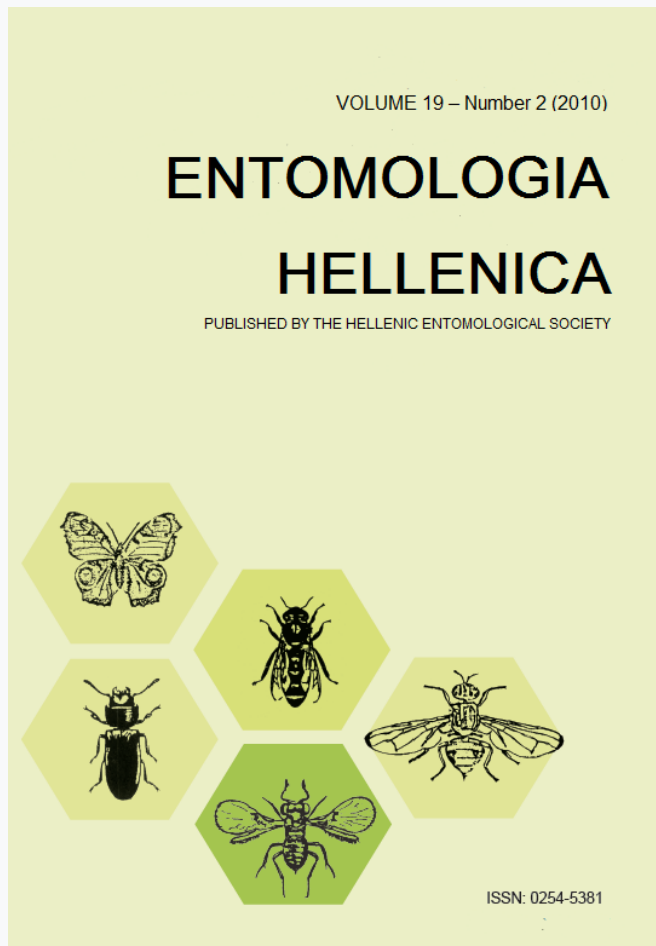


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Species richness and host-plant diversity are positively correlated in Coccidae

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ABSTRACT

The interactions between insect herbivores and their hosts are among the most fundamental biological associations. Although there are many data available on the host associations of scale insects, there have been few attempts to synthesize the available information. Here we examine host associations of Coccidae, the third most species-rich family of scale insects. We compare host-plant data for most species of coccids that were available from online databases, especially ScaleNet, and the literature, with species richness estimates for host-plant families. Similar to most insect groups, coccids showed high host specialization with about 64% of species recorded from only a single plant family. Analysis of the relationship between species richness of host-plant families and the number of species of coccids recorded on these plants showed a significant positive correlation between host-plant species richness per angiosperm plant family and coccid species richness ($P < 0.0001$). This is expected under a null model in which host use is randomly distributed across families according to plant species richness of the families. However, the presence of several exceptions (Orchidaceae and Asteraceae in particular) warns that host associations in coccids might be more complex than the correlation analysis suggests.

KEYWORDS: host specialization, insect-plant interactions, scale insects, soft scales.

Introduction

Plants and insects are species-rich and abundant, representing a large proportion of the world's biodiversity. There is little doubt that herbivorous insects play an important role in plant evolution (Strauss and Zangerl 2002), and these interactions are likely to be reciprocal (Ehrlich and Raven 1964, Winkler and Mitter 2008). Therefore, understanding the relationships between insect herbivores and their hosts is crucial for understanding the evolution of biodiversity.

There is a high degree of host specialization in insects (e.g. Wilcox 1979, Janzen 1988, Strauss and Zangerl 2002), with esti-

mates of about 80% of herbivorous insects being restricted to a single host-plant family (Schoonhoven et al. 2005). However, there appears to be considerable variation in host-specificity among insect groups (e.g. Novotny et al. 2002). Although the host associations of many insect groups have been studied (Wilcox 1979, Crawley 1985, Janzen 1988, Bernays and Graham 1988), scale insects (Hemiptera: Sternorrhyncha: Coccoidea) have not yet received much attention. Coccids are herbivorous and the superfamily is the most diverse in Sternorrhyncha (Gullan and Martin 2009), with nearly 8,000 described species (Ben-Dov et al. 2009). The family Coccidae, or "soft scales" or "coc-

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cids”, is the third most species-rich family within Coccoidea. It is estimated to include over 1,150 described species that occur on more than 200 families of host plants (Ben-Dov et al. 2009), especially on trees and woody shrubs (Ben-Dov 1993).

