Freshwater ecosystems and aquatic insects: A paradox in biological invasions

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Freshwater ecosystems and aquatic insects: a paradox in biological invasions

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Biological invasions have increased significantly in response to global change and constitute one of the major causes of biodiversity loss. Insects make up a large fraction of invasive species, in general, and freshwaters are among the most invaded ecosystems on our planet. However, even though aquatic insects dominate most inland waters, have unparalleled taxonomic diversity and occupy nearly all trophic niches, there are almost no invasive insects in freshwaters. We present some hypotheses regarding why aquatic insects are not common among aquatic invasive organisms, suggesting that it may be the result of a suite of biological, ecological and anthropogenic factors. Such specific knowledge introduces a paradox in the current scientific discussion on invasive species; therefore, a more in-depth understanding could be an invaluable aid to disentangling how and why biological invasions occur.

1. Introduction

Biological invasions represent one of the most significant components of global change and are widely accepted among the leading causes of biodiversity loss and ecosystem alteration [1,2]. Many species reach new areas every year (becoming non-native species, i.e. species introduced beyond their native/historical range [3]), with different fates: most of them are not able to survive while very few establish and can become invasive (sensu [4]). In the context of biological invasions, insects are one of the groups with the highest number of invasive species [5], and freshwaters are among the most invaded ecosystems, with major threats to aquatic biota that create future conservation challenges [6–9]. The majority of the 126 000 freshwater animal species are insects (60.4%) [10], which dominate inland waters and occupy almost all trophic niches [11]. However, interestingly, they are almost absent as invasive species, which are represented mainly by crustaceans, fish and molluscs [6]. Here, we hypothesize about the causes why invasive species are not common among aquatic insects despite their enormous diversity and multiple adaptations to freshwater life.

2. Economic interest in moving aquatic insects is currently limited

Hundreds of freshwater species have deliberately been moved outside their native ranges by humans, mainly because of their economic importance (i.e. food or recreation) [12]. The human-mediated spread of fish [13], crayfish [14] and amphibians [15] has a long history. For example, the carp (*Cyprinus carpio* (Linnaeus, 1758)) was deliberately introduced by the Romans in many regions of Europe [16]. However, among the 27 most widely distributed non-native animals for aquaculture in Europe, not one is an insect [17]. Nowadays, despite the fact that the actual and potential value of aquatic insects as food is not negligible outside of Europe and North America, they have a relatively limited economic importance at international scale and the interest in consuming them is restricted to particular countries or taxa [18]. Moreover, hundreds of deliberate releases of terrestrial insects as part of biological control efforts can be listed [19], being an important cause of insect introductions; however, no true aquatic insects have been used with this aim, with the exception of a limited number of semiaquatic weevils [20]. Finally, except for some large-sized aquatic beetles and bugs used as aquarium pets, and chironomids for aquarium fish food, no commercial value is known for aquatic insects [21].

3. Associations between aquatic insects and host-plants are extremely rare

Many invasive terrestrial insects are strictly associated with particular host-plants of agricultural or ornamental importance. When these host-plants are intentionally or unintentionally translocated, these insects are moved around as stowaways with the plants [22]. However, herbivory on macrophytes is usually considered of minor importance in the energetic pathways of aquatic systems, in comparison with phytoplankton filtering, benthic algae grazing or detritus processing [23], so it is rare to find aquatic insects associated with host-plants. In addition, despite there being several ornamental aquatic plants in trade (some of which very invasive), the number of plants of commercial interest is undoubtedly smaller in aquatic than in terrestrial environments. In this context, only few semiaquatic invasive weevils (not truly aquatic coleopterans [24]) are associated with plants of commercial interest (e.g. [25,26]).

