



## Original article

## Relative abundance of an invasive alien plant affects insect–flower interaction networks in Ireland

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## ABSTRACT

1. Invasive alien flowering plants may affect native plant pollinator interactions and have knock on impacts on populations of native plants and animals. The magnitude of these impacts, however, may be modified by the relative abundance of the invasive plant and the number of flowers it presents.
2. We tested this by examining the structure of insect–flower interaction networks in six sites with increasing levels of invasion by *Rhododendron ponticum* in Ireland.
3. Neither flower-visiting insect abundance, species richness nor diversity were related to *R. ponticum* flower abundance, but the composition of insect communities was. The total number of flowers in a site increased with the relative abundance of *R. ponticum* flowers but the number of co-flowering native plant species in these sites was low (<6), making interaction networks relatively small.
4. As a result, changes in interaction network properties (connectance, interaction evenness and network level specialisation), which correlated with *R. ponticum* flower abundance, were a result of the small network size rather than due to changes in the resilience of networks.
5. Overall, we conclude that the impacts of invasive alien plants on native plant–pollinator interactions are not only species specific, but site specific, according to the abundance of flowers produced by both the invasive and the native plants.

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## 1. Introduction

Invasion by non-native plant species has often been linked with ecological changes to native species populations and communities, but impacts on ecosystem functions and services have, until recently, been less well studied (Vilà et al., 2011). Non-native, invasive plants have the potential to affect native plant–pollinator interactions, and thus pollination services in invaded communities, in several ways. They may alter the availability of nectar and pollen resources for native flower-visitors: either by out-competing native plants which provide forage resources, or by providing alternative additional resources themselves; and they can thus affect the abundance of pollinating animals in an invaded habitat

(e.g. Morón et al., 2009). Furthermore, non-native invasive plants may affect the pollination of native plants by disrupting patterns of foraging of native flower-visitors: either by luring them away from native plants and reducing pollination through competition, or by enhancing the overall attractiveness of native plants and facilitating enhanced pollination (reviewed in Bjerknes et al., 2007; Morales and Traveset, 2009). Additionally, non-native invasive plants may have indirect impacts on plant–pollinator interactions by affecting other ecological processes and causing changes to microclimates, soil nutrient status, microhabitats for nesting, etc. Although some pair-wise studies have demonstrated negative impacts of invasive plants on native plant fitness as a result of competition (e.g. Brown et al., 2002; Chittka and Schurkens, 2001), it has become clear that this is not always the case (Bjerknes et al., 2007; Morales and Traveset, 2009). The biological traits and abundance of the alien species, as well as the composition of the native flowering-plant and insect communities, affect the magnitude and direction of impacts (Bartomeus et al., 2008; Nienhuis et al., 2009; Stout and

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Morales, 2009). Hence, whilst floral abundance can affect competitive and facilitative interactions among native plants (Rathcke, 1983), it can also affect competitive interactions between aliens and natives as well (Dietzsch et al., 2011; Muñoz and Cavieres, 2008), and is likely to affect the interactions at a community level and hence the entire structure of the insect–flower interaction network (Stang et al., 2006).

It is recognized that insect–flower interaction networks have robust architectural properties (Bascompte et al., 2003, 2006), and display asymmetry (with specialist insects interacting with generalist plants and vice versa) and nestedness (where specialists interact with species that form a subset of those that interact with generalists) (Bascompte and Jordano, 2007; Vázquez et al., 2009). These properties can give networks stability (Bascompte et al., 2006; Petanidou et al., 2008) and resilience in the face of species extinctions (Kaiser-Bunbury et al., 2010; Memmott et al., 2004). Networks appear to be able to cope with invasion by non-native plants, which can become well integrated into insect–flower interaction networks (Lopezaraiza-Mikel et al., 2007; Memmott and Waser, 2002; Morales and Aizen, 2006; Vilà et al., 2009). Integration occurs as generalist native flower-visitors include the invasive alien plants in their diet (Olesen et al., 2002), and in pollinator-limited systems, this can result in competition for pollinators between invasive alien and native plants (Traveset and Richardson, 2006). This integration can also affect the structure of the network (Bartomeus et al., 2008; Kaiser-Bunbury et al., 2011). For example, insect–flower interactions are generally asymmetric, in terms of the number of species to which a given species is connected: the specialists (who have a low number of links between species) tend to interact with generalists (who have a high number of links). Since successful non-native plants tend to have generalist flowers which can attract a range of native flower-visitors (Memmott and Waser, 2002; Stout et al., 2006; but see Parker, 1997; Valentine, 1978), they may affect the interaction evenness of the network (i.e. the distribution of interactions between species in the network), particularly if they produce an abundance of flowers.