The occurrence of polyphagy, defined here as the ability to use more than one plant family, versus family-level monophagy within a certain herbivore group, is the outcome of different evolutionary histories. High levels of specialization in which most of the group members are restricted to one host-plant family or even to one genus, plus the existence of a strong positive correlation between the host-plant and herbivore species richness, would suggest that either cospeciation, host shifting with niche-filling, or both (Menken and Roessingh 1998) are the major forces shaping the evolution of insect-plant associations. Under both scenarios, the insect herbivore species diversity on a plant group is expected to be positively correlated with the species richness of that plant group. However, the absence of a positive correlation would indicate the existence of host-use biases. In order to investigate the pattern of host-plant use among Coccidae, this study aims to: (1) determine the levels of family-level monophagy, which is defined here as coccid species occurring on a single plant family, and (2) determine whether host-plant use can be explained by the species richness of plant families alone.

Materials and Methods

Host specificity

Host-plant data for 1,035 described species (excluding subspecies and species of unknown host use) of Coccidae were downloaded from the scale insect database, ScaleNet (Ben-Dov et al. 2009). Classification of angiosperm families, and the number of species recognised in each host-plant family, followed the angiosperm classification of APGII (APG 2003) and Stevens (2008); Judd et al. (2008) was used for gymno-

sperms and “The Fern Pages” (Australian National Botanic Gardens website) (CPBR 2004) was used for other land plants, here referred to as “non-seeded land plants”. Coccid species were scored as being either family-level monophagous (occurring on only a single host-plant family) or polyphagous (occurring on two or more host-plant families). Additionally, for family-level monophages, the number of genera on which the coccid species had been reported was recorded. Although Miller and Miller (2003) defined monophagous, oligophagous and polyphagous coccid species as those that have host ranges encompassing 1 to 2, 3 to 10, and greater than 10 plant families, respectively, the reason why they used these definitions is unclear. Therefore, family-level monophagy and polyphagy are used in this paper to categorise coccid species in terms of their host use in order to avoid ambiguous and arbitrary sorting, and to enable comparisons with broader studies that have used this definition e.g. Schoonhoven et al. (2005).

Correlations between coccid host-use and species richness of host-plant family

We used GraphPad Prism 5.03 (GraphPad Software 2009) for all statistical analyses, implementing two-tailed tests in all instances. Prior to testing for correlations between coccid species numbers on host plant families and the species richness of these plant families, we assessed the fit of the data (both Y and X variables independently) to a Gaussian (normal) distribution using the D’Agostino and Pearson normality test (D’Agostino and Stepenes 1986). If the data are not normally distributed, a non-parametric test is required (LeBlanc 2004). We conducted tests of normality and correlation separately for coccids on angiosperms, gymnosperms, non-seeded land plants and all host plants combined (eight data partitions in all). The first two host groups each represent monophyletic lineages of plants (Bowe et al. 2000), whereas the third is a non-mo-

nophyletic group (Smith et al. 2006) that we used for convenience as there were too few observations of coccids on each of the constituent host groups (ferns, spike-mosses and horsetails) alone.

