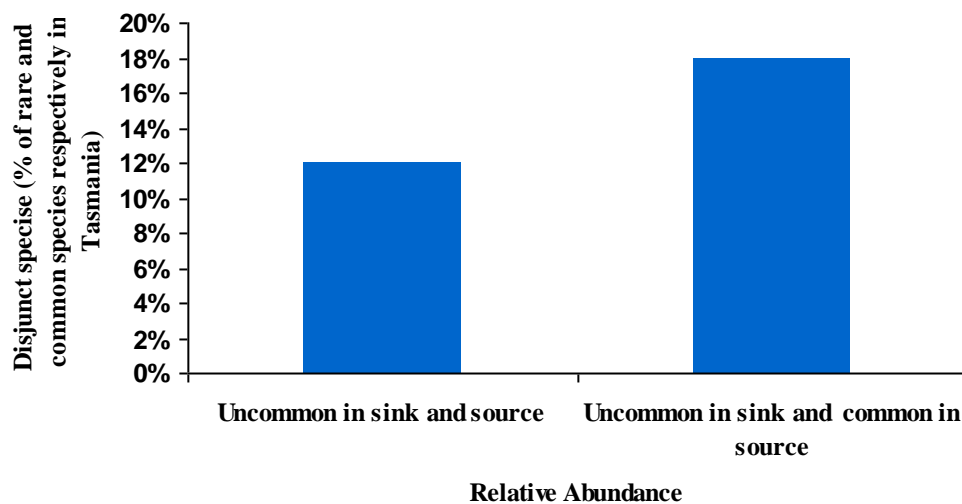
Fig. 3. Rare and common disjunct species (dispersers for which long distance dispersal from Tasmania to New Zealand is apparent) in sink and source regions, expressed as proportions of the total number of species in their category

Table 3. Observed (Obs.) and expected (Exp.) number of within-species disjunctions (long distance dispersal from Tasmania to New Zealand) according to relative abundance in sink and source regions. Results from the analysis of deviance are given (G, P)

Class	Obs.	Exp.	% Gain in Representation	G value
Uncommon in sink and source	21	13	+38%	
Uncommon in sink, common in source	31	39	-25%	10.09,
Common in sink and source	98	90	+8%	P < 0.01
Common in sink, uncommon in source	21	29	-38%	

Relative abundance in disjunct species by altitudinal range

47% of the disjunct species maintained restricted altitudinal ranges in both the sink and source locations while 21% of the species had widespread altitudinal ranges in both locations (Fig. 4). Both were significantly over-represented (P<0.001; Table 4). 24% had expanded their altitudinal range in the sink, with only 8% failing to do so (Fig. 4). These species were significantly under-represented (P<0.001; Table 4).
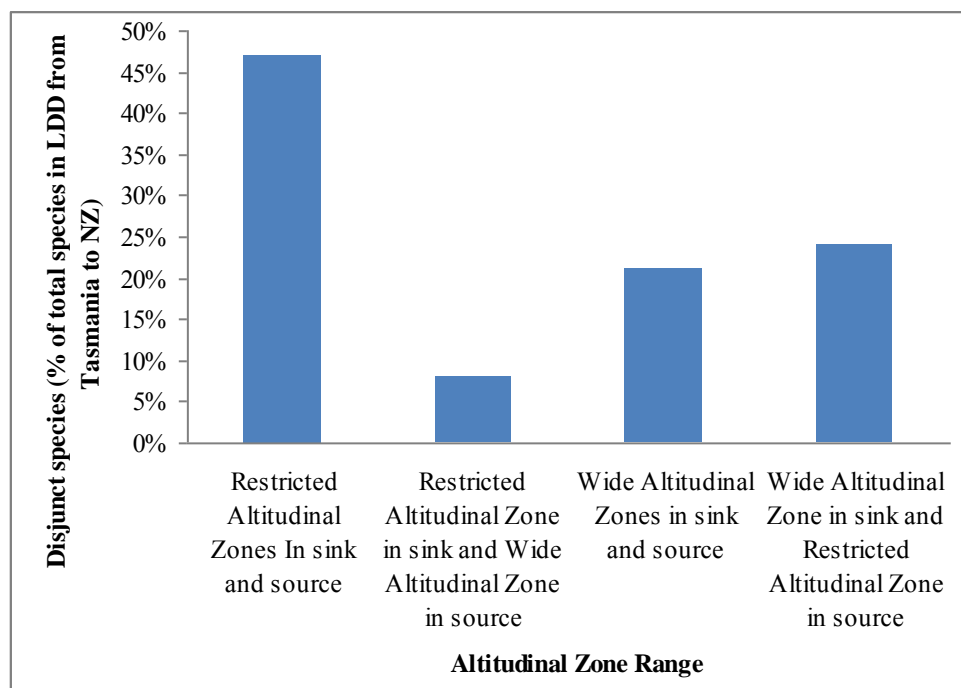
Fig. 4. Disjunct species by altitudinal range in sink and source regions expressed as proportions of total number of species

Table 4. Observed and expected number of within-species disjunctions (long distance dispersal from Tasmania to New Zealand) according to altitudinal zone range in sink (New Zealand) and source (Tasmania). Results from the analysis of deviance are given (G, P)

Class	Observed	Expected	% Gain in Representation	G value, P
Narrow in both sink and source	81	67	+17%	
Narrow in sink and wide in source	41	55	-34%	21.14,
Wide in both sink and source	36	22	+39%	P<0.001
Wide in sink and narrow in source	14	28	-100%	

DISCUSSION

What is the relationship between within-species disjunctions and relative abundance?

The evidence (Fig. 1, Table 2) that the frequency of within-species disjunctions is greater for species that are common suggests a positive relationship between species abundance and frequency of dispersal. Although species do vary in relative abundance through time and source size therefore fluctuates, this strong positive relationship would suggest the presence of an underlying relationship between relative abundance and dispersal - there is no reason to suspect that this relationship is due to some bias. In New Zealand and Tasmania, approximately 30% of the disjunct flora are uncommon and this modest percentage stands in strong contrast against 70% of the disjunct flora that are common (Fig. 1). The effects of differences in sample sizes of the cumulative flora (Table 2) and differences in the land area size for Tasmania (90,587 km^2) and New Zealand (268,021 km^2) on these frequencies appear to be minimal. This apparent stability of relative abundance maintained in the two different floras underscores the ecological conservatism of disjunctions. Indeed, physiological traits underlying relative abundance of disjunct species are believed to be evolutionarily stable (Huntley *et al.*, 1989; Svenning, 2003; Qian & Ricklefs, 2004). Climatic requirements are relatively consistent for disjunct species, especially those pre-adapted for alpine environments. For instance, species of *Donatia, Phyllachne, Scleranthus,* and *Oreobolus,* all of which have within-species disjunctions, exemplify the physiological and climatic adaptations that conservatively delineate their distributions in New Zealand and Tasmania (Gibson & Kirkpatrick, 1985;

Wagstaff & Wege, 2002; Smissen *et al.*, 2003). Exposed to climatic extremes of their alpine and subalpine environments, these disjunct species condense their shoots and internodes tightly, forming the cushions up to 3 metres or more that categorise them as cushion plants (soft mat and bolster forms) (Gibson & Kirkpatrick, 1985). The consistent trend in the New Zealand and Tasmanian frequencies highlighted in Figure 1 is further reinforced by the patterns of representation in disjunction and relative abundance: observed values for common disjunct species on both islands were significantly over-represented (Table 2).

On the other hand, the statistically significant under-representation of uncommon disjunct species in both New Zealand and Tasmania (Table 2) supports the concept of rarity as a consequence of limited dispersal. If rarity was not related to limited dispersal, then we would have expected the within-species disjunctions of rare species to be as well represented as common species in both island floras, whereas the results have proved otherwise. Such a link between rarity and limited dispersal has also been established for several Australasian taxa (Coates *et al.*, 1999; Rossetto *et al.*, 2008), although it has yet to be applied specifically and broadly to disjunct taxa, and not without assessing the impact of specialised habitat requirements and genetic bottlenecks on relative abundance. However, the over-representation of non-disjunct uncommon species in New Zealand and Tasmania (Table 2) may be attributable to specialised habitat requirements and genetic bottlenecks (numbers in the population must be very low) characterising their distributions. Outside of plants, limited dispersal has been found to be formative in the structure of freshwater fish communities (Drakou *et al.*, 2009), and when acknowledged with environmental and species heterogeneity, in birds and land snails (Steinitz *et al.*, 2006).

To what degree does habitat availability dictate rarity in disjunct species here? Rossetto *et al.* (2008) suggested that a disparity exists between the distribution of a rare species with limited dispersal and the availability of suitable habitats. Therefore, even if the proportion of potential habitats does exceed that of realised niches, the species still retains its narrow distribution, despite having successfully navigated physical barriers to establish disjunct populations. It seems reasonable

to anticipate and expect dispersal to be a primary factor in the relative abundance of within-species disjunctions, although such generalisation, like elsewhere, should be taken cautiously. Thus if dispersal is reasoned to be a driving force behind the relative abundance of within-species disjunctions in Tasmania and New Zealand, then its success is tied to source size.

Are within-species disjunctions related to source and sink sizes?

The data in Fig. 3, Table 3 implies that source size does affect the probability of dispersal, because species that are common in the source area show significantly higher rates of disjunction than species that are rare in the source area in the disjunct flora experience greater transoceanic movement. A larger source size can correlate to more disseminule production, and in turn translates to a higher probability of successful dispersal. However, having a large source size does not always lead to colonisation success and habitat suitability, nor does it guarantee long-distance survival and viability of disseminules upon their arrival in a sink area. In all, disjunct species do not always fulfill their potential range within the sink.

A number of the species that are more abundant in the source area than in the sink area are vagrants as defined by (De Lange & Molloy, 1995) and (De Lange & Norton, 1998) (Table 5): ‖taxa whose presence within the New Zealand botanical region is naturally transitory…which have failed to establish themselves significantly beyond their point of introduction through reproductive failure or for quite specific ecological reasons." The occurrence of vagrant species validates the metapopulation theory utilising the ‗rescue effect‗ principle (Edwards & Westoby, 1996; Duncan *et al.*, 1999). Vagrant species can be viewed as ‗sink‗ populations still extant due to steady immigration from ‗source‗ productions (Brown & Kodric-Brown, 1977; Gotelli, 1991). They exemplify species unfit for persistence, but exist solely by chance or transient conditions. Based on their reduced abundance and distribution, vagrant species represent the consequence of disseminule limitation

Disseminule limitation occurs in two stages: source populations produce less seeds, and dispersal of viable seeds become limited (Clark *et al.*, 1998; Nathan & Muller-Landau, 2000; Muller-Landau *et al.*, 2002; Ehrlén *et al.*, 2006). Such overriding effect of disseminule quantity on colonisation success and habitat suitability revisits the definition of rarity as a manifestation of limited dispersal. Although suitable ecological conditions are present, the disseminule quantity arriving at the destination is insufficient to ensure establishment. Its influence in relative abundance has been acknowledged (Turnbull *et al.*, 2000; Rees *et al.*, 2001; Bolker *et al.*, 2003), but supported with weak empirical evidence. On a localised scale, disseminule availability proved to have a strong correlation with relative abundance in an eleven-year analysis of disseminule recruitment while environmental conditions and species heterogeneity were less relevant (Ehrlén *et al.*, 2006). Replicating the long-term analysis of disseminule recruitment is unfeasible, given the distances and barriers involved in within-species disjunctions, although the correlation between disseminule availability and relative abundance is suggested by the eleven of the twenty disjunct taxa in Asteraceae (Appendix 1), a family known for its profligacy, having common trans-Tasman distributions.

Table 5: Vagrant Species in New Zealand (via Tasmania)

Family	Species	Reference
Aizoaceae	*Disphyma clavellatum*	(De Lange *et al.*, 2009)
Asteraceae	*Senecio australis*	(De Lange *et al.*, 2009)
Chenopodiaceae	*Atriplex cinerea*	(De Lange *et al.*, 1998)
Convolvulaceae	*Wilsonia backhousei*	(Jane & Sykes, 1995; De Lange *et al.*, 2009)
Droseraceae	*Drosera peltata*	(De Lange *et al.*, 2009)
Gleicheniaceae	*Sticherus tener*	(De Lange *et al.*, 2009)
Onagraceae	*Epilobium gunnianum*	(De Lange *et al.*, 2009)
Orchidaceae	*Myrmechila formicifera*	(De Lange *et al.*, 2009)
Orchidaceae	*Myrmechila trapeziformis*	(De Lange *et al.*, 2009)
Orchidaceae	*Pterostylis nutans*	(De Lange *et al.*, 2009)
Orchidaceae	*Simpliglottis valida*	(De Lange *et al.*, 2009)
Orchidaceae	*Thelymitra malvina*	(De Lange *et al.*, 2009)
Phrymaceae	*Mazus pumilio*	(Heenan & Forester, 1997; De Lange *et al.*, 2009)
Plantaginaceae	*Gratiola pubescens*	(De Lange *et al.*, 2009)

Is there an effect of ecological release?

On the other hand, disseminule limitation in a source population does not necessarily equate to a diminished distribution in the sink area if ecological release, the expansion of habitat and resource of a species grows in areas of lower interspecific competition (Van Valen, 1965; Schoener, 1989), is critically involved. Ecological release can be a powerful mechanism for species successful in the sink destinations. However, the significant under-representation of the observed 21 disjunct species that are more common in sink than the source areas does not support ecological release as a success factor in species arriving in new areas (Table 3).

