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Direct and indirect effects of an invasive omnivore crayfish on leaf litter decomposition

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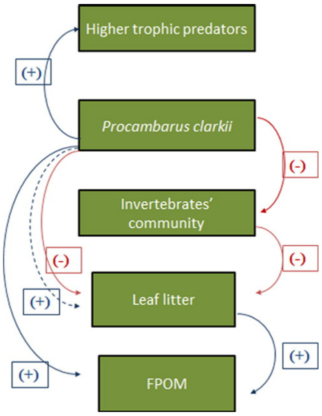
HIGHLIGHTS

- *Procambarus clarkii* is one of the most problematic IAS in European freshwaters.
- We assessed the direct and indirect effects of *P. clarkii* on leaf decomposition.
- *P. clarkii* affected basal resources by direct consumption of leaf litter.
- *P. clarkii* indirectly affected leaf decomposition through invertebrate consumption.
- Effects of *P. clarkii* on other invertebrates may be time dependent.

GRAPHICAL ABSTRACT



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ABSTRACT

Invasive alien species (IAS) can disrupt important ecological functions in aquatic ecosystems; however, many of these effects are not quantified and remain speculative. In this study, we assessed the effects of the invasive crayfish *Procambarus clarkii* (Girard, 1852) on leaf litter decomposition (a key ecosystem process) and associated invertebrates using laboratory and field manipulative experiments. The crayfish had significant impacts on leaf decomposition due to direct consumption of leaf litter and production of fine particulate organic matter, and indirectly due to consumption of invertebrate shredders. The invertebrate community did not appear to recognize *P. clarkii* as a predator, at least in the first stages after its introduction in the system; but this situation might change with time. Overall, results suggested that the omnivore invader *P. clarkii* has the potential to affect detritus-based food webs through consumption of basal resources (leaf litter) and/or consumers. Recognizing that this IAS is widespread in Europe, Asia and Africa, and may attain high density and biomass in aquatic ecosystems, our results are important to develop strategies for improving stream ecosystem functioning and to support management actions aiming to control the invasive omnivore *P. clarkii*.

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1. Introduction

In freshwaters, particularly in forest streams, allochthonous organic matter from riparian zones is the major source of energy and carbon to aquatic biota (Wallace et al., 1997; Suberkropp, 1998). The decomposition of plant litter is a fundamental process conducted by microbial communities, such as fungi and bacteria, as well as by invertebrate shredders (Gessner et al., 1999; Pascoal et al., 2005). The decomposition of plant litter results in the formation of carbon dioxide, mineral compounds, dissolved organic matter (DOM), and fine particulate organic matter (FPOM) that will be used by other organisms (Gessner et al., 1999). The role that some species, such as omnivores, can play in top-down and bottom-up control of plant litter decomposition is a key question to investigate (Greig & McIntosh, 2006). The biotic interactions between different groups of decomposers plus interactions between organisms within the same group may also have an important role in plant-litter decomposition (Gessner et al., 2007). Because omnivores are able to feed on more than one trophic level, they represent a deviation on trophic-cascade theory that may also lead to large effects on community structure (Diehl, 1993; Polis & Strong, 1996). Omnivores' broad diets allow them simultaneously to fill the trophic position of primary consumers up to top predators (Dorn & Wojdak, 2004). Nevertheless, much debate exists about how the dominance of omnivory changes the energy flow through a food web (Yodzis, 1984; Polis & Strong, 1996; McCann et al., 1998; Thompson et al., 2007).

The relationship between biodiversity and ecosystem functioning (BEF) has been one of the most exciting research fields in ecology over the past two decades (Hooper et al., 2005; Cardinale et al., 2012; Tilman et al., 2014). Most studies dealing with BEF, including those using plant litter decomposition in freshwaters, have focused on what happens when species are lost (Pascoal et al., 2010; Geraldes et al., 2012; Fernandes et al., 2013, 2015). However, this can be just part of the problem because at the local scale an increase in species number may also occur due, for example, to the introduction of invasive alien species (IAS) (Sousa et al., 2011). Indeed, many ecosystems show unprecedented rates of species introductions mediated by human activities, and freshwaters are not an exception (Strayer, 2010). IAS modify the structure and functioning of ecosystems because they change abiotic conditions (light availability, nutrient levels, heat transfer, habitat complexity and physical disturbance) and biotic interactions, and thus affect several attributes of native communities, such as diversity, spatial distribution, density and biomass (Grosholz, 2002; Byrnes et al., 2007; Simberloff et al., 2013; Gutiérrez et al., 2014). In addition, IAS impacts depend on the time after invasion, their position in the trophic chain and also on the characteristics of the invaded ecosystem (Strayer, 2012).

