



REVIEW

Seed dispersal systems in the New Zealand flora

Michael J. Thorsen^{a,*}, Katharine J.M. Dickinson^a, Philip J. Seddon^b

^aDepartment of Botany, University of Otago, Dunedin 9054, New Zealand

^bDepartment of Zoology, University of Otago, Dunedin 9054, New Zealand

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Abstract

Knowledge of the dispersal mechanisms used by plants is important in phylogenetic, ecological, biogeographical, and conservation studies. Here we attempt to assign dispersal mechanisms to the entire flora-2595 plant species of the New Zealand Botanical Region. Anemochory is the most frequent dispersal mechanism, utilised by 79% of species. The next most frequent mechanisms are endozoochory (33%), hydrochory (28%), epizoochory (26%), and ballistic (8%). Polychory is common, particularly in monocotyledonous and dicotyledonous families and hydrochorous, epizoochorous, and ballistically dispersed species. Epizoochory is more common in New Zealand than in other regions, and species using this dispersal mechanism are over-represented among threatened species. Frugivory is less common than previously reported, and is under-represented among threatened species. Some mechanisms are poorly known, and entanglement and capsulivory are dispersal mechanisms apparently unique to New Zealand. Dispersal mechanisms reflective of New Zealand's distinctive assemblages of large flightless birds and reptiles are not apparent. A pattern of reduction in dispersal-related structures is evident in some genera. The mechanisms utilised by some species are ambiguous. Thus there remains a need for further investigation of the dispersal mechanisms utilised by plants in New Zealand.

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*Corresponding author. Tel.: +64 3 4822802.

E-mail address: mike.esr@xtra.co.nz (M.J. Thorsen).

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Introduction

Dispersal is a critical process in the life history of plants. It allows plants to colonise new locations and, through the heterogeneous distribution of propagules, dispersal influences patterns of propagule and seedling predation, seedling establishment and survival, and ultimately the density and distribution of the next generations of adult plants (Webb, 1998; Willson and Traveset, 2002; Fuentes, 2000; Nathan and Muller-Landau, 2000; Wang and Smith, 2002). The spatial pattern of propagule dispersal therefore is the template from which biotic communities develop (Schupp and Fuentes, 1995). Plants use a range of motive forces to achieve dispersal of their propagules. Some of these, such as wind and water, are environmentally pervasive and utilised by a range of species. Others, such as frugivory, are specific to a particular group of organisms and a degree of coevolution has developed between disperser guild and plant dispersal systems (Herrera, 1985, 1992, 1998; Wheelwright, 1991; Jordano, 1995; Burns, 2006).

The mechanisms used for propagule dispersal in the flora of New Zealand are poorly known (Godley, 1985; Webb and Simpson, 2001). Much current knowledge is derived from ecological studies or regional propagule rain studies (e.g. Beveridge, 1964; Spence, 1990; Wardle, 1991; Burrows, 1994b,c; Sem and Enright, 1996; Dungan et al., 2001; Outred, 2002). A lack of reliable information on dispersal mechanisms is not restricted to New Zealand however, with most papers making inferences from the structure of the propagule (Ridley, 1930; van der Pijl, 1982; Hughes et al., 1994). For some traits (e.g. fleshy fruit), this assumption can be justified. However, some propagules display no obvious adaptations, and are difficult to link to a known dispersal agent. This situation may have arisen as a result of the disperser becoming extinct (Janzen and Martin, 1982; Janzen, 1986; Barlow, 2000), or where novel dispersal mechanisms are involved such as ingestion by weta (large, flightless insects in the order Orthoptera, endemic to the New Zealand archipelago; Burns, 2006; Duthie et al., 2006). Even so, 27% of the propagules of New Zealand gymnospermous and dicotyledonous

genera show no specialised adaptation for dispersal (Webb and Simpson, 2001).

Knowledge of the dispersal mechanisms used by plants is important in phylogenetic, ecological, biogeographical, and conservation studies. For example, propagule dispersal may shape an island's flora by favouring colonists with the capacity to achieve long-distance dispersal (Carlquist, 1967; Stebbins, 1971; Price and Wagner, 2004; Burns, 2005). On arrival, different selection pressures may ultimately result in changes to the dispersal mechanism (Carlquist, 1967). One expected change to island colonists is a decrease in dispersal ability in response to limited habitat availability and loss of prior dispersal linkages (Carlquist, 1974; Price and Wagner, 2004). This loss of dispersal ability can occur in only a few generations (Cody and Overton, 1996; Blair and Wolfe, 2004), and is evident in the flora of Hawai'i (Carlquist, 1967, 1980; Price and Wagner, 2004).

The New Zealand flora includes elements originating from both transoceanic immigrants and original Gondwanan inhabitants, which have undergone intense selection and evolution under fluctuating environmental conditions (Lloyd, 1985; Pole, 1994; Macphail, 1997; Lee et al., 2001; Lockhart et al., 2001; McLoughlin, 2001; McGlone et al., 2001; Stöckler et al., 2002; Wagstaff et al., 2002; Winkworth et al., 2002; Gardner et al., 2004; de Queiroz, 2005; Rogers and Walker, 2005; Gibbs, 2007). Dispersal mechanisms within the New Zealand flora are presumably modifications of those of the original occupants. It is argued that many species in New Zealand have originated from transoceanic immigration (Lockhart et al., 2001; Wagstaff et al., 2002; Winkworth et al., 2002; Gardner et al., 2004). Thus an over-representation of mechanisms derived from those taxa capable of achieving transoceanic dispersal would be expected (Lloyd, 1985; Burrows, 1994a).

The lack of mammals and the predominance within the New Zealand fauna of birds, reptiles, and invertebrates may have caused certain dispersal mechanisms to proliferate, especially given the diversity and density of ground-dwelling bird species, many of considerable body mass (Holdaway et al., 2001; Worthy and Holdaway, 2002; Bond et al., 2004) and the likely

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