Is disjunction related to ecological niche breadth?

The significant over-representation of both common and uncommon species in both source and sink areas (Table 3) can be interpreted as a consequence of common species having greater ecological niche breadth than uncommon species. While reproductive success sometimes constrains the dispersal of uncommon species, habitat availability can be a limiting factor if the niche threshold, the range of ecological tolerance, is low. Since uncommon species retain restricted altitudinal zones in both sink and source areas ($P<0.001$) (Table 4), they exemplify constraints from specific ecological requirements and an inability to bridge areas of less suitable habitats. Simply an alpine or montane specialist is less capable of expanding its range into lowland or coastal areas. Thus, a narrow habitat range can be a signifier of a species' relative abundance and revisits the principles of limited dispersal, lower reproductive rate, and habitat availability detailed earlier.

Habitat ranges have been applied successfully to test predictions for the distribution and patterns of local endemism in New Zealand alpine species (McGlone *et al.*, 2001). In their study of New Zealand alpine flora (disjunct and non-disjunct), McGlone *et al.* (2001) confirmed that specialist alpine species (n=114, 35%) are significantly under-represented among long-distance dispersers and argued that because these species have specific habitat requirements, they will

be less successful in colonizing less than ideal habitat through long-distance dispersal. In contrast, generalists are overrepresented because they are able to occupy a wide range of habitats outside the alpine zones. These results are consistent with the over-representation of species with wide altitudinal ranges in source and sink (Fig. 4, Table 4). They support the strong tendency of generalists to retain their ecological advantages in new territory. Studies of interspecific correlations between niche range and relative abundance have produced divergent conclusions, albeit in two different geographic regions. Rare and common species in southern Western Australia did not reveal any significant differences in their niche range (Burgman, 1989). In contrast, a positive relationship between niche range and relative abundance was demonstrated for herbaceous species in central England (Thompson *et al.*, 1998). The divergence in these results highlights the influence of habitat types and species composition on dispersal and colonisation success and there is no reason not to anticipate the same for the Tasmanian disjunctions.

Future implications

The strong correlation in relative abundance and within-species disjunctions in Tasmania and New Zealand reinforces the growing relevancy of long distance dispersal in historical biogeography. Moreover, the results here raise several questions for future studies. Do disjunct species have higher reproductive rates than their non-disjunct equivalents? Are there any differences in evolutionary rates between highly dispersible and less dispersible species? Such questions call for the application of molecular methods to test the alternative explanation of age differences between disjunct and non-disjunct species. Disjunct species may be older than the non-disjunct species and their temporal advantage means that they have an equal probability of being dispersed as much as widespread and abundant younger, but non-disjunct species do. However, phylogenetic studies of Tasmanian and New Zealand flora are incomplete and therefore do not present a complete picture to test this hypothesis. When these studies do develop fully in the future, the results should prove to be interesting. Vegetation types of similar floristic composition in New Zealand and southern Andes (South America) have

been assessed for their proportions of ancestral and modern phylogenetic groups (Ezcurra *et al.*, 2008), and while this assessment is valuable in a broad context, the relative abundance and ecological drivers for within-species disjunctions are not presented. A farther consideration is tabulating climatic conditions (annual precipitation, mean annual temperature, monthly temperatures) and correlating them to the disjunct species, an approach used by Qian and Ricklefs (2004) to evaluate the geographical and climate distributions of disjunct vascular genera in eastern Asia and North America. Nonetheless, the Tasmanian and New Zealand disjunctions present an interesting examination of relative abundance and dispersal in the long distance dispersal model, highlighting the importance of successful dispersal and post-dispersal colonisation in biogeography.

CHAPTER 3: AN INVESTIGATION OF FEATURES RELATED TO LONG DISTANCE DISPERSAL, BASED ON DISJUNCT SPECIES BETWEEN NEW ZEALAND AND TASMANIA

INTRODUCTION

The ability of a plant species to transcend physical barriers and environmental challenges, as well as establish disjunct populations depends not only on the effectiveness of their dispersal mechanisms, but also ecological traits that may affect the establishment of species once dispersal has occurred. Such dispersal can occur through various processes, which van der Pijl (1982) was among the first to categorise: anemochory (wind dispersal), hydrochory (water dispersal), ectozoochory (adhesive dispersal on animals), endozoochory (dispersal through digestion), and autochory (ballistic dispersal). Plants can also disperse by gravity dispersal, which is often typified as a lack of such specialized mechanisms.

Specialised dispersal mechanisms can lead to wider geographic distributions. For example, one study of Australian plants showed that species dependent on vertebrate dispersal colonized more areas than those with non-specialised dispersal features (Oakwood *et al.*, 1993), and a comparison of *Acacia* and *Eucalyptus* species with similar seed sizes revealed respective advantages in having avian dispersal and wings for wind dispersal (Edwards & Westoby, 1996).

The success of disjunct species in colonising islands and other distant landmasses is also contingent on the survival of their disseminules (seed, fruit, or any vegetative tissue that produces another individual) during the ‚journey', the suitability of the sites reached for establishment of an individual of the species, and their capability of the initial immigration population to expand. The last step of expansion is crucial for disjunct species that have traits to promote high abundance and overcome challenges simultaneously, with some exceptions reserved for those with already restricted distributions. Many traits that may relate success in establishment are diverse, ranging from growth (such as habit, longevity), reproductive characters, (such as sexuality and disseminule size) and abiotic and biotic relationships (habitat, especially related to successional

characteristics; dependency on other organisms such as pollinators and altitudinal zone). Molecular analyses, bolstered by the growing acceptance of long distance dispersal as a key player in the South Hemisphere biogeography, make some acknowledgment of the importance of traits, but to date no overall consensus has been reached in characterising long distance dispersal and traits. The modelling of long distance disseminule dispersal is in its infancy and has shifted from the standard dispersal syndromes towards unusual climatic occurrences and generalised long distance dispersal vectors (Cain *et al.*, 2000; Nathan, 2006). Large-scale studies on the relationship between long distance dispersal and ecological and morphological traits are rarer, despite methods that quantify long distance dispersal by capitalising on individual movements and combining modelling and empirical tools (Greene & Calogeropoulos, 2002; Nathan *et al.*, 2003). Two major studies have focused on taxa in the Northern Hemisphere: the Tvärminne Archipelago in southern Finland (Hayren, 1914; Luther, 1961) and Surtsey Island, near Iceland (Fridriksson, 1975). An analysis of ecological and morphological traits and long distance dispersal in the Southern Hemisphere has been confined to vascular species (excluding orchids) of Tasmania, also native to New Zealand, allowing for the assumptions that these within-species disjunctions are attributed to long distance dispersal rather than vicariance, and variation in rates of speciation is randomly organised in correlation to many of the major dispersal traits (Jordan, 2001).

Admittedly, a methodology that amalgamates different disjunct species and disparate, multiple traits for robust relationships with long distance dispersal is not without risks. Previous studies instead have concentrated on connecting the studies within one genus or a few closely related genera in one region (Aizen & Patterson, 1990; Murray & Gill, 2001; Murray *et al.*, 2002). Focusing on the within-species disjunctions of New Zealand and Tasmania, as well as the climatic and vegetation similarities between both islands (See Chapter 1) minimises the context-dependent variability encountered in similar studies on rarity-common associated traits for taxa on different continents. Murray *et al.* (2002) emphasised the importance of distinguishing those traits that allow species to become abundant and widespread and those traits related to constancy at low abundance or

limited ranges, but this differentiation is more pertinent at a local scale, a scope outside of our study.

This study uses information gleamed from literature to assess the within-species plant disjunctions between New Zealand and Tasmania (293 vascular plant species) to ecological and morphological traits. The traits in these disjunct species were compared with those of non-disjunct species for their significance in long distance dispersal. The main objective was to identify and determine which traits that distinguished the disjunct and non-disjunct species reliably, were not significantly different for both species, or related independently in a specific context (family, habitat preferences).

MATERIAL AND METHODS

The study group is the same as utilised in Chapter 2. Each species was scored for each of the following trait. Where the trait varied between the two regions (i.e. the same species scored different values in the different regions), a separate variable was scored for each region.

Group: Species were categorised as conifer, dicot, monocot, or fern (Allan, 1961; Curtis, 1963; Curtis, 1967; Moore & Edgar, 1970; Curtis, 1975, 1979; Curtis & Morris, 1994; Edgar & Connor, 1999; Buchanan, 2009).

Family: Families were based on Angiosperm Phylogeny Group (2003).

Habit: Species were categorised as woody perennial (tree, shrub, or woody vine); annual monocot; perennial monocot; annual dicot; or perennial dicot herb (Allan, 1961; Curtis, 1963; Curtis, 1967; Moore & Edgar, 1970; Curtis, 1975, 1979; Curtis & Morris, 1994; Edgar & Connor, 1999; Buchanan, 2009).

Habitat: Species were categorised as belonging to one of six categories (Allan, 1961; Curtis, 1963; Curtis, 1967; Moore & Edgar, 1970; Curtis, 1975, 1979; Curtis & Morris, 1994; Edgar & Connor, 1999; Buchanan, 2009). For those that occurred in more than one habitat, two or more categories were recognized.

coastal: not aquatic, but near the sea or the tidal zone with some salt exposure (e.g. cliffs, heathlands, wet ledges) (Johnson & Brooke, 1989)

saltmarsh/estuarine: wetlands near the sea or within the tidal distance; coastal waters partially enclosed by land and semi-diluted by freshwater (Johnson & Brooke, 1989).

freshwater aquatic: fully to partially submerged in lacustrine (lakes or open rivers dammed), palustrine (wetlands exclusive of saltmarsh, estuarine and tidal wetlands, open water bodies, and covered wet ground) and riverine (rivers, streams, and margins with flowing water) environments that are not exposed to tidal or coastal waters (Johnson & Brooke, 1989)

bog/wet peat: peatlands fed by rainwater or/and moving ground-water; swamps; waterlogged soils (Johnson & Brooke, 1989).

forest: conifer-broadleaf forest characterised by broadleaf angiosperm trees intermittently mixed with emergent conifers, and beech forest defined by continuous layer of southern beeches with no emergents (Poole & Adams, 1986; Dawson & Lucas, 2000); no differentiation were made between two types of forest in New Zealand.

open forests, grasslands, and heathlands: open to sparse canopy of trees usually in drier areas; graminoids or forbs; graminoids or forbs intermixed with trees and shrubs.

Dioecy: Species were categorised as whether they were dioecious or not. (Allan, 1961; Curtis, 1963; Curtis, 1967; Moore & Edgar, 1970; Curtis, 1975, 1979; Curtis & Morris, 1994; Edgar & Connor, 1999; Buchanan, 2009)

The ability of a species to produce viable disseminules through self-fertilisation can affect its likelihood of colonisation and perpetuation through long distance dispersal. Ba7ker (1967) suggested that self-compatible hermaphrodites had a higher probability of establishing themselves after long distance dispersal due to the need for only one propagule to establish a population (Baker's law).

The endemic New Zealand flora is considered to have a high proportion of gender dimorphism (Heine, 1937; Carlquist, 1966b; Godley, 1975, 1979; Lloyd, 1985b; Webb & Kelly, 1993b); dioecy occurs in approximately 12-13% of the species, and most of the species within 10-11% of the genera (Godley, 1979). In addition, dioecism has been tentatively correlated with perennial habit and woodiness, generalist pollination (wind pollination, water pollination, and white, yellow, and green flowers), and fleshy fruitedness (Sakai & Weller, 1999). Webb *et al.* (1999) discovered that 23% of the genera have gender dimorphism, but 40% of these genera have species or populations lacking this feature. They inferred that gender dimorphism originated autochthonously in 17 of the 83 genera. Outside of New Zealand, high levels of gender dimorphism and dioecism has been documented in the Hawaiian flora (respectively 17.9% and 11.4%) (Sakai *et al.*, 1995). Various explanations have been incited for high island dioecism (Carlquist, 1966b; Bawa, 1980; Thomson & Barrett, 1981; Bawa, 1982; Baker & Cox, 1984; Lloyd, 1985b; Sakai *et al.*, 1995; Sakai & Weller, 1999), but overall none has been conclusive or comprehensive.

Disseminule Size: The size of the disseminule can influence the probability of long distance dispersal particularly if wind or water is the species' means of dispersal. Jordan (2001) revealed that significantly high proportions of disjunct species had disseminules within the two small size categories. Disseminule size, based on the back converted log of the sum of the length and width of the disseminule excluding appendages, was organized according to the following categories: <0.25 cm; 0.25-0.40 cm; 0.40-0.75 cm; 0.75-1.0 cm; 1.0-2.0 cm; 2.0-4.0 cm; >4.0 cm. The sizes were obtained and standardized from floras (Allan, 1961; Curtis, 1963; Curtis, 1967; Moore & Edgar, 1970; Curtis, 1975, 1979; Curtis & Morris, 1994; Edgar & Connor, 1999; Webb & Simpson, 2001; Buchanan, 2009) and Webb and Simpson (2001) provided an invaluable compilation of seeds of New Zealand gymnosperms and dicots.

