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SHORT COMMUNICATION

Can monophagous specialists mediate host plant choices in generalist planthoppers (Hemiptera: Delphacidae)?

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Abstract. 1. A preference experiment was set up with two planthopper species (Hemiptera: Delphacidae) to test the influence of competition on host plant choice.

2. The delphacid *Javesella pellucida* was chosen as a generalist and the rarer *Ribautodelphax imitans* as a monophagous specialist, which feeds on the grass, tall fescue *Schedonorus arundinaceus*.

3. In the absence of the specialist, the generalist showed a marked preference for tall fescue. In some experiments, however, the introduction of the specialist resulted in a shift of preference to an alternative plant if the specialist was established prior to the introduction of the generalist.

4. This experiment supports the hypothesis that specialist herbivores can potentially alter the host plant choices of generalists, which may lead to differing host plant use patterns in insect communities.

Key words. Auchenorrhyncha, competition, insect–plant interactions, planthopper, rarity.

Introduction

Interspecific interactions are important because they mediate community composition and have far-reaching impacts on the long-term stability of complex insect–plant networks, and how they are structured (Frank van Veen *et al.*, 2005; Denno & Kaplan, 2007; Kaplan & Denno, 2007). Studies of direct competition, particularly among phytophagous groups, have largely been focussed on fitness, fecundity rates, growth, and survival (reviewed by: Denno *et al.*, 1995; Kaplan & Denno, 2007). Competition, however, can affect factors not solely attributed to community and population fitness, such as host plant and microhabitat use and position on plants (Ferrenberg & Denno, 2003).

Within phytophagous insect communities, generalists and specialists coexist (Bernays, 1998), with the majority of species being specialist (Tallamy, 2004). Moreover, most studies of competition between species, specialist or generalist, centre on those directly sharing resources (Denno & Kaplan, 2007; Kaplan & Denno, 2007; Ali & Agrawal, 2012), with little work carried out on how competition affects host plant utilisation. The majority of previous work focussed on host displacement, where non-native species have displaced their native counterparts (Kenis *et al.*, 2009) or where there is resulting niche shift or death of an outcompeted species under experimental conditions (Kaplan & Denno, 2007). In order to understand other aspects of the roles that specialists have on generalists, there is a need for more experimental work.

Two-species experiments are useful models because they can elucidate potential community effects at a level more accurately measured under controlled conditions rather than more observational field-based studies (Kaplan & Denno, 2007). This paper looks at one such system, an interaction between two co-occurring grass-feeding planthopper species (Hemiptera: Auchenorrhyncha: Delphacidae), and the influence of one species feeding on the other's preferred host within mesocosms. The species used were a generalist, *Javesella pellucida* (Fab.) (Nickel & Remane, 2002), and a specialist, *Ribautodelphax imitans* (Ribaut.), which is only known to feed on tall fescue *Schedonorus arundinaceus* (Schreb.) (den Bieman, 1987; Nickel & Remane, 2002; JNCC, 2010; Dittrich, 2016; Dittrich & Helden, 2016). It was hypothesised that, because the specialist was adapted to utilising one grass species efficiently, it would drive a host plant shift in the generalist. Thus, we tested the paradigm that there is a potential trade-off between using many

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resources adequately and being able to move between them and avoid competition versus being able to use one resource better than all others, thus outcompeting any potential competitors (McPeek, 1996; Noriyuki & Osawa, 2012). We tested this with experiments in which we observed the host choice of the two delphacid species in single- and mixed-species culture.

Methods

In order to determine the life cycles and abundance of the test specialist *R. imitans* and the test generalist *J. pellucida*, bi-monthly randomised suction samples were taken on Coe Fen, Cambridge, U.K. (52.198885, 0.118247) between April and October 2011, consisting of 40 x 10 local subsamples each (full details can be found in Dittrich, 2016; Dittrich & Helden, 2016). Each subsample consisted of one full-power 16-s suck with a Vortis™ suction sampler (Arnold, 1994; Brook *et al.*, 2008). The catch was emptied into a canvas sweep net, and all adult Auchenorrhyncha (both Cicadellidae and Delphacidae) were removed by pooter for later identification. Throughout 2011, live specimens were also obtained for insect cultures, and the offspring following F2 generation were used in these experiments.