Results and Discussion

Host-specificity

Coccids were recorded from 200 plant families – 171 angiosperms, 10 gymnosperms and 19 non-seeded land plants. On angiosperms, approximately 63% of coccid species were restricted to only one plant family (Fig. 1A) and most of these (about 90%) were recorded from only one plant genus. About 37% of coccid species are polyphagous on angiosperms (Fig. 1A), including notorious agricultural pests such as *Ceroplastes rubens*, *Parasaissetia nigra*, *Saissetia coffeae* and *Saissetia oleae*, which have broad host ranges of more than 20 plant families. Fewer coccids feeding on gymnosperms are specialists and approximately 48% are polyphagous (Fig. 1B). This finding is consistent with the hypothesis that gymnosperms are not ancestral hosts of scale insects (Danzig 1980, Gullan and Kosztarab 1997), although dated phylogenies are required to fully test this. There are few coccid species (30) reported on non-seeded land plants and the majority of these are polyphagous (about 83%) (Fig. 1C). Of the five species of coccid on non-seeded land plants that exhibit family-level monophagy, two have only a single host record (*Alecanopsis filicum* and *Pulvinaria satoi*). The other three, *Kilifia diversipes*, *Pounamococcus cuneatas* and *Saissetia carnosae*, have at least two collection records and so their inferred host-use associations might be more reliable.

The finding that the majority of coccids are dietary specialists is in line with reports for other insect groups (Schoonhoven et al. 2005). However, the level of family-level

monophagy in coccids (about 64%) is lower than that reported for other herbivorous insects, such as aphids (76%; Schoonhoven et al. 2005) and Nepticulidae (Lepidoptera) (over 90%; van Nieukerken 1986). Furthermore, the estimate of family-level monophagy here is likely to be an over-estimate, given that there are only single host records for many coccid species listed in ScaleNet (Ben-Dov et al. 2009). With increased sampling, some of these might be found to be polyphagous.

Despite relatively conservative host ranges for most coccid species, some species are extremely polyphagous, with eight species recorded from more than 50 plant families. Interestingly, it is these eight species that use non-seeded land plants as hosts in addition to other plant families. In consideration with the low total number of coccids on non-seeded land plants, it appears that it might be difficult for coccids to use these plants, perhaps because of the high concentrations of secondary compounds in them (e.g. Lawton 1982, Patra et al. 2008).

Correlations between coccid host-use and species richness of host-plant family

In all eight data partitions, only species richness of non-seeded land plant and gymnosperm families passed the test of normality and, therefore, the non-parametric Spearman correlation test (LeBlanc 2004) was used throughout for tests of correlation. There was a significant positive correlation between coccid species occurrence and both angiosperm (Spearman r (r_s) = 0.61; df = 169; P < 0.0001) (Fig. 2A) and gymnosperm (r_s = 0.67; df = 8; P = 0.034) (Fig. 2B) host family species richness. That is, species-rich plant families typically are hosts to more coccid species than are the species-poor plant families. This finding is the same as that found for galling insect diversity, which is also