Disseminule Type: The eastward movement (west wind drift) has given credence to specific disseminule types specialized for long distance dispersal. Buoyancy is certainly a limiting factor in determining the chances of success, and observations

that a higher frequency of disseminules with plumosity (hairs, wings, pappus) and flotation features will exist in long distance dispersed flora, although Jordan's (2001) results implied that these features are not over-represented empirically. Vertebrate dispersal cannot be discounted as well – seeds can survive intact and unhindered in digestive tracts of birds and mammals before they are either regurgitated or expelled through droppings. By having sticky (viscous, hooked) or fleshy characteristics, zoochorous seeds instead may hitchhike on the fur or feathers, carried long distances, and finally released once the destination has been reached (Van Der Pijl, 1982).

Viability of drifted seeds in New Zealand and Australia have not been thoroughly investigated, although seeds of legumes and coastal flora are more likely to remain viable after dispersal by ocean currents than those originating from flora inland and away from the coast, and having limited relative abundance (Hacker, 1990; Smith, 1990, 1991, 1992). A comparison of disjunctions by genus and species in New Zealand and Tasmania, and correlating them to habitat or altitudinal zone can produce preliminary conclusions and assumptions about viability.

The binary classification scheme, in which each plant species are classified by their specific dispersal mode or not (i.e. disseminules with plumosity are deemed wind dispersed), has been criticized for its limitations because it excludes species with no clear dispersal traits and overlooks the variable dispersal potential (Bakker, 1960; Plummer & Keever, 1963; Stöcklin & Baumler, 1996; Tackenberg, 2003a; Tackenberg *et al.*, 2003b). This shortcoming has been addressed by comparing the rates of dispersal of taxa with the traits with those for taxa lacking the traits. However, few methods for addressing the species variation in dispersal potential have been established, although (Tackenberg *et al.*, 2003b) have formulated a system for wind dispersal potential. The system, which is dependent on two traits of the plant species (falling velocity and initial release height of the diaspores) and two context-specific parameters (reference distance and weather conditions), does not match the comprehensive scope of the binary

classification scheme. The limitations of the binary scheme are offset by the inclusion of other traits independent of disseminule type.

Data was collected from the same references used for disseminule size.

Fleshy Fruit: Presence/ Absence. The fruit was deemed fleshy if it was described as a berry, drupe, or having fleshy, pulpy, or succulent tissue.

Because avian dispersal is one common mechanism by which seed plants disseminate themselves in isolated islands or landmasses, fleshy fruitedness has often been considered as a chief characteristic of species with the capacity for long distance dispersal. Their conspicuous presence had led to the idea that the frequency of fleshy fruitedness is unusually high on island or disjunct flora. However, such an idea can be misleading because the New Zealand flora does not have an unusual high frequency of fleshy-fruitedness in its entirety or when measured against other temperate floras (Lord, 1999; Jordan, 2001).

The occurrence of fleshy fruits appears to be more common in forest communities, although their frequency in alpine communities appear to be less clear. Given that the tropics worldwide have a high representation of fleshy-fruited species (Heywood, 1978; Howe, 1986; Snow & Snow, 1988), the frequency of flesh-fruitedness in North Island (New Zealand) and New South Wales and Queensland (Australia) may be similar or within the same range. The vegetation of the North Island, with its lowland rainforests, is more subtropical in character than that of South Island with its extensive montane *Nothofagus* forests, alpine and subalpine grasslands and heathlands. Furthermore, a number of disjunct genera are shared between North Island and New South Wales and Queensland (Table 1).

Associated with fleshy fruitedness is their mode of seed dispersal by vertebrates, known as endozoochory (Van Der Pijl, 1982) or ants, termed myrmechory (Berg, 1975). Where there is high frequency of fleshy-fruited species in a given area, a strong correlation with vertebrates is predicted. A number of Tasmanian plants are dependent on lizards for pollination and seed dispersal (Potter, 2001). Avian

frugivory is a common feature of lowland rainforests in mainland Australia and New Zealand (Green, 1993; Burrows, 1994b). For instance, the rose-crowned fruit-dove (*Ptilinopus regina*), topknot pigeon (*Lopholaimus antarcticus*), and white-headed pigeon (*Columba leucomela*) feed on *Beilschmiedia elliptica* while the New Zealand counterpart, *kererū* (*Hemiphaga novaeseelandiae*) feast on *B. tarairi* (Dijkgraaf, 2002; Lord, 2004). Myrmechory is a more common phenomenon in Australia, especially among species in dry heath and sclerophyll vegetation. Because Tasmania does have dry heath and sclerophyll vegetation, the low frequency of fleshy-fruited species with vertebrate dispersal may be offset by those with ant dispersal. However, this variation may not influence the frequency significantly enough to establish a possible link between fleshy-fruitedness and vertebrate dispersal.

Hooked/Sticky Disseminules: Presence / Absence. Hooked and sticky traits often reflect external transport by animals, known as epizoochory (Van Der Pijl, 1982).

Plumosity: Presence / Absence - disseminules with noticeable hairs, plumes, pappus, and wings. Such seeds are often considered to be wind-dispersed, though it is recognised that many seeds with relatively small wings (i.e. ones that do not increase fall times markedly) may not result in significant wind dispersal.

STATISTICAL ANALYSES

The data were compiled in MS Excel 2003 worksheets, and analyses of the trans-Tasman disjunct species and their ecological and morphological correlates were carried out, using MS Word Excel 2003's PivotTable and PivotChart Report.

RESULTS

293 species (excluding bryophytes) are native to both Tasmania and New Zealand, and this represents 17% of the Tasmanian flora and 14% of the New Zealand flora. In Tasmania, 3% of the trees and shrubs are disjunct, while 21% of the perennial dicots, 20% of the annual dicots, 18% of the perennial monocots, and 18% of the annual monocots were disjunct (Fig. 5). The trees and shrubs were

significantly under-represented (P<0.001) and the annual dicots were significantly over-represented (P<0.05) (Table 6). In New Zealand, 3% of the trees and shrubs, 13% of the perennial dicots, 23% of the annual dicots, 19% of the perennial monocots, and 60% of the annual monocots are disjunct. Again the trees and shrubs were significantly under-represented (P<0.001), but perennial dicots were significantly over-represented (P<0.05) (Table 6).
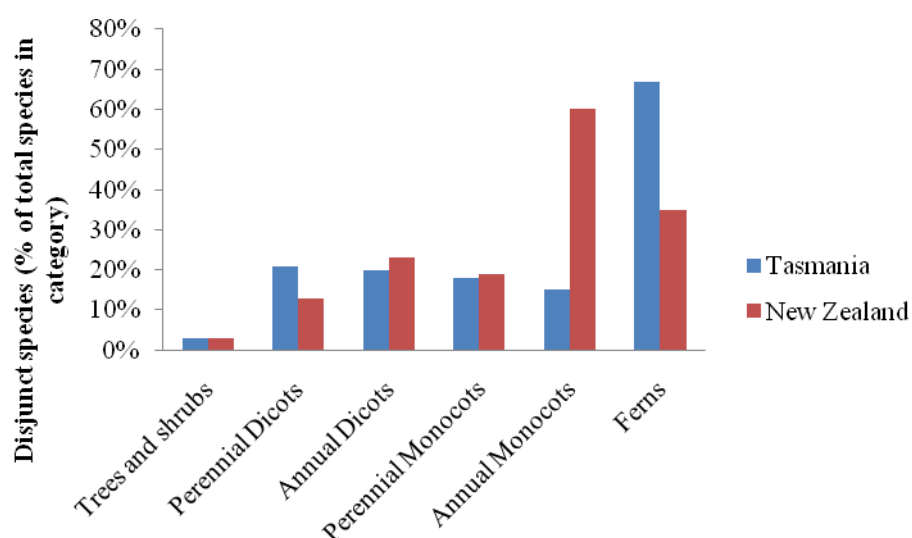
Fig. 5. Disjunct species by habit in New Zealand and Tasmania expressed as proportions of the total number of species.

Table 6. Observed (Obs.) and expected (Exp.) numbers of within-species disjunctions by habit in New Zealand and Tasmania. Results from the analysis of deviance are given (G, P)

Class	Observed	Expected	% Gain/Loss Representation	G
New Zealand				
Trees and Shrubs	17	90	-400%	99, P < 0.001
Perennial Dicots	77	86	-12%	1, P > 0.05
Annual Dicots	23	14	+39%	7, P < 0.05
Perennial Monocots	103	75	+27%	17, P ≤ 0.001
Annual Monocots	6	19	-216%	22, P ≤ 0.001
Ferns	67	26	+61%	77, P < 0.0001
Tasmania				
Trees and Shrubs	17	88	-417%	99, P < 0.001
Perennial Dicots	77	64	+17%	4, P < 0.05
Annual Dicots	23	20	+13%	0.6, P > 0.05
Perennial Monocots	103	97	+6%	0.6, P > 0.05
Annual Monocots	6	7	-16.6%	0.1, P > 0.05
Ferns	67	82	-18.0%	184, P > 0.05

New Zealand had high proportions of disjunct species in freshwater aquatic (57%), saltmarsh and estuarine (42%), and coastal habitats (38%) (Fig. 6). Except for the salt marsh and estuarine, they are significantly over-represented ($P<0.001$). Tasmania had higher proportions of disjunctions in forest (24%), significantly over-represented, and open forests, grasslands, and heathlands (38%), significantly under-represented, than New Zealand. A similar high incidence can be seen in disjunct species inhabiting lowland and alpine regions of New Zealand respectively (Fig. 6, Table 7).
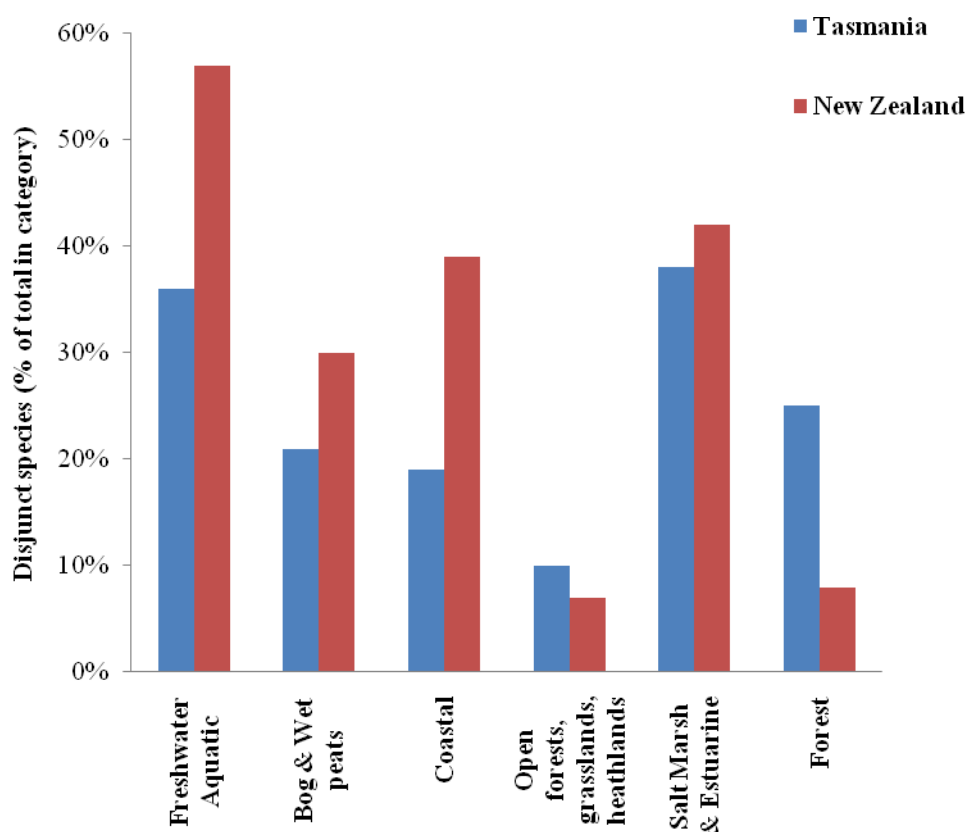

Fig. 6. Disjunct species by habitat in New Zealand and Tasmania expressed as proportions of the total number of species.