Most studies of the impacts of invasive aliens on native plant–pollinator networks were not designed to consider the abundance of the invading species as a factor (but see Kaiser-Bunbury et al., 2011). Aizen et al. (2008) compared highly and lightly invaded subwebs, but most studies have attempted to compare invaded and non-invaded sites (Bartomeus et al., 2008; Vilà et al., 2009), and/or invaded sites and ones where the invader had been experimentally removed (Lopezaraiza-Mikel et al., 2007). Invaders in networks examined by Vilà et al. (2009) were all found at relatively low abundance (<40% cover). Kaiser-Bunbury et al. (2011) showed that more highly invaded sites were more vulnerable to loss of flower-visiting taxa and interactions were less evenly distributed among the species in the communities. They concluded that non-native species are likely to have more effect on network structure at higher levels of invasion (Kaiser-Bunbury et al., 2011). At high abundance, aliens may have more impact on plant–pollinator networks via a variety of mechanisms, including: i) vegetative competition may exclude some native plants from networks altogether, ii) there may be increased competitive effects of the alien on native plants in terms of pollinator attraction (Dietzsch et al., 2011; Muñoz and Cavieres, 2008) and iii) the alien may directly impact on the pollinator community, depending on trait complementarity with native pollinators (Nienhuis and Stout, 2009; Stang et al., 2006, 2009). In this study, we explored the impacts of abundance of an invasive plant on plant–pollinator network structure, using *Rhododendron ponticum* as a model invasive species.

*Rhododendron ponticum*, introduced from the Iberian peninsula in the late 18th Century (Milne and Abbott, 2000), invades woods,

bogs and heathlands in Britain and Ireland (Brown, 1953; Colak et al., 1998; Cross, 1981; Erfmeier and Bruelheide, 2010; Stephenson et al., 2006). It can form dense thickets which shade out native plants (Cross, 1975, 1981), and produces a massive floral display which is visited and pollinated by a range of native insects (Stout, 2007a; Stout et al., 2006). Hence it has the potential to affect native plant–pollinator interactions. Comparisons of lightly invaded (<20% cover) and uninvaded networks revealed no differences in plant–linkage level (generality), connectance or nestedness (Vilà et al., 2009). However, other studies have shown that as abundance increases (up to 98% cover), it has a greater negative effect on the pollination of the native plant, *Digitalis purpurea* (Dietzsch et al., 2011).

This study aimed to use quantitative network descriptors to investigate the effect of increasing *R. ponticum* invasion on plant–pollinator networks in Irish heathlands. In particular, we were interested in determining whether increasing invasion affected network connectance, insect and plant linkage, the evenness of interactions between species in the network, network specialisation and the asymmetry of interaction strengths of species pairs (Tylianakis et al., 2010). Specifically we tested the hypothesis that *R. ponticum* abundance at a site will affect, i) flowering–plant species richness and native flower abundance; ii) flowering–visiting insect richness, abundance and community composition; and iii) network structure as quantified by standard network descriptors.

## 2. Materials and methods

### 2.1. Plant and insect sampling

Six heathland sites (approximately 100 m × 50 m) in the Knockmealdown Mountains, Co. Tipperary, Ireland were selected according to the overall level of invasion by *Rhododendron ponticum* (Table 1). Sites were ≥1 km apart to reduce the chances of insect overlap among sites (Knight et al., 2005), were at a similar altitude and aspect, and represented relatively homogeneous heathland habitat in an attempt to standardize the native plant communities and abiotic conditions at each site. Sites were numbered according to increasing *R. ponticum* floral abundance: site 1 had the lowest abundance and site 6 the highest (see below for how abundance was determined).

Each site was sampled four times between May 15th and June 18th 2009 during peak *R. ponticum* flowering, when weather conditions were suitable for flower-visiting insect activity (>14 °C and dry). Each site was visited at least once in the morning (9.00–12.00), midday (12.00–15.00) and afternoon (15.00–18.00) to reduce potential temporal biases. Sampling was conducted using random transect walks (mean ± SD: length – 264.56 ± 86.6 m; time taken to walk – 89.78 ± 7.10 min; rate – 2.97 m/min ± 1.0) (Gibson et al., 2011; Westphal et al., 2008). On each walk, all flowering plants and flower-visiting insects within 1 m of the

**Table 1**

Location and altitude of study sites. Sites are numbered according to increasing proportion of *Rhododendron* in the flowering community (Rhodo % = percentage of total flower units that were *Rhododendron*); site 1 had the lowest abundance and site 6 the highest.

Site number	Location	Elevation (m)	Rhodo%
1	N 52.21740°; W 007.93547°	268	13.0
2	N 52.20986°; W 007.92971°	206	25.6
3	N 52.25747°; W 007.94792°	262	76.1
4	N 52.23923°; W 007.95780°	271	82.9
5	N 52.24838°; W 007.95879°	375	90.3
6	N 52.26378°; W 007.96076°	95	98.0

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