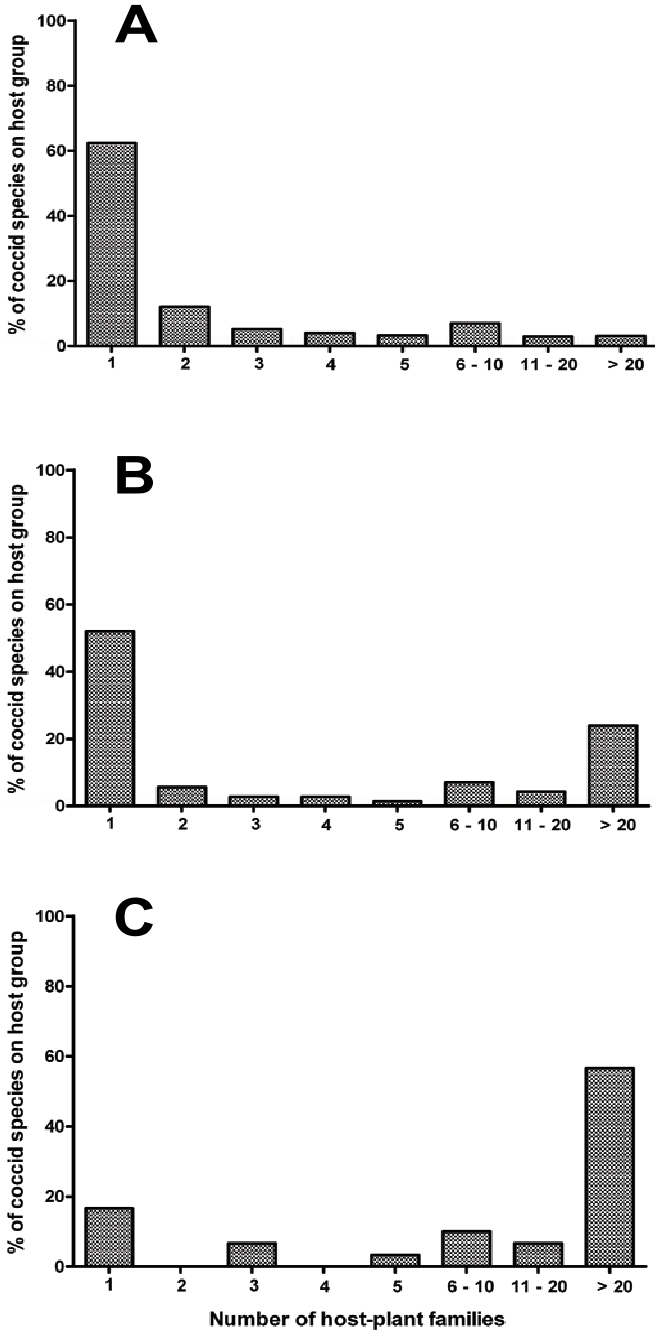


FIG. 1. Histograms of host ranges of coccids on angiosperms (A), gymnosperms (B) and non-seeded land plants (C).

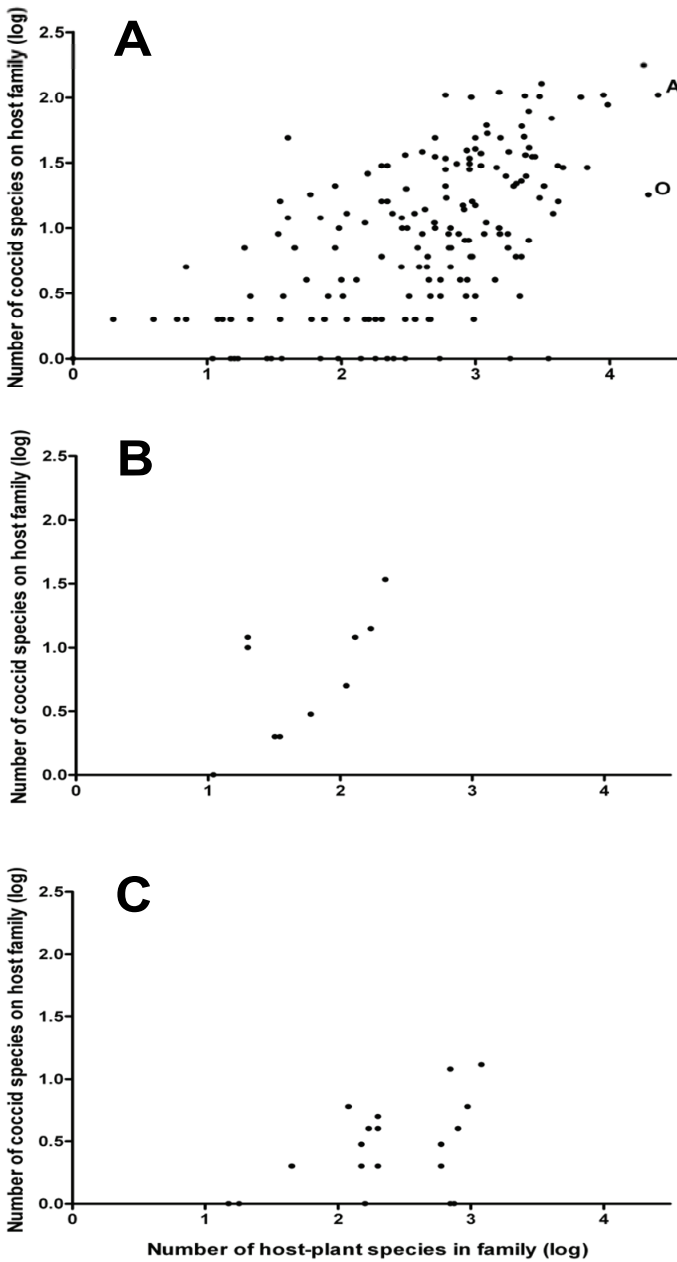


FIG. 2. Scatter plot of the number of species per host-plant family (X axis) and the number of coccid species on each family (Y axis) of angiosperms (A), gymnosperms (B) and non-seeded land plants (C) (A = Asteraceae and O = Orchidaceae). Both X and Y axes are logarithmically transformed (base = 10).