Table 7. Observed (Obs.) and expected (Exp.) numbers of within-species disjunctions by habitat in New Zealand and Tasmania. Results from the analysis of deviance are given (G, P)

Class	Observed	Expected	% Gain/Loss Representation	G
Tasmania				
Freshwater Aquatic	17	4	+76%	46, P < 0.001
Salt Marsh & Estuarine	10	13	-30%	15, P < 0.001
Coastal	40	15	+63%	53, P < 0.001
Bog & Wet Peats	106	49	+54%	93, P < 0.001
Forest	39	65	-67%	15, P < 0.001
Open forests, grasslands, and heathlands	81	15	+81%	92, P < 0.001
New Zealand				
Freshwater Aquatic	20	10	+50%	14, P<0.001
Salt Marsh & Estuarine	16	7	+56%	13, P<0.001
Coastal	29	26	+10%	0.40, P>0.05
Bog & Wet Peats	109	87	+20%	9, P<0.001
Forest	42	29	+31%	7, P<0.001
Open forests, grasslands, and heathlands	80	133	-66%	43, P<0.001

Proportions of disjunct species with hooks, barbs, or sticky seeds, plumes and hairy seeds, and fleshy fruits were greater in the overall extant Tasmanian vascular flora than the New Zealand flora (Fig. 7). Disjunct species having plumes, hairy seeds, and large pappus represented only 11% of the extant Tasmanian flora whereas only 6% of the disjunct flora in New Zealand had the same traits (Fig. 7). These wind-dispersed features were significantly under-represented (P<0.05) (Table 8). Disjunct species with hooks, barbs, or sticky seeds defined only 19% of the Tasmanian flora and 10% of New Zealand flora. However, the former were under-represented and the latter over-represented, although they are not statistically significant (P>0.05) (Table 8). Significantly under-represented (P<0.05), disjunct species with fleshy fruits occurred in 9% of the Tasmanian flora, but only 4% of the New Zealand flora (Table 8).
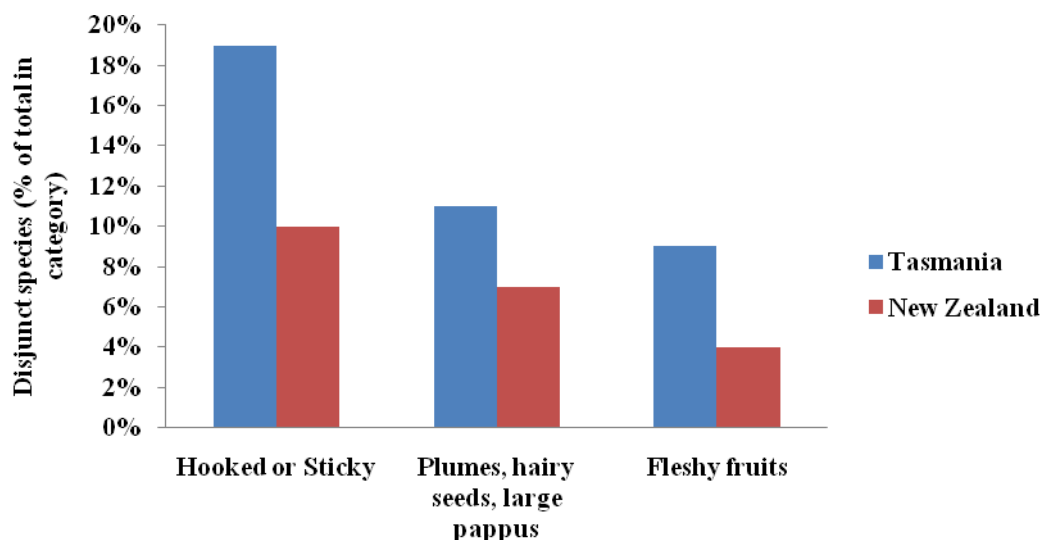
Fig. 7. Disjunct species in New Zealand and Tasmania by presence of specialised dispersal features expressed as proportions of the total number of species

Table 8. Comparison of observed and expected numbers of within-species disjunctions in New Zealand and Tasmania by known specialised dispersal features. Results from the analysis of deviance are given (G, P)

Class	Observed	Expected	% Gain/Loss Representation	G
New Zealand				
Hooks, sticky seeds, etc	22	31	-40%	4, P>0.05
Plumes, hairy seeds, large pappus	21	43	-104%	15, P<0.05
Fleshy fruits	11	41	-272%	32, P<0.05
Tasmania				
Hooks, sticky seeds, etc	22	19	+13.6%	0.3, P>0.05
Plumes, hairy seeds, large pappus	21	32	-52%	5, P<0.05
Fleshy fruits	11	22	-100%	7, P<0.05

Disjunct species having specialised dispersal traits (hooks, sticky seeds, etc, plumes, hairy seeds, large pappus, and fleshy fruits) constituted 3% each of the Tasmanian and New Zealand floras (Fig. 8). The presence of specialised dispersal traits was under-represented (Table 9). In contrast, disjunct species having no specialised dispersal traits represented 14% of Tasmanian flora and 11% for the

New Zealand flora (Fig. 8). The lack of specialised dispersal traits was over-represented for both areas (Table 9).
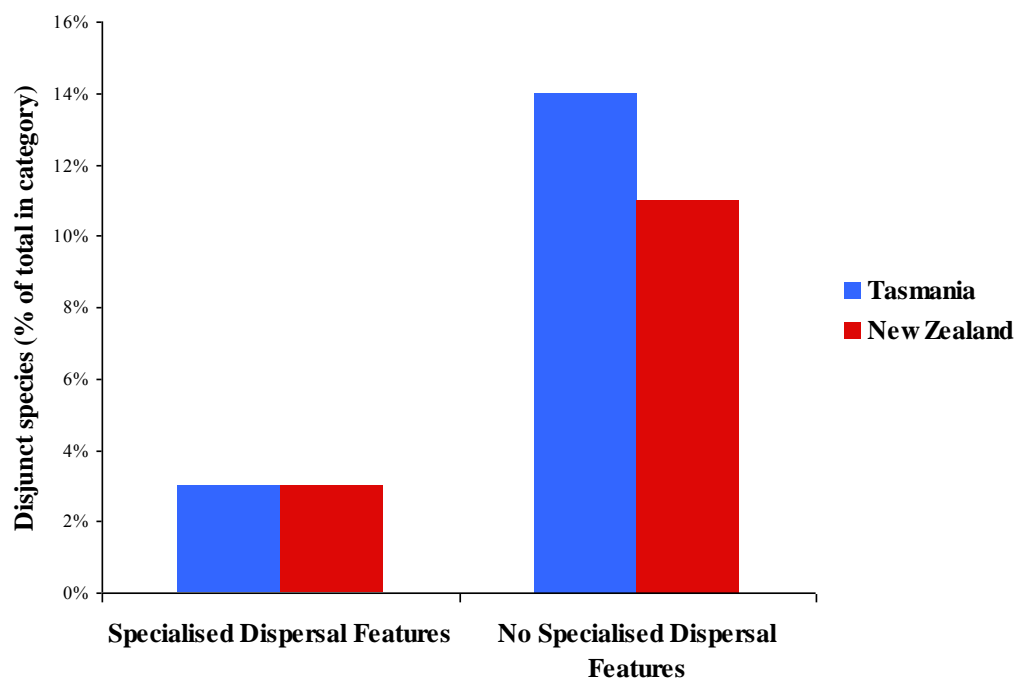
Fig. 8. Disjunct species in New Zealand and Tasmania by presence and absence of specialised dispersal features expressed as proportions of the total number of species

Table 9. Comparison of observed and expected numbers of within-species disjunctions in New Zealand and Tasmania by known specialised dispersal features. Results from the analysis of deviance are given (G, P)

Class	Observed	Expected	% Gain/Loss Representation	G
New Zealand				
Specialised Dispersal Features	54	116	-114%	G=64,
No specialised dispersal features	239	177	+26%	P<0.001
Tasmania				
Specialised Dispersal features	54	74	-37%	G=8, P<0.05
No specialised dispersal features	239	219	+8%	

Higher proportions of disjunct species were not dioecious in Tasmania and New Zealand than those that were dioecious (Fig. 9). Thus, dioecy is under-represented at 3% in Tasmania and New Zealand (Table 10).
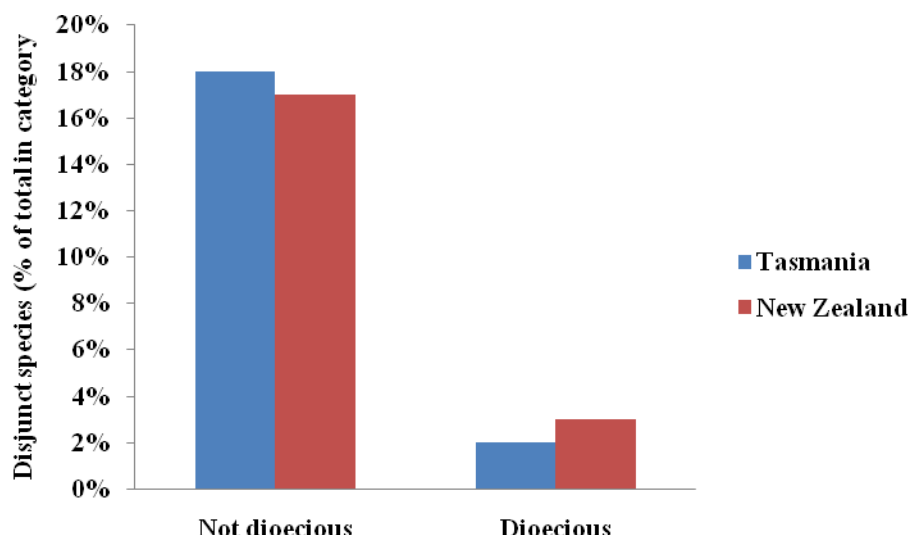
Fig. 9. Disjunct species in New Zealand and Tasmania by dioecy expressed as proportions of the total number of species.

Table 10. Comparison of observed and expected numbers of within-species disjunctions in New Zealand and Tasmania by dioecy. Results from the analysis of deviance are given (G, P)

Class	Observed	Expected	% Gain/Loss Representation	G
New Zealand				
Dioecious	7	33	-371%	P<0.001
Not Dioecious	286	260	+9%	
Tasmania				
Dioecious	7	11	-57%	P>0.05
Not Dioecious	286	281	+2%	

High proportions of disjunct species in Tasmania and New Zealand (24% to 37%) were in Caryophyllaceae, Chenopodiaceae, Cyperaceae, and Juncaceae (Fig. 10). 8% of the Tasmanian Asteraceae were disjunct in Tasmania and 13% of New Zealand members of this family were likewise (Fig. 10).
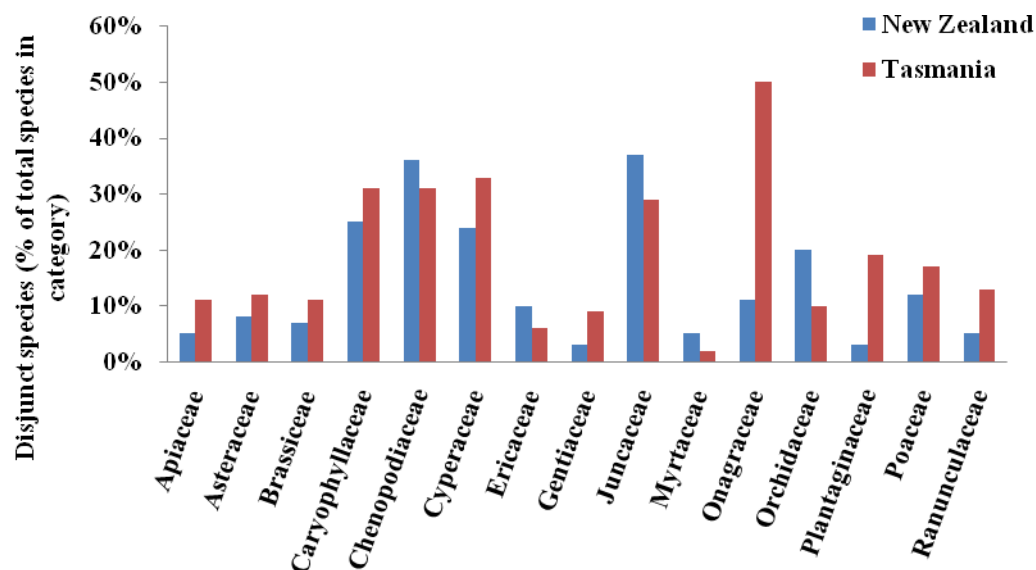
Fig. 10. Disjunct species in New Zealand and Tasmania by family expressed proportions of the total number of species in each family in each region

Proportions for each disseminule size category were generally within similar range for both New Zealand and Tasmania, except for 30% of disseminules in disjunct species for 0.75-1.00 cm in New Zealand (Fig. 11). Only the first two smallest categories (<0.20 cm and 0.20-0.40 cm) were statistically significant ($P<0.05$) in New Zealand while the remaining three categories (0.40-0.75 cm., 0.75-1.00 cm, 1.00-4.00 cm) in New Zealand and Tasmania were not significant ($P>0.05$). As predicted, the smallest disseminule size range (<0.20 cm) was over-represented for disjunct species in both New Zealand and Tasmania (Table 11). An inverse relationship developed between the disseminule size category and the number of disjunct species – an increase in disseminule size range meant a decrease in the resultant number of disjunct species (Table 11).
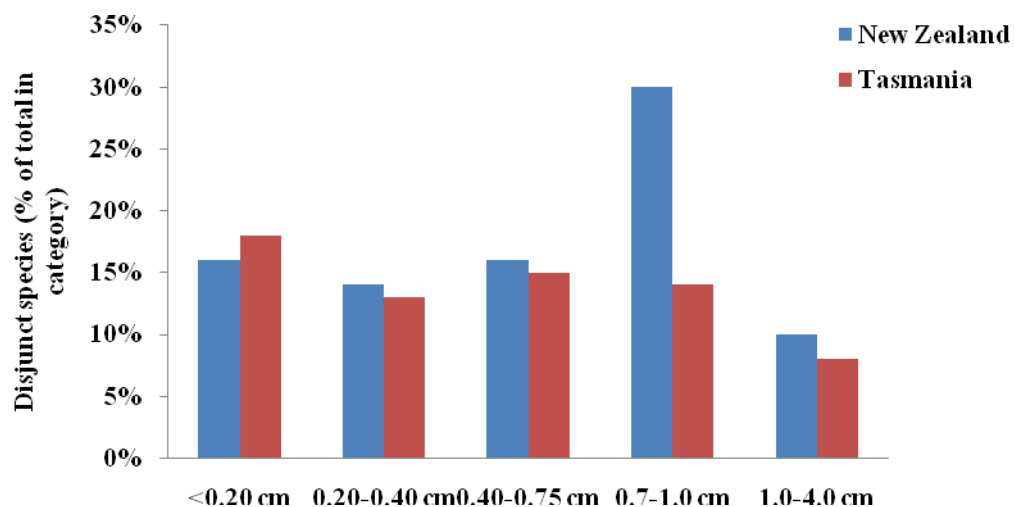
Fig. 11. Disjunct species in New Zealand and Tasmania by disseminule size expressed proportions of the total number of species in category.