A host preference experiment was set up using two grass species, tall fescue *S. arundinaceus* and Yorkshire fog *Holcus lanatus* (L.), within mesocosms. The latter plant was chosen because it was the second most common plant on the study site (after tall fescue) and one to which the generalist had a strong positive response in laboratory trials (Dittrich, 2016). Tall fescue was chosen because of the host plant's relationships with the specialist (Dittrich, 2016; Dittrich & Helden, 2016). Approximately 10 tall fescue and Yorkshire fo*g* seeds were planted 3 cm apart in 900-mL (60 × 150mm) round, clear, polyethylene terephthalate containers with a 5-micron mesh affixed to the top held in place with an elastic band, preventing insect escape. Growth was thinned to a pair of plants, one of each species, and the experiments started when plants had three tillers of growth. There were two experimental treatments used: one where the specialist species was allowed to first settle on plants before the generalist species was added and one where the generalist species were allowed to establish on plants before the specialist was added.

In the first test (generalists established), eight mesocosms were set up; in each, 10 generalists were allowed to establish themselves. After 1 week, 10 specialists were added to those mesocosms containing the generalists. The host plant choice of the generalists was recorded immediately before and 48 h following this introduction. Planthoppers were observed to move quite readily between their feeding positions through the course of a day, so a period of 48 h was considered a reasonable interval between recording.

For the second test (specialists established), eight mesocosms were set up, each with 10 specialists, which were allowed to establish for 1 week, after which 10 generalists were then added. The host plant choices were recorded immediately before and 48 h after introduction of the generalist.

A difference in the feeding preference of the generalist was tested before and after the addition of the allospecific competitor within the same experimental mesocosm and between tests where the generalist was added first and where it was added last (at equal density). All statistics were performed using R (R Development Core Team, 2013). *t*-Tests were used, assuming equal variance, with all effect sizes provided with 95% confidence intervals (CI). An analysis of variance was used to check for differences in tall fescue preference between experiments in the absence of allospecifics between all tests.

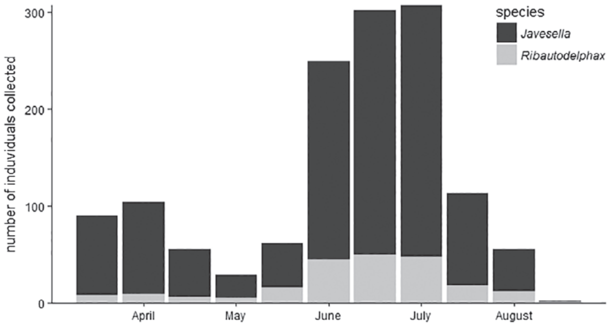

Figure 1. The numbers of the specialist *Ribautodelphax imitans* and the generalist *Javesella pellucida*, recorded throughout the growing season in 2011 on Coe Fen, Cambridge.

Results

The numbers of adult generalist *J. pellucida* recorded at Coe Fen during 2011 followed an almost identical phenological pattern to the specialist *R. imitans*. However, as expected, they were fewer in number (Fig. 1).

In the absence of specialists, generalists showed an overall choice preference for tall fescue where a mean proportion of 0.66 (95% CI = 0.57, 0.75) of the individuals settled. The preference for tall fescue did not differ from this average for generalists between experiments when allospecifics were absent ($F_{2,19}$. = 029, $P = 0.972$). On Yorkshire fog, mean proportions of 0.34 (95% CI = 0.25, 0.43) of individuals settled. There was a significant difference in proportions between host plants of 0.32 (95% CI = 0.26, 0.57; $t_{15} = 5.45$, $P < 0.001$; Fig. 2a).

There was no difference in the proportion of generalists on alternate host plants after the addition of the specialist to mesocosms where generalists were already established (non-significant mean difference of 0.06, 95% CI = −0.12, 0.54; $t_{15} = 0 : 60$; $P = 0.559$). However, overall preference for tall fescue changed in experiments where specialists were established on plants prior to their introduction. When generalists were added to experimental arenas with specialists already established, there was a marked change in preference, with a mean proportion of 0.23 (95% CI = 0.09, 0.37) individuals found on tall fescue. There was a significant reduction in difference in proportions of 0.41 (95% CI = 0.35, 0.77; $t_{15} = 13.70$; $P < 0.001$).

Generalist feeding preference between conditions where they were established first versus last in the presence of the specialist (at equal density) demonstrated an overall proportional reduction in preference for tall fescue of 0.36 (95% CI = 0.15, 0.58, $t_{15} = 3.7982$, $P = 0.003$, Fig. 2b).