positively correlated with host plant family richness (Gonçalves-Alvim and Fernandes 2001). In the coccid data, there are two comparisons that appear to differ greatly from others. Compared to the other angiosperm families in the study, the two most species-rich plant families, Orchidaceae and Asteraceae ("O" and "A" respectively in Fig 2A), are host to relatively few coccids. In contrast to the situation with the seed plants, there was no correlation between coccid host-use and species richness of non-seeded land plant families ($r_s = 0.42$; $df = 17$; $P = 0.076$) (Fig. 2C). When data from all host plant groups were combined, there was a significant positive correlation ($r_s = 0.60$; $df = 198$; $P < 0.0001$). This likely reflects the dominance of the angiosperm contribution (about 86 % of records) in the combined dataset.

It is evident that, like other herbivorous insects, the majority of coccids are restricted to a single host family. The significant positive correlation between the number of coccids on a plant family and the species richness of that plant family is as expected and is consistent with either the cospeciation model or the niche-filling model, or a mix of both.

The current study is based on species counts of coccids only and does not take account of phylogenetic relationships of species, nor of their hosts. This raises several points: are counts of coccid species on host plant families randomly distributed with respect to coccid phylogeny or are there radiations of coccids on particular host groups? In order to answer these questions, further studies need to include phylogenies of coccids and their hosts. In addition, it would be interesting to determine whether there are particular plant traits that determine host-use patterns in coccids. Thus, testing correlations of coccid species richness with alternative categories of hosts, such as integument characteristics, geographic distribution or abundance (instead of plant family richness), might prove informative.

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Συσχέτιση μεταξύ ποικιλίας φυτών ξενιστών και αφθονίας ειδών της οικογένειας Coccidae

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ΠΕΡΙΛΗΨΗ

Οι αλληλεπιδράσεις φυτοφάγων εντόμων και των φυτών ξενιστών τους είναι από τις πιο βασικές βιολογικές σχέσεις. Αν και υπάρχουν πολλά δεδομένα για τις σχέσεις κοκκοειδών εντόμων με τους ξενιστές τους, εντούτοις δεν έχουν γίνει πολλές προσπάθειες να δημιουργηθεί μια σύνθεση αυτών των πληροφοριών. Στην παρούσα εργασία εξετάζουμε τις σχέσεις φυτών ξενιστών με είδη της οικογένειας Coccidae που είναι η τρίτη σε αφθονία ειδών στην υπεριοικογένεια Coccoidea. Συγκρίναμε δεδομένα σχέσεων φυτών ξενιστών με είδη της παραπάνω οικογένειας που ήταν διαθέσιμα από ηλεκτρονικές βάσεις δεδομένων όπως το ScaleNet και από τη βιβλιογραφία και εκτιμήσαμε την αφθονία ειδών σε επίπεδο οικογένειας φυτών ξενιστών. Παρόμοια με άλλες ομάδες εντόμων τα είδη της οικογένειας Coccidae παρουσιάζουν υψηλή εξειδίκευση ως προς τον ξενιστή τους, με το 64% των ειδών να απαντώνται σε μία μόνο οικογένεια φυτών. Παρατηρήθηκε μια θετική συσχέτιση μεταξύ αφθονίας ειδών ανά οικογένεια φυτών αγγειοσπέρμων και αφθονία ειδών της οικογένειας Coccidae ($P < 0.0001$). Ωστόσο, η παρουσία αρκετών εξαιρέσεων (Orchidaceae και Asteraceae ειδικότερα) μας κάνει να πιστεύουμε ότι οι σχέσεις φυτών ξενιστών και ειδών της οικογένειας Coccidae είναι πιο περίπλοκη από ότι έδειξε η ανάλυση συσχέτισης.