Table 11. Comparison of observed and expected numbers of within-species disjunctions in New Zealand and Tasmania by disseminule size. Results from the analysis of deviance are given (G, P)

Class	Observed	Expected	% Gain/Loss Representation	G
New Zealand				
<0.20 cm	158	156	+1%	0.10, P>0.05
0.20-0.40 cm	45	49	-8%	0.43, P>0.05
0.40-0.75 cm	14	14	0%	0.00, P>0.05
0.75-1.00 cm	3	2	+33%	1.60, P>0.05
1.0-4.0 cm	1	2	-100%	0.24, P>0.05
Tasmania				
<0.20 cm	158	144	+10%	4.52, P<0.05
0.20-0.40 cm	45	57	-27%	4.07, P<0.05
0.40-0.75 cm	14	15	-7%	0.10, P>0.05
0.75-1.00 cm	3	3	0%	0.07, P>0.05
1.0-4.0 cm	1	2	-100%	0.72, P>0.05

DISCUSSION

Growth habit

The significant under-representation of disjunct woody species (P<0.001) in both New Zealand and Tasmania suggests that plant type can be an accurate signifier of dispersal success (Table 6). This is emphasized by the over-representation of

both disjunct annuals and short-lived perennials (Table 6). The lower rate of within-species disjunctions in woody species is very unlikely to be due to greater rates of evolution in these plants because rates of both molecular evolution and speciation are empirically lower in woody plants than herbs (Smith & Donoghue, 2008). Herbs have shorter life cycles than woody trees and shrubs, which require more time to reach mature reproductive stages. Therefore their greater reproductive prowess may result in more individuals and in turn, more populations, although longer-lived plants can overcome their slow maturity by producing prolific seeds held at taller heights, enhancing mobility. However, plant type itself cannot determine or dictate a plant's rate of success in long distance dispersal since it is dependent on the ability of the plant to colonise and establish new areas. The ability to exploit marginal sites efficiently and effectively is a competitive advantage for annual and short-lived perennials since woody shrubs and trees have to contend with persistent challenges in the time preceding their reproductive maturity, despite having higher tolerances of stress. Even in reproductive maturity, woody plants face fulfilling specific requirements for breaking dormancy for their dissemminules prior to germination and growth. In all, the very traits that secure the dispersal and colonisation success rate of disjunct species are uncommon in woody species.

Not surprisingly, ferns were over-represented in New Zealand and Tasmania (Table 6). Their spores are prodigious, light-weight, and easily mobile either by wind or water (Barrington, 1993). High proportions of ferns in floras of oceanic islands (Tyron, 1970) attest to their vagility.

Habitat Type

The high incidence of disjunct species in aquatic and coastal habitats (Fig. 6, Table 7) is not surprising since such habitats have long been considered to afford more opportunities for colonisation and dispersal mechanisms, like water and external transport by avian visitors, and readily distribute disseminules (McGlone *et al.*, 2001). Tasmania shares the same high incidence of disjunct species in such habitats (Jordan, 2001), and the congruence in habitat preferences of disjunct species only reinforces the prevalence of water as a vector for dispersal, local and

long distance (Jacobs & Wilson, 1996; Sanmartín *et al.*, 2007). Another trend convergent with that of Tasmania is the high frequency of disjunct species in bogs and wet peaty soils (Fig. 6, Table 7). A number of these taxa such as species of *Abrotanella* (Swenson & Bremer, 1997)*, Carpha* (Zhang *et al.*, 2003), *Donatia* and *Phyllachne* (Wagstaff & Wege, 2002), *Scleranthus* (Smissen *et al.*, 2003) have close counterparts in analogous habitats at mid-high latitude regions elsewhere in the Southern Hemisphere (Patagonia, Tierra del Fuego, alpine New Guinea, and a few scattered oceanic subantarctic islands) (Jordan, 2001). In contrast, the low incidence of disjunct species in closed forests (Fig. 6, Table 7) may be a consequence of competition and slow species turnover and thus fewer chances to establish these areas. This incidence reflects the dominance of herbs over woody plants in disjunctions. Even the high over-representation of ferns in New Zealand was insufficient (Table 6) to bolster the proportion of disjunct species in forests (Fig. 6), possibly reflecting the low dispersal rate of angiosperm and gymnosperm species. Nonetheless, the pattern is clear when compared with the high incidence of disjunct species in open forests, grasslands, and heathlands. Interestingly, the frequency of disjunct species in Tasmanian grasslands and heathlands (including forests, open and closed) is low and not significant (Jordan, 2001), but the inclusion of forests may have altered the result.

Dioecy

Since the reproductive success of dioecious species is tied to the presence of both sexes in vicinity of each other, the under-representation of dioecy in within-species disjunctions in both Tasmania and New Zealand (Fig. 9, Table 10) would be anticipated. Baker (1955, 1967) predicted that the initial influx of immigrant species on islands would be self-compatible due to the advantages of self-compatibility in early colonization. In line with Baker's hypothesis, Böhle *et al.* (1996) discovered a strong tendency for out-crossing among island plants, especially those in small populations, and self-incompatibility and heterostyly are exceptional rather than the rule on islands. Dioecy is not necessarily a common breeding system even if it appears unusually high in certain island floras, such as the Hawaiian flora (Sakai *et al.*, 1995).

Moreover, dioecy is infrequent in flowering plants where 4 to 6% of species are dioecious (Renner & Ricklefs, 1995; Richards, 1997; Barrett, 1998). In addition, given that herbs dominated the majority of the disjunct species, the frequency of dioecy would have been higher if woody plants dominated instead. It has been well established that trees are more likely to be dioecious (Waller, 1988; Schatz, 1990; Arroyo & Uslar, 1993; Richards, 1997; Adam & Williams, 2001).

Although the results appear incongruous with the high incidence of dioecy on certain island floras, they suggest that in-situ evolution of dioecy from lineages of self-compatible immigrants occurred. The other possibility is that dioecious species were among the first to colonize islands and later experienced low levels of extinction. Either explanation is the result of the interaction between high levels of dioecy and low rates of dioecious immigrant plants, although a stronger case may be made for the former from molecular work.

Disseminule Size

The over-representation of the smallest disseminule category (<0.20 cm) in New Zealand and Tasmania confirmed the trend in Jordan (2001), (Table 11). It emphasizes the importance of disseminule size in the organism's ability to disperse long distances, and the advantage of having small disseminules instead of large disseminules (with important exceptions, such as large floating seeds, such as coconuts, *Cocos nucifera,* and a range of species called sea beans, including *Mucuna* spp.) especially if wind is the dispersal vector. The families in which disjunct species belong can be revealing about their commonness in small disseminules. For instance, with their fine dust-like seeds, the Orchidaceae boost the observed number of disjunct species having less than 0.20 cm disseminules (Table 11). Similarly the Asteraceae have a high representation of species with less than 0.20 cm disseminules. Wardle (1991) observed that the New Zealand possesses a disproportionate number of species having small seeds and this fact led McGlone *et al.* (2001) to suggest that small seeds may be an immigration selection syndrome.

More telling are the dominant plant types in disjunctions, which in this case are annuals and short-lived perennials (Table 6). If disseminule size is a compromise between quantity (high numbers of seeds, each with limited resources) and quality (few numbers of larger seeds, each well-equipped with resources) (Leishman *et al.*, 2000), then it is reasonable that annuals and short-lived perennials would exploit the former and woody plants follow the latter. An association between annuals and short-lived perennials and small disseminules is expected, just like a correlation between woody plants and large disseminules (Moles *et al.*, 2007). However, there must be consideration for woody plants capable of producing vast quantities of wind-borne or water-borne small disseminules, despite their slow reproductive maturity.

Disseminule Type

Although not significant (P>0.05) (Table 8), the under-representation of hooked or sticky seeds does not support the concept that such seeds are heavily involved in immigration into the New Zealand flora, yet immigrant birds, which can transport hooked or sticky seeds, are frequently witnessed in New Zealand. In fact, levels of endemism in certain habitats corresponded to the frequency and presence of avian visitors, with low levels implying less isolation from immigration (McGlone *et al.*, 2001). Tasmania's over-representation of hooked or sticky seeds is surprising because its flora is supposedly less dependent on immigrant plant species than that of New Zealand. A plausible explanation for the representation differences could be that Tasmania, being the source population of immigrant species, has more realized niches for species with hooked or sticky seeds than New Zealand can afford to fulfill. The number of these species producing successful sink populations in New Zealand are likely uncommon. Plumes or hairy disseminules were both under-represented in both New Zealand and Tasmania, and such low incidence in New Zealand is unexpected since a large number of species are within the Asteraceae.

Fleshy-fruitedness

Fleshy-fruited disjunct species were significantly under-represented (Table 8), although the proportion may likely be higher if the data analysis encompassed within-genera disjunctions, rather than within-species disjunctions, from other oceanic islands and eastern Australia. For instance, the subtropical forests of New South Wales and Queensland share several frugivorous genera with the North Island of New Zealand. To some extent, fleshy fruits seem more common for woody species than herbs, and the under-representation is a reflection of the herbaceous habit for within-species disjunctions in New Zealand and Tasmania. However, Lord (1999) found no significance in fleshy-fruitedness between New Zealand flora and other temperate floras, as well as no correlation with selective immigration and endemism.

Relationships between disjunctions and fleshy-fruitedness

The conspicuous presence of fleshy-fruited species in New Zealand flora has resulted in the theory that fleshy-fruitedness is a distinct feature of the flora (Willson *et al.*, 1989; Webb & Kelly, 1993a; Burrows, 1994b). This theory has been disproved by Lord (1999), who discovered that the New Zealand flora does not have an unusual high frequency of fleshy-fruitedness in its entirety or when measured against other temperate floras, and the majority of the flora possessing fleshy-fruitedness tend to occur in alpine environments or were trees. Nor were fleshy-fruited New Zealand genera more likely than dry-fruited genera to appear in Australia.

Unpublished estimates of relative abundances of plants with different dispersal modes in East Gippsland, Victoria reveal no differences between those vertebrate-dispersed and those dispersed in other ways (Willson *et al.*, 1989).

Relationships between habitat and fleshy-fruitedness, and comparative surveys with other regions

The frequencies of fleshy-fruited species in New Zealand (36%) and Tasmanian (27%) forests fall within the range (N.Z. 27-60%, Chile 45-70%) for fleshy-fruited species in south temperate forests (Willson *et al.*, 1989). 28% of New

Zealand species with fleshy-fruits in alpine regions falls within the expected frequency range (17-48%) (Willson *et al.*, 1989). The proportion of fleshy-fruited species in alpine regions (38%) for Tasmania is slightly higher than the 30% or less of the fleshy-fruited species in Australian sclerophyll woodlands, heaths, and alpine communities (Willson *et al.*, 1989).

Relationships between plant type and fleshy-fruitedness, and geographical comparisons.

The observed value of 39% of woody species with fleshy fruits falls with the middle range of 27 to 60% of species with fleshy fruit observed in New Zealand forests by (Burrows, 1994a). Burrows (1994a) determined that the proportion of fleshy-fruited woody species in New Zealand (48%) is similar to that of the British Isles (48%), New England (44%), and Georgia/the Carolinas (48%), but lower than that of Japan (55%). After dividing the fleshy-fruited woody species into tree, shrub and vine subcategories, Burrows (1994a) and compared the frequencies again, New Zealand had at least 70% of tree species with fleshy fruits (40% of shrubs and 30% of vines). These proportions are similar to those in Chilean forests (70% of tree species, 64% of shrubs and vines) and in rainforests of New South Wales, Australia (70% of woody species are fleshy fruited). The lowland rainforests in New South Wales and southern Queensland have ~72% of woody species with fleshy fruits (Willson *et al.*, 1989). North Island (New Zealand) similarly shares the same proportion as New South Wales and southern Queensland.

Tasmania has a lower frequency of woody species with fleshy fruits at 18.8% and this low proportion reflects the fact that eucalypts are the forest dominants and canopy trees. 17% of the flora in forests, woodlands and scrubs in East Gippsland, Victoria, have fleshy fruits (Willson *et al.*, 1989).

When considered together with habitat and environmental conditions, latitudinal gradients can influence the frequency of fleshy-fruited species. Stewart and Chatham Islands, New Zealand, have different frequencies of fleshy-fruited species. The former has 17.4%, of which 64.4% are in forests, whereas the latter

has 7.7%, of which 13.2% are in forests. Willson *et al.* (1989) cited the higher proportion of fleshy fruits in forests of Stewart Island compared to those of Mt. Cook (South Island) due to moisture availability.

Vertebrate dispersal within woody species with fleshy fruits

Nearly 38% of woody species in New Zealand (36% with fleshy fruits) are dependent on vertebrate dispersal. This frequency of woody species with fleshy fruits dependent on vertebrate dispersal is at the low end of the observed ranges for other regions: neotropical and Australian dry tropical forests (35-70% of woody plants), North American deciduous forests (47-54% of woody plants), and Mediterranean scrublands (49-66%), although high frequencies over 70% are not unheard of in tropical rain forests (Willson *et al.*, 1989). The frequency in Tasmania (17%) is less than the worldwide norm, and may be attributed to a high proportion of myrmechorous species where ants likely displaced vertebrates as dominant dispersers.

