Insect and Angiosperm Diversity in Marine Environments: A Response to van der Hage

J. Ollerton; D. McCollin

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the washing process, despite the fact that the diameter was narrower than that proposed by other authors: 0·100 mm as opposed to 0·254 (Brenchley & Warington 1930) or 0·212 mm (Ter Heerdt *et al.* 1996). Smaller filter diameters would have increased the complexity of the washing process and hindered one of the objectives of this study: the elimination of the fine soil material. In certain cases the losses might be explained by the deterioration of seeds with soft coats during the sample washing stage. Drying subsamples C might have caused the death of seeds that had already begun the germination process (Fenner 1985) or induced dormancy (Pemadasa & Lovel 1975), although germinations were not detected for at least 1 week prior to drying. Moreover, no seeds were found in the subsequent hand-sorting process.

This study revealed a considerable reduction in the sample volume in treatment C (*c.* 60%) but because the samples were spread in layers of less than 0·5 cm, method C ultimately took up more greenhouse space than method NC, which used layers of *c.* 2 cm: similar to the depth used by other authors (Moore & Wein 1977; Brown 1992; Ortega 1994; Ortega *et al.* 1997).

In the present case, with a highly diverse community which has many small seeds and a large number of species, the washing procedure can cause seed losses during the sample division and preparation process. In conclusion, the selection of a seed bank analysis methodology is determined by the characteristics of the zone where the study is to be carried out.

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J. Traba, C. Levassor and B. Peco
Departamento Interuniversitario de Ecología
Facultad de Ciencias
Universidad Autónoma de Madrid
28049 Madrid, Spain

Insect and angiosperm diversity in marine environments: a response to van der Hage

Why are insects and vascular plants rarely encountered in the marine environment? Recently van der Hage has addressed these questions and suggested a causal link between the two (van der Hage 1996). In summary, the argument goes that insects have not colonized the sea because they tend to have closely coevolved relationships with angiosperms and angiosperms, by far the most diverse group of vascular plants, have in turn only rarely entered the seas because water pollination (hydrophily) is 'inefficient'. Thus, angiosperms could not hope to reproduce successfully in the marine environment and, without their abundance, insects can never be successful at sea. This hypothesis gives a novel twist to an old conundrum and is superficially attractive. Closer examination, however, reveals some problems. The main arguments against the van der Hage hypothesis are as follows:

1. Insect evolution pre-dates that of the angiosperms by some 200 million years (Labandeira & Sepkoski 1993).

What was preventing these earliest insects from colonizing the seas? It may be that the early insects were intimately associated with the land plants of the time, but even if this were so, it argues against the angiosperms being the key to the lack of marine insects.

2. If marine insect diversity is limited by the absence of angiosperms, why have no insects followed seagrasses into the oceans? One might expect that the freshwater antecedents of seagrasses and their associated herbivores would continue their relationship as the proto-seagrasses colonized first brackish, estuarine waters and then coastal habitats.

3. Water pollination by angiosperms, though relatively rare, has evolved independently in several groups (Cox 1993). As van der Hage notes, pollination by water currents in a manner analogous to wind currents is inefficient. This is probably why it seldom occurs — most hydrophilous pollination occurs in two dimensions at the water surface and/or involves pollen masses or elongated pollen (Cox 1993). The few plant species which employ three-dimensional dispersal of single pollen grains into water are usually self-pollinated (Proctor, Yeo & Lack 1996). Many aquatic plants are wind pollinated (anemophilous) and traits associated with anemophily (reduced corolla, exerted stigmas and stamens, etc.) are likely to represent prerequisite pre-adaptations to hydrophily. Anemophily itself is comparatively rare in the angiosperms, and so for that reason alone hydrophily is also uncommon. Marine water-pollinated plants (i.e. the seagrasses) are abundant, successful species: there is no suggestion that their reproductive systems are in any way inefficient or ineffective.

In summary, we would argue that the link between angiosperm and insect rarity in marine ecosystems is coincidence rather than causation. In ending his article, van der Hage asks 'Why are [predatory, parasitic and detritivore] insects not found in the sea?'. Surely the most parsimonious answer is that it is for the same reason(s) herbivorous insects are not found in the sea. We can offer no explanation as to why this is so, but we do have two alternative, and not mutually exclusive, hypotheses to explain the rarity of angiosperms in aquatic ecosystems.

First of all, many fresh water, but no marine, aquatic plants are insect pollinated. The reason for this may lie in mechanical restrictions related to flower presentation in a tidal environment. In order to display a dry, undamaged flower to a potential pollinator, a marine plant would have to invest in structures tall enough to keep the flower out of the water during heavy swell at high tide, but strong enough to withstand considerable buffeting by wind and waves. Such structures would represent massive investments for plants in the face of an uncertain pollination environment — insects flying near the coast tend to keep to the land and seem to exhibit behavioural responses which prevent them from being blown out to sea (Russell & Wilson 1996). These two factors alone would preclude the establishment of viable populations of marine angiosperms.

Second, the marine environment, from a plant's perspective, is an environment of severe stress (problems associated with high salinity and regular inundation) and high disturbance (damage to flowers, leaves and stems from wind and wave action). Under Grime's (1979) three strategy model, habitats exhibiting severe stress and high disturbance are unlikely to be successfully colonized by plants.

In truth, the absence of flowering plants from the oceans is probably the result of a combination of these factors and others that we cannot yet imagine. In ecology, single factors are rarely enough to explain large-scale phenomena.

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J. Ollerton & D. McCollin
School of Environmental Science, Nene College, Northampton NN2 7AL, UK

Insect and angiosperm diversity in marine environments: further comments on van der Hage

Van der Hage (1996) has addressed the possibly related questions of why insects, and angiosperms, are rarely encountered in the marine environment. The argument can be summarized as follows: insects have not colonized the sea because they have closely coevolved relationships with angiosperms, and angiosperms have only rarely entered the sea because pollination in water is relatively ineffective. Hence, angiosperm sexual reproduction in the marine environment could not be successful and, without abundant angiosperms, insects could not be successful in the sea. The stimulating contribution of van der Hage raises a number of points, two of which are addressed below.

1. While the (marginally) marine insects and the seagrasses share a taxonomic paucity, with only a few marine species relative to the number in freshwater plus terrestrial habitats, they differ markedly in their contributions to biomass, productivity, nutrient cycling and habitat structuring. Thus, marine insects make a minimal impact relative to their closest marine arthropod (crustacean) ecological analogues, the