4. Aquatic insects usually lack adaptations for overland or maritime transport.

Successful invasive taxa are typically known to have high potential of dispersal, with strategies that allow them to survive adverse conditions [27]. Passive or accidental transport of aquatic organisms could occur through wet (transport into ballast waters or attached to vessels) or dry pathways (transport into dry containers or attached to goods or overland vehicles). Aquatic insects generally lack adaptations that allow them to survive during passive transport through such pathways (e.g. resting eggs or stages, euryhaline tolerance, ability to adhere to vessels, resistance to prolonged periods of drying or reduced oxygen levels [28–30]). Some mosquitoes (Diptera: Culicidae) are an exception, being able to survive in small amounts of water in containers, and having high reproductive rates with desiccation-resistant eggs and fast development [31]. For example, *Aedes albopictus* (Skuse, 1894) and A. japonicus japonicus (Theobald, 1901) are known to have spread worldwide via the international trade of used tyres [32]. Other exceptions could be the corixid *Trichocorixa verticalis verticalis* (Fieber, 1851), which tolerates high levels of conductivity and high water temperatures and has important flight ability [33,34], and the gerrid *Rhagadotarsus kraepelini* (Breddin, 1905), which is known forhaving a resting egg stage and long- and short-winged morphs [35].

5. Aquatic insects seem to have less diverse reproductive strategies than terrestrial ones

Invasive species are frequently associated with a high reproductive capacity that ensures establishment and persistence after the initial introduction [22]. In this perspective, asexual reproduction, as well as other reproductive strategies, such as haplodiploidy, is a trait that may ease the establishment [36], because a single individual can begin the invasion process. A good example is the European solitary bee, *Lasioglossum leucozonium* (Schrank, 1781), which most probably colonized North America as a lone singly mated female [37]. However,although many successful terrestrial invasive insects are parthenogenetic or haplodiploids, such as aphids, leaf miners,weevils, ants or bees [37], these particular reproductive traits are almost absent in aquatic insects [38].

6. Aquatic insects usually have an aquatic and a terrestrial stage

Most successful freshwater invasive taxa complete their life cycle in the water and lack a terrestrial or aerial stage [39]. Bycontrast, the presence of aquatic and terrestrial life-phases is extremely common among aquatic insects [40]. This 'amphibious' life cycle could represent an insurmountable problem, not for invasiveness but for survival, establishment or spread because suitable habitats should be found in both terrestrial and aquatic environments. Moreover, the aerial stage is generally short and coincides with the reproductive phase, thus

reducing their fitness and potential for further dispersion.

7. Many aquatic insects live in running water

environments

Running waters are highly heterogeneous ecosystems, characterized

by a constant and gradual change of environmental

conditions, such as the width, depth, water temperature and

flow conditions [23]. Many aquatic insects are restricted to

lotic habitats, which may limit their ability to spread, because

in order to do so the conditions of the invaded environment

should be similar to those of the original area. Finally, as

reflected by the number of endemisms, most aquatic insects

from lotic habitats seem to have lower dispersal abilities

compared with lentic ones [41], which can be of importance

in post-invasion spread.

8. Final remarks

Invasive aquatic insects seem to be an exception rather than a

rule. This paradox represents an important and representative

case of study and clearly highlights the central role played

by humans in biological invasions. The scarcity of successful

invasive aquatic insects is likely the result of their particular

bio-ecological traits and, specially, of the lack of direct human

interest in moving aquatic insects. Other factors, such as the

difficulty of identifying them morphologically and the lack of

comprehensive information on their original distribution

ranges (as happens, for example, for many chironomids [42]), may also contribute to an underrepresentation of invasions by aquatic insects [43]. Furthermore, among the 32 different pathways facilitating the establishment of invasive taxa in the wild [44], only a few, particularly those related to human actions (e.g. aquarium/aquaculture trade and ship ballast waters) could be applicable to aquatic insects. Therefore, from a biological point of view, the most successful invasive aquatic insects would not be only those with particular bio-ecological traits [3,45], but also those with a high potential to exploit human transportation systems.

From a broader perspective, the hypotheses proposed here can help to stimulate future research in this topic. In particular, such research should address the new scenarios emerging with global climate change. Freshwater ecosystems are facing dramatic transformations by global change, increasing the homogenization of aquatic environments worldwide [46] and favouring species invasiveness (e.g. [44,46]). In addition, the increasing interest in entomophagy in some regions and the growing industry of aquatic insect farming [47] will also increase future species invasiveness. Future research needs to explore not only the effects of invasive species, but also the mechanisms that drive their occurrence in new areas. This will help to prevent invasions worldwide through the most cost-effective means.

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