Specialised Dispersal Traits versus No Specialised Dispersal Traits

The significant over-representation of disjunct species lacking specialized dispersal traits (Table 9) confirms the clear cases of where long distance dispersal has been demonstrated in species without such traits. *Scleranthus* does not have any distinguishing dispersal traits and is capable of long distance dispersal as evidenced by its occurrence in both Australia and New Zealand (Smissen *et al.*, 2003), and *Abrotanella*, which lacks evident dispersal traits, is capable of long distance dispersal (Swenson & Bremer, 1997).

Direction of dispersal

Although these results were presented in Chapter 2, they are pertinent to this discussion. The inferred patterns of dispersal (of movement from Tasmania to New Zealand being approximately nine times more common than dispersal in the opposite direction; Figure 2) are consistent with West wind drift.

Overall Patterns

Of the traits evaluated, only growth habit, habitat, small seeds, relative abundance, and unisexual plants emerged as strong predictors of long distance dispersal for the New Zealand and Tasmanian flora, making it difficult to formulate generalizations about dispersal-mediated traits (Table 12).

Table 12. Summarised results of seed morphology, habitat, pollination and habit traits for long distance dispersal in Tasmania and New Zealand.

Class		TASMANIA Representation	Significance	NEW ZEALAND Representation	Significance
Seed Morphology	Small seeds	Over	Yes	Over	No
	Hooks, sticky seeds	Over	No	Under	No
	Plumes, hairy seeds, large pappus	Under	No	Under	Yes
	Fleshy fruits	Under	Yes	Under	Yes
	No specialized dispersal traits	Over	Yes	Over	Yes
Habitat	Freshwater aquatic	Over	No	Over	Yes
	Salt marsh/ estuarine	Over	No	Over	Yes
	Coastal	Over	No	Over	Yes
	Bog/wet peat	Over	No	Over	Yes
	Grasslands, heathlands, open forests	Under	Yes	Over	Yes
	Forest	N/A		Under	Yes
Pollination	Dioecy	Under	Yes	Under	Yes
Habit	Trees and shrubs	Under	Yes	Under	Yes
	Perennial Dicots	Over	Yes	Over	No
	Annual Dicots	Over	No	Over	Yes
	Perennial Monocots	Over	No	Over	No
	Annual Monocots	Under	No	Under	No
	Ferns	Over	No	Over	Yes
Relative abundance	Common species	Over	Yes	Over	Yes
Dispersal direction	Tasmania to New Zealand	Over	Yes	-	-

While it is easy to dismiss morphological dispersal syndrome as a reliable predictor of long distance dispersal due to the scarcity of consistent empirical data on long distance dispersal, to do so would be overlooking the fact that long distance dispersal operates by different standards from local or short distance dispersal. Higgins *et al.* (2003) noted that what would be applicable across the smaller scales of localized dispersal does not necessarily pertain to long distance dispersal. The evaluated traits are placed within the context of seeing which ones are important in shaping the within-species disjunctions of Tasmania and New Zealand, which demonstrated a strong directional bias towards the latter (Chapter 2).

In line with countless studies, especially those in endemism (Thorne, 1969; Koechlin *et al.*, 1974; Wagner *et al.*, 1990; Crisp *et al.*, 1999), woody plant habit can reliably predict a species' reproductive potential and the same applies for within-species disjunctions (Table 12). Habitat is a consistent predictor as well since ecological or niche conservatism, strongly supported by phylogenetic studies (Crisp *et al.*, 2009), is a major determinant of a species' habitat. Boggy, coastal and freshwater aquatic habitats exemplify the type of open habitat prone to immigrants (Table 11), and several vagrant species in New Zealand arrived through these habitats (Table 5). Similar correlations between habitat and dispersible species have been established (Jordan, 2001; McGlone *et al.*, 2001). As small seeds are amenable to dispersal by wind, attachment, and ingestion, the higher likelihood of disjunct species with small seeds (Table 11) reinforces the recurring trends of previous studies (Ridley, 1930; Grime, 1977, 1979; Grime *et al.*, 1988). The dynamics of sexual system evolution are notoriously more complex than seed size, given that transitions from dioecy towards monoecy have occurred in several genera, such as *Fuchsia* (Onagraceae; Systma *et al.*, 1991) and *Iphigenia/Wurmbea* (Colchicaceae; Case *et al.*, 2008) and they are associated with long distance dispersal. Yet as Schaefer and Renner (2010) have discovered for *Momordica* (Curcubitaceae), sexual reversals can be incorrectly attributed to long distance dispersal when plant-pollinator relationships, relative abundance, and habitat can inform such changes instead. Hence such inaccuracies stresses the importance of revising parochial view of morphological dispersal syndrome and

long distance dispersal in favour of a one that weighs ecological and genetic relationships (i.e. relative abundance, sink-source interactions, phylogenetic inferences) carefully with morphological dispersal syndromes. Nathan (2005) urged advancing integration of different approaches to address the complexity of the long distance dispersal.

There is some empirical support for the local, albeit limited, association between morphological dispersal syndromes and long distance dispersal (Aizen & Patterson, 1990; Oakwood *et al.*, 1993; Peat & Fitter, 1994), but while concurring that standard syndromes can be involved, Higgins *et al.* (2003) consider their effects masked by common non-standard mechanisms. Furthermore, these cases merely confirm Higgin's view of specific syndromes being unpredictive. A phylogenetically independent contrast (PICs) analysis of Australian vascular flora revealed no general differences in disseminule mass between species with similar morphological dispersal syndromes and their distribution, although avian dispersal for *Acacia* and winged features in *Eucalyptus* seemed to be prerequisites for wider distributions (Edwards & Westoby, 1996).

Where common non-standard mechanisms concealed the predictive nature of standard syndromes, plant families can be predictive as certain families are well known for their dispersible species. It seems appropriate that a species' family can be informative for gauging the likelihood of disjunctions (Fig. 10). However, the larger the number of species found in a family, the harder it is to attribute long distance dispersal and direction of dispersal unless relationships are clarified through phylogenetic studies. It is likely that the presence of strong associations of apparent dispersibility with families may indicate that these families possess dispersal traits that are not obvious.

Thus, Jordan (2001) acknowledged the limitation of a model using observable traits, given that several dispersal traits are neither known nor understood, although the allowance of family and habitat compensates for this deficit.

Although the dispersal traits do not infer the direction of dispersal, strong empirical evidence for the west wind drift from recent molecular studies

(Chiswell *et al.*, 2003; Waters & Roy, 2004; Donald *et al.*, 2005; Waters, 2008) helps overcome some of the limitations of trait-based analyses even if they do not provide a general theory. The pattern observed in the current study, in which within-species disjunctions showed a 19-fold bias for eastward movement (i.e. Tasmania to New Zealand) over westward movement (Fig. 2) bolsters these arguments. Some of this evidence not only comes from vascular plants (See references in Appendix 1), but also buoyant macroalgae in which the rafting mechanism transports coastal invertebrates between land masses (Waters, 2008). Irrespective of the organisms studied, the west wind drift provides a powerful motive for performing comparative trait analyses because it links the southern continents, placing long distance dispersal in favour instead of vicariance. Given that the Tasmanian and New Zealand within-species disjunctions are not the solitary representative of the long distance dispersal phenomenon between oceanic islands and continental masses and other examples, such as Africa and Madagascar do exist elsewhere, it is possible that a clearer and stronger picture of trait-based roles will emerge once the species disjunction data are collated.

In addition, autocorrelation may have contributed to some of the relationships observed here. For instance, there may be relationships between relative abundance and some other traits. Shrubs and trees are more to be likely rare than herbs in Great Britain (Kelly & Woodward, 1996) and Australia (Oakwood *et al.*, 1993), and both the woody habit and rarity show negative relationships with disjunction. Whether this is a direct consequence of woodiness, longevity (Eriksson & Jakobsson, 1998) or actual abundance is not clear. Furthermore, dispersal trait/rarity relationships can vary among different vegetation types in distinct geographical areas. Seed size-abundance relationship can be inconsistent – for example, among sand dune annuals, rare species tended to have larger seeds than common species (Rees, 1995; Guo *et al.*, 2000), yet no correlation was discerned in other studies (Eriksson & Jakobsson, 1998; Bruun, 2001; Leishman & Murray, 2001). Nonetheless, the significant relationships between disjunction (and therefore inferred dispersal potential) and traits lay the foundation for further testable hypotheses.

CHAPTER 4: CONCLUSIONS

Although vicariance has clearly influenced distributional patterns of species, long distance dispersal also plays a significant role in disjunctions—organisms are capable of dispersing across transoceanic distances after the landmasses became isolated by continental drift. Increased evidence for long distance dispersal has come primarily from estimates of molecular divergence times, which are too recent and variable to attribute to vicariance, although potential problems may exist in assumptions derived from such estimates (Arbogast *et al.*, 2002; Sanderson, 2002). More persuasive arguments for a greater role of long distance dispersal have arrived from the recognition of oceanic currents and wind patterns in the dispersibility of organisms (Muñoz *et al.*, 2004; Sanmartín *et al.*, 2007; Waters, 2008).

In particular, the within-species disjunctions between New Zealand and Tasmania are especially applicable for understanding the processes involved in shaping the flora. These disjunctions demonstrate a positive relationship between dispersal and relative abundance and driven by the source size to a certain extent. With careful consideration of the interacting factors within the geographic region, they are more likely to have niche and ecological versatility, if not a higher success rate of colonisation. A few disjunctions exhibit an inverse relationship between source and sink sizes, and equilibrium between these sizes may be reached once the temporal period for successful colonisation and reproduction is fulfilled unless other limitations superimpose. However, there was no evidence for any significant ecological release suggesting that this process has a minor role in the success of disjunctions in sink areas. These results refute the claim that ‚hypotheses based on abundance distributions alone rarely provide satisfactory elucidation of underlying causes‘ (Sagarin *et al.*, 2006).

Underscoring Lloyd‘s prescient conclusion that ‚…future studies will show that, for most characters, the distinctive New Zealand character states have been acquired in New Zealand predominantly through species selection rather than individual selection (1985a),‖ the within-species disjunctions in New Zealand and

Tasmania compel one to reveal any correlations with dispersal-mediated ecological and morphological traits in other Southern Hemisphere island flora. These traits constitute the non-random aspect of the otherwise complex and random phenomenon of long distance dispersal. Certain traits, especially dioecy and habitat type are consistent with the predictions, while others, like fleshy fruitedness and disseminules with hooks show no relationship with disjunction. Fleshy-fruitedness may be a better predictor of disjunct taxa having ancestral subtropical and tropical forbearers and equivalent climes, as suggested by Burrows (1994a), than those taxa derived from temperate ancestors and climes, but are clearly a poor predictor of disjunction in the remainder of the flora.

The frequency of within-species disjunctions between northern New Zealand and subtropical Australia raises the interesting question of whether the rates of evolution proceed faster than elsewhere or dispersal is less infrequent at higher latitudes (Fischer, 1960; Mittelbach *et al.*, 2007). Once again, a better resolution of this question will come within time as more phylogenetic understanding of the flora in northern New Zealand and subtropical Australia develops. Despite the unclear association between hooked disseminules and long distance dispersal, disseminule size is an obvious candidate for greater dispersibility. As confirmed in other studies, plant type (especially herbs versus woody plants) remains a reliable predictor of a dispersible species having disjunct distributions. Overall, the mixed results among trait-related inferences likely stems from the temporal and environmental variation of the dispersal events for the ancestral taxa – for instance, ancestral woody species, especially trees, may have found the late Miocene-Pliocene more conductive than the Pleistocene period for dispersal and colonization (McGlone *et al.*, 2010).

Although the role of long distance dispersal model in the assembly of floras is emphasized here, the contribution of vicariance should not be underestimated. Going as far as Poleʻs suggestion that the New Zealand flora may be largely largely the product of long distance dispersal based on fossil evidence (1994) may be overstating the role of long distance dispersal, given that vicariance is still relevant for some disjunct distributions. Skewed towards Gondwana and plate

tectonics, the vicariance model warrants a scope revised towards localised and small-scale vicariant events. For instance, there is the effect of Bassian Isthmus, which linked Tasmania to mainland Australia during the Pleistocene low sea-levels, on the development of endemic and disjunct species (Davies, 1974). This land bridge permitted the influx of mainland Australian flora into Tasmania, which simultaneously reduced and enhanced endemism. The shift from a vicariant-centric view to a long distance dispersal one signals a more critical and crucial examination of molecular dating and fossil evidence on divergence times and in turn, a more balanced view of historical biogeography involving vicariance and dispersal rather than one where the former was *a priori* preference. This view is reflected in Ronquist's DIVA (dispersal-vicariance analysis) approach (1997), allowing for inferences on the probabilities of both dispersal and vicariant events, and Donoghue and Moore's (2003) methodology follows the same perspective.

In conclusion, the results of this study indicate that relative abundance and long distance dispersal-mediated traits should be given significant heft in biogeographical analyses. It is clear that plant type and disseminule size and the availability of susceptible habitats and features for successful establishment and reproduction at the destination are all critical. Long distance dispersal may be interpreted as a random process occurring intermittently, if not steadily, throughout a biota history, but it relies on a nonrandom preference towards specific ecological and morphological traits. Stanley (1975) and Grantham (1995) alluded to this preference as a form of species selection, which Lomolino (1996) defined _selective immigration.' However, because long distance is not only a random, but also a rare process, the lack of evolutionary pressure or significance for the process must be acknowledged as well (Matthew McGlone pers. comm.).