The red-swamp crayfish *Procambarus clarkii* (Girard, 1852), from the family Cambaridae, is one well-known IAS in freshwater ecosystems. It is native to the center and south of the United States of America and the northeast of Mexico. This species has been a matter of concern in several countries, including Portugal, due to their ecosystem engineering activities and disruption of several biotic interactions, which ultimately cause several impacts on ecosystem functions and services (Gherardi & Holdich, 1999; Rodriguez et al., 2005). This crayfish species is omnivorous, highly active, and it is well known for playing a key role in the food web (Holdich, 2002). *P. clarkii* is listed in Europe as one of the 100 worst invasive species (DAISIE database, http://www.europe-aliens.org) with some authors considering this crayfish as one of the ten most problematic IAS (Tablado et al., 2010). In Portugal, *P. clarkii* is widespread from the north to south and west to east colonizing almost all inland aquatic ecosystems (Sousa et al., 2013).

Reductions in invertebrates due to crayfish consumption may have cascade effects on lower trophic levels. This top-down effect can be important not only because of direct consumption but also due to possible indirect non-consumptive interactions, where fierce predators change the behavior of the prey (Lima & Dill, 1990). In this way, prey may consider the risk of being predated as an activity with costs and respond according to that risk (Brown et al., 1999). An interesting hypothesis that has been raised is that the prey behavior and the perception of risk may change if the predator is a native or a non-native species (Sih et al., 2010). A naivety effect has been found in native prey in response to introduced predators, with great declines in density and biomass being reported in distinct organisms (e.g. fishes: McLean et al., 2007; Kuehne & Olden, 2012; invertebrates: Freeman & Byers, 2006; Edgell & Neufeld, 2008). Finally, crayfish may also compete with invertebrates for direct consumption of plant litter due to its omnivore behavior and also compete with other predators for invertebrate prey (Gherardi, 2006).

Although *P. clarkii* is distributed almost worldwide, there is a lack of studies addressing the effects of this IAS on detritus-based food webs and the mechanisms underlying such effects. Given this gap we carried out laboratory and field experiments to test the following hypotheses: i) *P. clarkii* has a top-down control on plant litter decomposition in forest streams, directly by consuming leaf litter and/or indirectly by consuming invertebrate shredders; and ii) invertebrate shredders change their feeding behavior in the presence of *P. clarkii* due to the risk of being predated, but the response depends on their naivety (i.e. recognizing or not the crayfish as a potential predator).

2. Materials and methods

2.1. Laboratory experiments

We collected males of *P. clarkii*, with approximately 8 cm of total length (from the rostrum tip to the telson rear edge), in the Minho River (Portugal) near the village of Vila Nova de Cerveira (41°57'N, 8°44'W). We also collected a common invertebrate shredder in streams of North Portugal, *Sericostoma* sp. larvae (Trichoptera, Sericostomatidae) with approximately 1 cm of total length, in the upper reach of the Cávado River. This site is located 10 km downstream of the town Montalegre, Portugal (41°48'N, 7°51'W) and there are no records of *P. clarkii*, or any other crayfish species, in this river stretch. Animals of both species were kept under starvation for 24 h before the beginning of the experiments.

In a first mesocosm experiment, we assessed the effects of *P. clarkii* on: i) the consumption of leaf litter in the absence or presence of *Sericostoma* sp., and ii) the abundance of *Sericostoma* sp. To this end, we manipulated the presence/absence of the crayfish and the abundance of the invertebrate shredder as follows: control with no *Sericostoma* sp. and no crayfish; low abundance of *Sericostoma* sp. (6 individuals) with or without 1 crayfish; high abundance of *Sericostoma* sp. (12 individuals) with or without 1 crayfish; and 1 crayfish with no *Sericostoma* sp. Each treatment was replicated 4 times and the experiment ran for 21 days ($N = 24$) under controlled temperature (15 °C) and photoperiod (12 h in the dark and 12 h with light). For each treatment, aquariums ($40 \times 23 \times 25$ cm) were filled with river gravel and pebbles (size 850 μm–60 mm) previously washed and autoclaved (120 °C, 20 min). Aquariums were filled with 3 L of water and equipped with an aeration system. Sets of four grams of alder (*Alnus glutinosa* Gaertn.) leaves collected in the autumn were weighted, placed in mesh bags and submerged in deionized water for 36 h to promote the leaching of soluble compounds. After that, the leaves were removed from the mesh bags and placed in the aquariums. To ensure the presence of natural microbial communities, 10 disks of alder leaves (12 mm diameter) were previously colonized for one week in a low-order stream and then placed in the aquariums at the beginning of the experiment (following Fernandes et al., 2015). One third of the water volume of each aquarium was renewed every 7 days. The retrieved water was filtered through a 53 μm sieve to collect FPOM. Then, FPOM from each replicate was centrifuged (10 min, 14,000 rpm; Sigma 4–