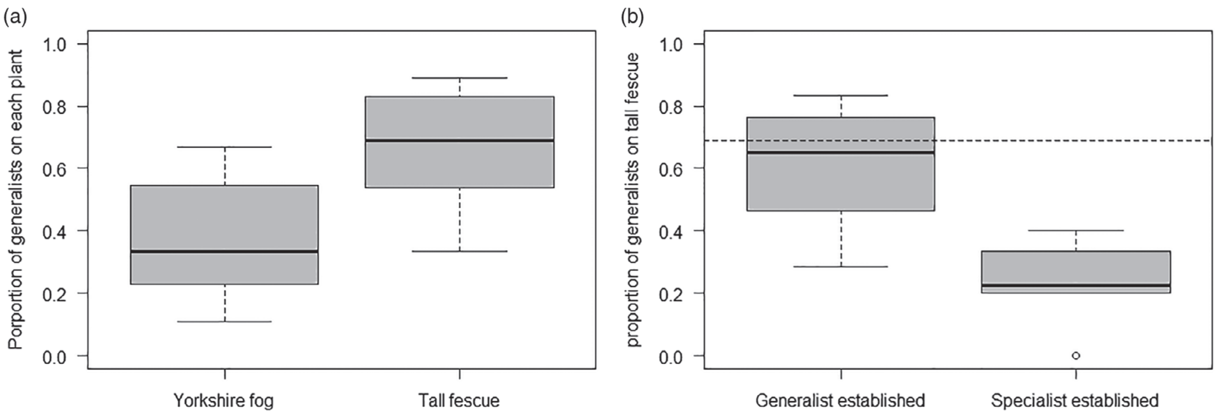

Figure 2. (a) Food preference of the generalist planthopper *Javesella pellucida* on either plant species Yorkshire fog *Holcus lanatus* and tall fescue *Schedonorus arundinacea*; (b) the difference in preference for tall fescue, between experiments where the generalist was established first and where the specialist was established first, when both species were present at ratios of 10 : 10 generalists to specialists. The dashed line represents the average proportion of generalists established on tall fescue in the absence of specialists with 10 individuals per mesocosm.

Discussion

When established before the generalist, the specialist planthopper *R. imitans* affected the host plant preference of the generalist *J. pellucida*, supporting our hypothesis. However, this pattern was not apparent if the generalist established first, where there was no change in preference. Both species' adult phenology is similar, and adults are spatiotemporally sympatric in the field (Dittrich *et al.*, 2013; Dittrich & Helden, 2016), although the egg incubation periods for the specialist *R. imitans* may be slightly shorter (Raatikainen & others, 1967; Dittrich, 2016). Faster development may lead to earlier establishment on food plants and, in some species, is indicative of competitive advantage or numerical dominance (Krijger *et al.*, 2001; Hunter & Yeargan, 2014). Specialist species dictating the specific feeding niches of others, based on their own feeding ecology, however, may provide a broader explanation as to how generalists and specialists coexist within insect herbivore communities.

Host choice mediated by interspecific interactions is not widely studied. However, it may have much farther-reaching implications for understanding how insect herbivore communities are constructed and how generalist and specialist interactions help to shape them. Of the two study species, *R. imitans* is rare, and *J. pellucida* common, and it stands to reason that, where the two coexist, the community position of *J. pellucida* may be different to sites where the two species do not coexist. Moreover, due to the rarity of *R. imitans*, it is likely that the two species co-occur less frequently than when *J. pellucida* – the very widespread generalist – is found without *R. imitans* (Le Quesne, 1960; Gaston, 1994; Nickel, 2003). If most species in grassland communities are monophagous and rare, particularly in the case of the planthoppers (Delphacidae) (Gaston, 2010; Denno & Perfect, 2012), it is likely that these interactions play a part in shaping how communities of herbivorous insects differ from one location to the next and between a range of different hosts.

The lottery hypothesis proposed by Chesson and Warner (1981), in which temporal environmental fluctuations lead to the coexistence of competing species, is supported here. In our paper, the competing specialist is at an advantage if it arrives first. However, in systems where non-equilibrium dynamics are at play, the recruits to vacant space may vary in time, and it is these fluctuations that enable coexistence (Munday, 2004). Similar colonisation competition trade-offs, where disturbances shape community structure may be common, such as in the heavily disturbed grasslands in which our study species were found (Levins & Culver, 1971; Beisner *et al.*, 2003; Munday, 2004). Conversely, as grasslands are one of our most human-impacted habitats, the interactions that are described within this paper may decrease in their frequency, together with insect biodiversity, as disturbance increases.

The importance of monophagous herbivore species within communities is not unstudied (Harrison *et al.*, 2008; Mouillot *et al.*, 2013). However, the range of roles that these species fill is not fully understood, as highlighted by the finding of our work. It may be the case that rarer insect specialists have an important role in modifying the host plant choices of generalists. The influence of one species on how others utilise feeding location on single hosts is known to some extent (Denno *et al.*, 2003; Ferrenberg & Denno, 2003), and how direct competition affects the fitness of species through direct plant-mediated and indirect effects is also well studied (Denno *et al.*, 1995; Kaplan & Denno, 2007). This case of host-mediated choice, however, is unique and warrants further investigation, particularly in field studies, and presents an interesting line of enquiry that may enable a greater understanding of wider community effects.

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Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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