The correlations established here represent a data subset that can be compared with other potential datasets for similar within-species disjunctions in oceanic islands, such as New Zealand, Madagascar, and the Chatham Islands, where recent temporal lineages of modern biotas have been revealed. Quantifying the degree of long distance dispersal or any dispersal accountable for a flora may be further elucidated from phylogenetic studies, genus by genus, family by family,

and while a considerable number of phylogenetic studies on the Australian and New Zealand flora do exist (See Appendix 1), many remain to be investigated. Once the robust phylogenies of the Australian and New Zealand vascular flora gain more depth and diversity, incorporating this information will be important, given the likely presence of cryptic lineages and species within the widespread disjunctions.

A holistic approach that considers both ecological and historical biogeographic viewpoints, and involving molecular analysis then would be the best approach for a critical evaluation of long distance dispersal, a process that encompasses random and non-random elements, and the same can be applied to future historical biogeographical studies.

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APPENDIX. Vascular plant species considered to occur naturally in both Tasmania and New Zealand.

Family	Genus	Species	Relative Abundance (0= Rare; 1 = Common)		Inferred Disperal Event		
			NZ	TAS	Direction	Cause	Reference
Aizoaceae	*Disphyma*	*crassifolium*	1	1	Tasmania -> NZ		
	Tetragonia	*implexicoma*	0	1	Tasmania -> NZ		
	Tetragonia	*tetragonioides*	0	1	Tasmania -> NZ		
Amaranthaceae	*Alteranthera*	*denticulata*	1	0	Tasmania -> NZ		Heenan & de Lange (2004)
Apiaceae	*Apium*	*prostratum*	1	1			
	Daucus	*glochidiatus*	0	0	Tasmania -> NZ	Only native species in NZ.	
	Eryngium	*Vesiculosum*	1	1			
	Hydrocotyle	*pterocarpa*	0	0			
Asteraceae	*Argyrotegium*	*nitidulum*	0	0	Tasmania -> NZ		Smissen *et al.* (2004)
	Brachyscome	*radiata*	1	0	Tasmania -> NZ		Denda *et al.* (1999)
	Centipeda	*cunninghamii*	1	0			
	Centipeda	*elatinoides*	1	0			
	Centipeda	*minima*	0	1			
	Cotula	*australis*	1	1			
	Cotula	*coronopifolia*	1	1			
	Euchiton	*collinus*	1	1	Tasmania -> NZ		Bayer *et al.* (2002)
	Euchiton	*involucratus*	1	1	Tasmania -> NZ		Bayer *et al.* (2002)
	Euchiton	*sphaericus*	1	1	Tasmania -> NZ		Bayer *et al.* (2002)
	Euchiton	*traversii*	1	1	Tasmania -> NZ		Bayer *et al.* (2002)
	Lagenifera	*montana*	0	0			

Family	Genus	Species	Relative Abundance (0= Rare; 1 = Common)		Inferred Disperal Event		
			NZ	TAS	Direction	Cause	Reference
	Lagenifera	*stipitata*	0	1			
	Picris	*angustifolia*	0	0			
	Pseudognaphalium	*luteo-album*	1	1	Tasmania -> NZ	Recent arrival and radiation in NZ	Breitwieser *et al.* (1999)
	Senecio	*biserratus*	1	1			
	Senecio	*glomeratus*	1	1			
	Senecio	*hispidulus*	1	1			
	Senecio	*lautus (=pinnatifolius)*	1	1			
	Senecio	*minimus*	1	1			
	Senecio	*quadridentatus*	1	1			
Boraginaceae	*Myosotis*	*australis*	1	0	NZ -> Tasmania	Multiple long-dispersals	Winkworth *et al.* (2002)
Brassicaceae	*Lepidium*	*flexicaule*	1	1	Tasmania -> NZ		Mummenhoff *et al.* (2004)
	Lepidium	*desvauxii*	0	0	Tasmania -> NZ		Mummenhoff *et al.* (2004)
Callitrichaceae	*Callitriche*	*antarctica*	0	0			
Campanulaceae	*Lobelia*	*anceps*	1	1			
Caryophyllaceae	*Colobanthus*	*affinis*	1	0			
	Colobanthus	*apetalus*	1	1			
	Scleranthus	*brockiei*	1	1	Tasmania -> NZ		Smissen *et al.* (2003)

Family	Genus	Species	Relative Abundance (0= Rare; 1 = Common)		Inferred Disperal Event		
			NZ	TAS	Direction	Cause	Reference
	Scleranthus	*biflorus*	1	1	Tasmania -> NZ		Smissen *et al.* (2003)
	Spergularia	*tasmanica*	1	1	Tasmania -> NZ		Adams *et al.* (2008)
Centrolepidaceae	*Centrolepis*	*ciliata*	1				
	Centrolepis	*strigosa*	0	1			
	Gaimardia	*setacea*	1	0			
Chenopodiaceae	*Atriplex*	*billardieri*	0	0	Tasmania -> NZ		Kadereit *et al.* (2005)
	Atriplex	*cinerea*	0	1	Tasmania -> NZ		de Lange *et al.* (1998); Kadereit *et al.* (2005)
	Chenopodium	*ambiguum*	1	1	Tasmania -> NZ		Kadereit *et al.* (2005)
	Sarcocornia	*quinqueflora*	1	1	Tasmania -> NZ		Kadereit *et al.* (2005)
Clusiaceae	*Hypericum*	*pusillium*	1	1			
Convolvulaceae	*Calystegia*	*marginata*	0	0	Tasmania -> NZ		Martin (2001)
	Calystegia	*sepium*	1	0	Tasmania -> NZ		Martin (2001
	Calystegia	*soldanella*	1	0	Tasmania -> NZ		Martin (2001
	Dichondra	*repens*	1	1	Tasmania -> NZ		Martin (2001
	Wilsonia	*backhousei*	0	0	Tasmania -> NZ		Martin (2001
Crassulaceae	*Crassula*	*helmsii*	0	1			
	Crassula	*moschata*	1	0			
	Crassula	*peduncularis*	0	0			
	Crassula	*sieberiana*	1	1			
Curcubitaceae	*Sicyos*	*australis*	0	0	Tasmania -> NZ		Wardle (1968)
Cyperaceae	*Baumea*	*arthrophylla*	1	1	Tasmania -> NZ		
	Baumea	*articulata*	1	0	Tasmania -> NZ		

Family	Genus	Species	Relative Abundance (0= Rare; 1 = Common)		Inferred Disperal Event		
			NZ	TAS	Direction	Cause	Reference
	Baumea	*juncea*	1	1	Tasmania -> NZ		
	Baumea	*rubiginosa*	1	0	Tasmania -> NZ		
	Bolboschoenus	*caldwellii*	1	1	Tasmania -> NZ		
	Bolboschoenus	*medianus*	1	0	Tasmania -> NZ		
	Carex	*appressa*	1	1	Tasmania -> NZ		
	Carex	*breviculmis*	1	1	Tasmania -> NZ		
	Carex	*capillacea*	0	0	Tasmania -> NZ		
	Carex	*fascicularis*	1	1	Tasmania -> NZ		
	Carex	*flaviformis*	1	1	Tasmania -> NZ		
	Carex	*gaudichaudiana*	1	1	Tasmania -> NZ		
	Carex	*inversa*	1	1	Tasmania -> NZ		
	Carex	*pumila*	1	1	Tasmania -> NZ		
	Carpha	*alpina*	1	1	Tasmania -> NZ		
	Eleocharis	*acuta*	1	1	Tasmania -> NZ		
	Eleocharis	*gracilis*	1	1	Tasmania -> NZ		
	Eleocharis	*pusilla*	0	1	Tasmania -> NZ		
	Eleocharis	*sphaecelata*	1	1	Tasmania -> NZ		
	Ficinia	*nodosa*	1	1	Tasmania -> NZ		
	Isolepis	*aucklandica*	1	1	Tasmania -> NZ		
	Isolepis	*cernua*	1	1	Tasmania -> NZ		
	Isolepis	*crassiuscula*	1	1	Tasmania -> NZ		
	Isolepis	*fluitans*	0	1	Tasmania -> NZ		
	Isolepis	*habra*	1	1	Tasmania -> NZ		
	Isolepis	*inundata*	1	1	Tasmania -> NZ		

Family	Genus	Species	Relative Abundance (0= Rare; 1 = Common)		Inferred Disperal Event		
			NZ	TAS	Direction	Cause	Reference
	Isolepis	*subtilissima*	1	1	Tasmania -> NZ		
	Lepidosperma	*filiforme*	1	1	Tasmania -> NZ		
	Lepidosperma	*laterale*	1	1	Tasmania -> NZ		
	Schoenoplectus	*pungens*	1	1	Tasmania -> NZ		
	Schoenus	*apogon*	1	1	Tasmania -> NZ		
	Schoenus	*brevifolius*	1	0	Tasmania -> NZ		
	Schoenus	*carsei*	0	0	Tasmania -> NZ		
	Schoenus	*fluitans*	0	1	Tasmania -> NZ		
	Schoenus	*maschalinus*	1	1	Tasmania -> NZ		
	Schoenus	*nitens*	1	1	Tasmania -> NZ		
	Tetaria	*capillaris*	1	1	Tasmania -> NZ		
	Uncinia	*elegans*	0	0	Tasmania -> NZ		
	Uncinia	*nervosa*	1	1	Tasmania -> NZ		
Donatiaceae	*Donatia*	*novae-zelandiae*	1	1	Tasmania -> NZ		Winkworth *et al.* (2002)
Droseraceae	*Drosera*	*arcturi*	1	1	Tasmania -> NZ		Williams *et al.* (1994)
	Drosera	*binata*	1	1	Tasmania -> NZ		Williams *et al.* (1994)
	Drosera	*peltata*	0	1	Tasmania -> NZ		Williams *et al.* (1994)
	Drosera	*pygmaea*	0	1	Tasmania -> NZ		Williams *et al.* (1994)
	Drosera	*spathulata*	1	0	Tasmania -> NZ		Williams *et al.* (1994)
Elatinaceae	*Elatine*	*gratioloides*	0	1	Tasmania -> NZ		Davis & Chase (2004)
Ericaceae	*Cyathodes*	*pumila*	1	1	Tasmania -> NZ		
	Gaultheria	*depressa*	1	1	Tasmania -> NZ		
	Leptecophylla	*juniperina*	1	1	Tasmania -> NZ		
	Leucopogon	*parviflorus*	0	1	Tasmania -> NZ		

Family	Genus	Species	Relative Abundance (0= Rare; 1 = Common)		Inferred Disperal Event		
			NZ	TAS	Direction	Cause	Reference
	Pentachondra	*pumila*	1	1	Tasmania -> NZ		
	Sprengelia	*incarnata*	0	1	Tasmania -> NZ		
Euphorbiaceae	*Poranthera*	*microphylla*	0	1	Tasmania -> NZ		Vorontsova *et al.* (2007)
Gentianaceae	*Sebaea*	*ovata*	0	1			
Geraniceae	*Geranium*	*potentilloides*	1	1	Tasmania -> NZ		Gardner (1984)
	Geranium	*retrorsum*	1	0	Tasmania -> NZ		Gardner (1984)
	Geranium	*sessiliflorum*	1	0	Tasmania -> NZ		Gardner (1984)
	Geranium	*solanderi*	0	0	Tasmania -> NZ		Gardner (1984)
	Pelargonium	*inodorum*	1	1	Tasmania -> NZ		Bakker *et al.* (1998)
Goodenaiceae	*Selliera*	*radicans*	1	1			
Haloragaceae	*Gonocarpus*	*micranthus*	1	1	Tasmania -> NZ		Moody & Les (2007)
	Gonocarpus	*monanthus*		1	Tasmania -> NZ		Moody & Les (2007)
	Myriophyllum	*pedunculatum*	1	1	Tasmania -> NZ		Moody & Les (2007)
Hemerocallidaceae	*Herpolirion*	*novae-zelandiae*	1	1	Tasmania -> NZ	Not close to either *Dianella* or *Phormium*	Wurdack & Dorr (2009)
Juncaceae	*Juncus*	*antarcticus*	1	1	Tasmania -> NZ		Bremer (2002)
	Juncus	*australis*	1	1	Tasmania -> NZ		Bremer (2002)
	Juncus	*caespiticius*	1	0	Tasmania -> NZ		Bremer (2002)
	Juncus	*holoschoenus*	1	1	Tasmania -> NZ		Bremer (2002)
	Juncus	*kraussii*	1	1	Tasmania -> NZ		Bremer (2002)
	Juncus	*pallidus*	1	1	Tasmania -> NZ		Bremer (2002)
	Juncus	*pauciflorus*	1	1	Tasmania -> NZ		Bremer (2002)
	Juncus	*planifolius*	1	1	Tasmania -> NZ		Bremer (2002)

