

1 | INTRODUCTION

When one starts to trace out the dependence of one animal upon another, one soon realises that it is necessary to study the whole community living in one habitat, since the interrelations of animals ramify so far.

— Charles Elton, *Animal Ecology* (1927)

From food and freshwater production to recreational and carbon sequestration, ecosystems provide a wide range of services of considerable value to humans. Unfortunately, the ability of ecosystems to provide these services is currently threatened by global change. Climate change and invasive alien species, in particular, are some of the most significant causes of ecosystem degradation. A necessary step to anticipate, prevent, and reverse ecosystem degradation is to understand the factors that determine their response to disturbances.

A substantial amount of ~~recent~~ research indicates that the way ecosystems respond to disturbances is strongly determined by the network of interactions formed by the species that inhabit it (Tylianakis, Didham, et al. 2008; Bascompte, Jordano, and Olesen 2006). This is so, because this network, which connects all organisms in an ecological community, underpins ecosystem functioning and structure, and, therefore, can modulate the resilience of ecosystem services to disturbances (Reiss et al. 2009; Dobson et al. 2006). However, we still do not understand enough about the processes that shape interaction networks in ecological communities to harness them for better ecological management. The central aim of my doctoral research is to shed light into outstanding questions about the factors that determine the structure of ecological networks and how can it be effectively leveraged for improved management of ecosystem services.

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In this thesis, I focus on the network of mutualistic interactions between plants and pollinators. These networks, which form the base of pollination systems, play a globally significant role in the maintenance of biodiversity and crop production (Bascompte and Jordano 2007; Klein et al. 2007). Pollination systems are locally critical too; for instance, two-thirds of New Zealand plants are pollinated by birds or insects (Cox and Elmqvist 2000), and this includes iconic native plants (like kōwhai and pōhutukawa), and economically important crops (like kiwifruit, apples and grapes). Regrettably, just like other species interactions, the relationship between plants and pollinators, are currently being disrupted by multiple drivers of human-driven global change at a worldwide scale (Cox and Elmqvist 2000).

A central concept of my thesis is that of species degree, essentially the number of interactions a species engages in an ecological community. The degree distribution of all species in a community is a fundamental way to describe ecological networks and underpins multiple metrics of network structure (Stouffer 2010). Broadly speaking, species with a large degree, and hence a large number of partners, are considered generalists while species with a small degree are considered a specialist.

Pollination networks are deemed to be relatively generalised when compared with other types of ecological networks. That is, pollinators tend to interact with a large number of plants and vice-versa, which biases the degree distribution. Previous theoretical work has suggested that this tendency of species to have a large degree and incidentally share a large number of partners, is responsible for the impressive biodiversity of pollination communities (Bastolla et al. 2009). This is so because, theoretically, this partner sharing increases the possible positive feedback loops between plants and pollinators, which offset the antagonistic interactions that may exist among each guild (Moeller 2004). These findings imply that coexistence of species is maximised when pollinator sharing is the highest. This implication is based on the assumption that pollination interactions are primarily mutualistic. However, there is ample empirical evidence going back to the end of the 19th century emphasising the competitive aspects of pollination and showing that plant reproduction de-

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pendes strongly on the quality of the mutualistic service (Mitchell et al. 2009).

In Chapter 2 I return to the longstanding view of pollination as a balance between facilitation and competition. Specifically, I explore how the sharing of partners, a common feature of generalised pollination networks, affects the quality of pollination and discuss its possible implications for network structure. A shortcoming of previous empirical evidence was that it focused primarily on pairs of species, or, at most, small subsets of ecological communities. However, ecological communities are highly diverse, and multiple confounding factors can also affect the quality of pollination (Flanagan, Mitchell, and Karron 2011). I, therefore, expand the analysis of competition for pollination to ecological communities using a comprehensive dataset collected by Hugo Marrero and collaborators in the Argentinean Pampas (Marrero, Medan, et al. 2016; Marrero, Torretta, and Medan 2014; Marrero, Torretta, Vázquez, et al. 2017).

In Chapter 2, I look at the possible implications that degree and pollinator sharing may have on network structure. However, neither the identity of the partners a species has nor the species degree is constant across the different ecological communities it inhabits (Gravel et al. 2018). It has been shown that the environment can affect the structure of ecological networks, but how exactly it does it, particularly in plant-pollinator communities, is not well understood (Tylianakis and R. J. Morris 2017). In Chapter 3 I investigate how the environment may influence species degree, the number of partners each species has, in an ecological community. To do that, I use a global dataset of pollination networks and complement it with information about the global climate and the occurrence of species. Importantly, I take into account how the environment may affect species degree through the presence or absence of possible partners or through the stresses it imposes on interacting species.

In Chapter 4 I move from how biotic and abiotic factors may determine the structure of ecological networks into how the structure may be used to inform ecological management. For this purpose, I build upon recent work from theoretical physics and engineering concerned with the control of complex networks (Liu