Family	Genus	Species	Relative Abundance (0= Rare; 1 = Common)		Inferred Disperal Event		
			NZ	TAS	Direction	Cause	Reference
	Juncus	*prismatocarpus*	1	0	Tasmania -> NZ		Bremer (2002)
	Juncus	*sarophorus*	1	1	Tasmania -> NZ		Bremer (2002)
Lemnaceae	*Lemna*	*minor*	1	1	Tasmania -> NZ		
	Wolffia	*australiana*	1	0	Tasmania -> NZ		
Lentibulariaceae	*Utricularia*	*australis*	0	0			
	Utricularia	*monanthos*	1	1	Tasmania -> NZ		
Lobeliaceae	*Lobelia*	*anceps*	1	1	Tasmania -> NZ		
Menythaceae	*Liparophyllum*	*gunnii*	0	0	Tasmania -> NZ		Tippery *et al.* (2008)
Myrtaceae	*Leptospermum*	*scoparium*	1	1	Tasmania -> NZ		Stephens *et al.* (2005)
Onagraceae	*Epilobium*	*billardierianum*	1	1			
	Epilobium	*gunnianum*	0	1			
	Epilobium	*hirtigerum*	0	1			
	Epilobium	*pallidiflorum*	1	0			
	Epilobium	*tasmanicum*	1	1			
Orchidaceae	*Calochilus*	*herbaceous*	0	1	Tasmania -> NZ		
	Calochilus	*paludosus*	0	1	Tasmania -> NZ		
	Calochilus	*robertsonii*	0	1	Tasmania -> NZ		
	Corunastylis	*nuda*	0	0	Tasmania -> NZ		
	Cryptostylis	*subulata*	0	1	Tasmania -> NZ		
	Gastrodia	*sesamoides*	1	1	Tasmania -> NZ		
	Microtis	*parviflora*	1	1	Tasmania -> NZ		
	Microtis	*uniflora*	1	1	Tasmania -> NZ		
	Myrmechila	*trapeziformis*	0	0	Tasmania -> NZ		
	Petalochilus	*alatus*	0	1	Tasmania -> NZ		

Family	Genus	Species	Relative Abundance (0= Rare; 1 = Common)		Inferred Disperal Event		
			NZ	TAS	Direction	Cause	Reference
	Plumatichilos	*tasmanicum*	0	1	Tasmania -> NZ		
	Pterostylis	*foliata*	0	1	Tasmania -> NZ		
	Pterostylis	*nutans*	0	1	Tasmania -> NZ		
	Simpliglottis	*cornuta*	1	1	Tasmania -> NZ		
	Simpliglottis	*valida*	0	1	Tasmania -> NZ		
	Sullivania	*minor*	0	1	Tasmania -> NZ		
	Thelymitra	*carnea*	1	0	Tasmania -> NZ		
	Thelymitra	*cyanea*	1	1	Tasmania -> NZ		
	Thelymitra	*ixioides*	0	1	Tasmania -> NZ		
	Thelymitra	*malvina*	0	0	Tasmania -> NZ		
	Thelymitra	*pauciflora*	1	1	Tasmania -> NZ		
Oxalidaceae	*Oxalis*	*exilis*	1	1			
	Oxalis	*magellanica*	1	1			
Phyrmaceae	*Mazus*	*pumilo*	0	1	Tasmania -> NZ		Heenan & Forester (1997)
	Mimulus	*repens*	0	1	Tasmania -> NZ		Beardsley & Olmstead (2002)
	Glossostigma	*elatinoides*	1	0			
Plantaginaceae	*Chionohebe*	*ciliolata*	1	0	NZ -> Tasmania	One ancestor that diversified in NZ	Wagstaff & Garnock-Jones (2000)
	Gratiola	*concinna (=nana)*	0	1			
	Gratiola	*pubescens*	0	0			

Family	Genus	Species	Relative Abundance (0= Rare; 1 = Common)		Inferred Disperal Event		
			NZ	TAS	Direction	Cause	Reference
	Plantago	*triantha*	0	1	Tasmania -> NZ		Tay (2008)
Poaceae	*Agrostis*	*muelleriana*	1	1	Tasmania -> NZ		
	Austrofestuca	*littoralis*	0	1	Tasmania -> NZ		
	Austrostipa	*stipoides*	1	1	Tasmania -> NZ		
	Bromus	*arenarius*	0	0	Tasmania -> NZ		
	Cenchrus	*caliculatus*	0	0	Tasmania -> NZ		
	Deschampsia	*caespitosa*	1	0	Tasmania -> NZ		
	Deschampsia	*gracillima*	0	1	Tasmania -> NZ		
	Deyeuxia	*quadriseta*	0	1	Tasmania -> NZ		
	Dichelachne	*crinita*	1	1	Tasmania -> NZ		
	Dichelachne	*inaequiglumis*	0	1	Tasmania -> NZ		
	Dichelachne	*micrantha*	1	1	Tasmania -> NZ		
	Echinopogon	*ovatus*	1	1	Tasmania -> NZ		
	Festuca	*rubra*	1	1	Tasmania -> NZ		
	Hierochloe	*redolens*	1	1	Tasmania -> NZ		
	Isachne	*globosa*	1	0	Tasmania -> NZ		
	Lachnagrostis	*billardierei*	1	1	Tasmania -> NZ		
	Lachnagrostis	*filiformis*	1	1	Tasmania -> NZ		
	Microlaena	*stipoides*	1	1	Tasmania -> NZ		
	Puccinellia	*stricta*	1	1	Tasmania -> NZ		
	Rytidosperma	*australe*	1	1	Tasmania -> NZ		
	Rytidosperma	*gracile*	1	1	Tasmania -> NZ		
	Spinifex	*sericeus*	1	1	Tasmania -> NZ		
	Sporobolus	*virginicus*	1	1	Tasmania -> NZ		

Family	Genus	Species	Relative Abundance (0= Rare; 1 = Common)		Inferred Disperal Event		
			NZ	TAS	Direction	Cause	Reference
	Trisetum	*spicatum*	1	1	Tasmania -> NZ		
Polygonaceae	*Muehlenbeckia*	*axillaris*	1	0			
	Persicaria	*decipiens*	1	0			
Potamogetonaceae	*Potamogeton*	*ochreatus*	1	1			
	Potamogeton	*pectinatus*	0	1			
Portulaceae	*Montia*	*fontana*	1	1			
Primulaceae	*Samolus*	*repens*	1	1			
Zannichelliaceae	*Lepilaena*	*bilocularis*	0	0	Tasmania -> NZ		
Ranunculaceae	*Ranunculus*	*acaulis*	1	0	NZ -> Tasmania	Estimated origin 5 mya	Lockhart *et al.* (2001)
	Ranunculus	*amphitrichus*	1	1	NZ -> Tasmania	as for *R. acaulis*	Lockhart *et al.* (2001)
	Ranunculus	*glabrifolius*	1	1	NZ -> Tasmania	as for *R. acaulis*	Lockhart *et al.* (2001)
Restionaceae	*Empodisma*	*minus*	1	1	Tasmania -> NZ		
Rhamnaceae	*Pomaderris*	*apetala*	0	1	Tasmania -> NZ		Ladiges *et al.* (2005)
Rhamnaceae	*Pomaderris*	*paniculosa*	0	0	Tasmania -> NZ		Ladiges *et al.* (2005)
Rhamnaceae	*Pomaderris*	*phylicifolia*	0	0	Tasmania -> NZ		Ladiges *et al.* (2005)
Rosaceae	*Acaena*	*novae-zelandiae*	1	1	NZ -> Tasmania		
	Acaena	*pallida*	1	1	NZ -> Tasmania		
Rubiaceae	*Coprosma*	*perpusilla*	1	1	NZ -> Tasmania		
Ruppiaceae	*Ruppia*	*megacarpa*	1		Tasmania -> NZ		
	Ruppia	*polycarpa*	1		Tasmania -> NZ		
Sapindaceae	*Dodonaea*	*viscosa*	1	1	Tasmania -> NZ		Harrington (2008)
Solanaceae	*Solanum*	*laciniatum*	1	1	Tasmania -> NZ		

Family	Genus	Species	Relative Abundance (0= Rare; 1 = Common)		Inferred Disperal Event		
			NZ	TAS	Direction	Cause	Reference
Stylidaceae	*Phyllachne*	*colensoi*	1	0	NZ -> Tasmania	Two dispersal events from Australia to NZ	Wagstaff & Wege (2002)
Thismiaceae	*Thismia*	*rodwayi*	0	0	Tasmania -> NZ		
Typhaceae	*Typha*	*orientalis*	1	1	Tasmania -> NZ		
Urticaceae	*Australina*	*pusilla*	1		Tasmania -> NZ		
	Parietaria	*debilis*	1	0	Tasmania -> NZ	Only native species in New Zealand	
	Urtica	*incisa*	1	1			
Violaceae	*Viola*	*cunninghamii*	1	1			
Zosteraceae	*Zostera*	*muelleri*	1	0	Tasmania -> NZ		
Adiantaceae	*Adiantum*	*aethiopicum*	0	1			
	Anogramma	*leptophylla*	0	0			
	Cheilanthes	*distans*	1	0			
	Cheilanthes	*sieberi*	1	0			
	Pellaea	*calidirupium*	1	0			
	Pellaea	*falcata*	0	1			
Aspleniaceae	*Asplenium*	*appendiculatum*	1	1	Tasmania -> NZ	Estimated divergence < 43 mya	Perrie & Brownsey (2005)
	Asplenium	*bulbiferum*	1	1	Tasmania -> NZ	as for *A. appendiculatum*	Perrie & Brownsey (2005)

Family	Genus	Species	Relative Abundance (0= Rare; 1 = Common)		Inferred Disperal Event		
			NZ	TAS	Direction	Cause	Reference
	Asplenium	*flabellifolium*	1	1	Tasmania -> NZ	as for *A. appendiculatum*	Perrie & Brownsey (2005)
	Asplenium	*flaccidum*	1	0	Tasmania -> NZ	as for *A. appendiculatum*	Perrie & Brownsey (2005)
	Asplenium	*hookerianum*	1	0	Tasmania -> NZ	as for *A. appendiculatum*	Perrie & Brownsey (2005)
	Asplenium	*obtusatum*	1	1	Tasmania -> NZ	as for *A. appendiculatum*	Perrie & Brownsey (2005)
	Asplenium	*trichomanes*	1	1	Tasmania -> NZ	as for *A. appendiculatum*	Perrie & Brownsey (2005)
	Pleurosorus	*rutifolius*	0	0			
Athyriaceae	*Cystopteris*	*tasmanica*	1	0			
	Diplazium	*australe*	1	0			
Azollaceae	*Azolla*	*filiculoides*	1	0			
Blechnaceae	*Blechnum*	*chambersii*	1	1			
	Blechnum	*fluviatile*	1	1			
	Blechnum	*minus*	1	1			
	Blechnum	*penna-marina*	1	1			
	Blechnum	*vulcanicum*	0	1			
	Doodia	*australis*	1	0			
Cyatheaceae	*Cyathea*	*cunninghamii*	1	0			
Dennstaedtiaceae	*Hypolepis*	*amaurorachis*	0	0			
	Hypolepis	*distans*	1	0			
Dryopteridaceae	*Lastreopsis*	*hispida*	1	0			

Family	Genus	Species	Relative Abundance (0= Rare; 1 = Common)		Inferred Disperal Event		
			NZ	TAS	Direction	Cause	Reference
	Rumohra	*adiantiformis*	1	1			
Gleicheniaceae	*Gleichenia*	*dicarpa*	1	1	ambiguous	Estimated divergence less than 55 mya	Perrie *et al.* (2007)
	Gleichenia	*microphylla*	1	1	ambiguous	As for *G. dicarpa*	Perrie *et al.* (2007)
	Sticherus	*tener*	0	1	ambiguous	As for *G. dicarpa*	Perrie *et al.* (2007)
	Ctenopteris	*heterophylla*	1	1			
	Grammitis	*billardierei*	1	1			
	Grammitis	*gunnii*	0	0			
	Grammitis	*magellanica*	1	1			
	Grammitis	*poepiggiana*	1	0			
	Grammitis	*pseudociliata*	1	0			
Hymenophyllaceae	*Crepidomanes*	*venosum*	1	1			
	Hymenophyllum	*australe*	0	1			
	Hymenophyllum	*cupressiforme*	0	1			
	Hymenophyllum	*flabellatum*	1	1			
	Hymenophyllum	*peltatum*	1	1			
	Hymenophyllum	*rarum*	1	1			
Lindsaeaceae	*Lindsaea*	*linearis*	1	1			
	Lindsaea	*trichomanoides*	1	0			
Lycopodiaceae	*Huperzia*	*australiana*	1	0			

Family	Genus	Species	Relative Abundance (0= Rare; 1 = Common)		Inferred Disperal Event		
			NZ	TAS	Direction	Cause	Reference
	Huperzia	*varia*	1	1			
	Lycopodiella	*diffusa*	1	1			
	Lycopodiella	*laterialis*	1	1			
	Lycopodiella	*serpentina*	0	0			
	Lycopodium	*deuterodensum*	1	1			
	Lycopodium	*fastigiatum*	1	1			
	Lycopodium	*scariosum*	1	1			
	Phylloglossum	*drummondii*	0	0			
Marsileaceae	*Pilularia*	*novae-hollandiae*	0	0			
Ophioglossaceae	*Botrychium*	*australe*	0	0			
	Botrychium	*lunaria*	0	0			
Osmundaceae	*Todea*	*barbara*	0	1			
Polypodiaceae	*Microsorum*	*pustulatum*	1	1			
Psilotaceae	*Tmesipteris*	*elongata*	0	0			
Pteridaceae	*Histiopteris*	*incisa*	1	1			
	Pteridium	*esculentum*	1	1			
	Pteris	*comans*	1	1			
	Pteris	*tremula*	1	0			
Schizaceae	*Schizaea*	*bifida*	1	0			
	Schizaea	*fistulosa*	1	1			
Thelypteridaceae	*Pneumatopteris*	*pennigera*	1	0			

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