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Global warming may lower thermal barriers against invasive species in freshwater ecosystems – A study from Lake Constance

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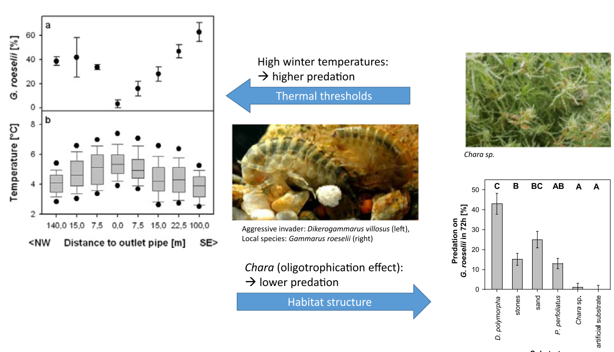
HIGHLIGHTS

- Coexistence between globally successful invader and 'weak' established species
- Low winter temperatures provide thermal shelter.
- Global warming threatens thermal barrier possibly leading to extinction until 2085.

GRAPHICAL ABSTRACT



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ABSTRACT

European freshwater ecosystems are increasingly invaded by exotic animal and plant species. Apart from increased connectivity between previously separated watersheds, the increasing temperature of the hydrosystems favors the spread of exotic species. The freshwater fauna of Central Europe is still shaped by the cold-adapted animal assemblages resulting from the last glaciation. It is less diverse, and the species are putatively less performant competitors, compared to the warm-adapted, species-rich fauna of the Ponto-Caspian realm, from which many current aquatic invaders are coming. Our study analyses potential mechanisms explaining the coexistence between one of the most impacting aquatic invaders of the past decades, the 'killer shrimp' *Dikerogammarus villosus* and the previously dominating amphipod *Gammarus roeselii* in Lake Constance, using laboratory predation experiments and field surveys. Our results indicate two key drivers for coexistence: low winter temperatures and the substrate structure of the alga *Chara* sp. At temperatures below 6 °C, the predation pressure on *G. roeselii* was strongly reduced; *G. roeselii* can therefore disperse throughout the littoral in winter, avoiding predation by *D. villosus*. Artificial heating of a section of the lake shore, however, resulted in local extinction of *G. roeselii* by *D. villosus*. The macroalga *Chara* sp. completely inhibited predation by *D. villosus* on *G. roeselii*. Climate change scenarios indicate that global warming might destroy this thermal refuge during winter until 2085. For the survival of *G. roeselii* it will then be crucial, which part of the *Chara* population will maintain epigeic plant parts during winter. The complex interplay between thermal and physical refuges for native species in the context of climate change and changing trophic status of freshwater systems, as disentangled by our study, shows that ecosystem management and restoration strategies need to better consider multiple stressors (and their rather complex mitigation strategies).

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1. Introduction

Biological invasions occur more and more often, and their global economic effect often exceeds the effects of environmental pollution (Lövei, 1997; Vitousek et al., 1997). Invasive species have been identified as one of the major threats of freshwater ecosystems in the last decades (Sala et al., 2000). Even single species invasions can change entire ecosystems such as the introduction of the Ponto-Caspian mussel *Dreissena polymorpha* in the Great Lakes in North America (e.g. Ludyanskiy et al., 1993; Ward, 1985). Many factors influence the success of freshwater invaders, e.g. homogenization of habitat structures, weakening of the native assemblages by pollution, 'invasional meltdown' by mutual subsidies from different invasive species, and diseases and parasites brought by the invaders, which are new to the native species (Keller et al., 2011; Leuven et al., 2009). The synchrony of improved water quality and increased temperature trends, currently found in many European water systems, may provoke confounding effects in freshwater invertebrate assemblages (Floury et al., 2013).

Climate change is known to influence natural communities (e.g., Urban et al., 2016), but it can also increase the impact of invasive aquatic species, e.g. their competitive and predatory effects on native species, or the virulence of some diseases, thus requiring new prevention and control strategies (Rahel and Olden, 2008). Climate change also affects aquatic ecosystem processes, e.g. by changing discharge regimes including prolonged droughts and ephemerisation of previously running waters, or by producing heat waves. Those may act as "windows of opportunity" for the establishment of invasive species, including parasites, such as the mass development of the "swimmer's itch", *Trichobilharzia franki*, in Lake Constance during the heat wave in summer 2003 (Fiedler et al., 2005). In our study, we focus on the effects of increasing water temperature on the success of a recent invader (*Dikerogammarus villosus*), which has caused considerable changes in the benthic invertebrate assemblages in Europe.

European freshwater ecosystems are recently heating up due to Climate Change and inflowing cooling or waste water. For example, long sections of the River Rhine hardly ever cool below 5 °C in winter (Schöll, 2000). A recent study on 475 sites in seven river basins of Germany has revealed a mean warming trend of 0.03 °C year^{-1} during the 1985–2010 period (Arora et al., 2016), the Loire River has increased approximately 0.8 °C year^{-1} (Moatar and Gailhard, 2006); prealpine lakes (Lake Constance, Lake Zurich) have been increasing by 0.021–0.054 and Lake Stensjön (Sweden) as much as 0.157 °C year^{-1} during the 1970–2008 period (Adrian et al., 2009).

Considering the biogeographical situation of Central Europe, these temperature trends are specifically worrying because its freshwater fauna derives in large parts from glacial relics (i.e. cold-stenothermous species) and the post-glacial recolonization by natural dispersal has been relatively slow, because river and lake ecosystems have been separated from their southern and south-eastern correlates by basin divides acting as geographical barriers (Dehling et al., 2010; Illies, 1978). The increased passability of these barriers due to canal construction (specifically the canal connecting the Rhine and Danube basins) and reduced environmental quality (water pollution, habitat degradation), combined with the increased water temperatures represent a scenario that is very favorable for a fast colonization of central European hydrosystems such as the Rhine river by non-native species (Beisel et al., 2017). Higher temperatures generally seem to increase the success of thermophilous, ponto-caspian invaders in Central Europe (Fruh et al., 2012; Gergs and Rothhaupt, 2015) but at the upper thermal limit (temperatures above 25 °C), alien freshwater crustaceans do not seem to perform better than their local congeners (Maazouzi et al., 2011, Verberk et al., 2018 and literature therein). Low water temperatures during winter may represent a thermal barrier for the thermophilic invaders and a temporal "window of opportunity" for the native fauna to survive. For example, populations of the invasive Asian clam *Corbicula fluminea* became considerably reduced during the cold winter 2012/13 in the Loire River (Wantzen and Richard, 2016). Global warming, however, may break down these thermal barriers.

One of the most alarming invasive freshwater invertebrate species in Europe is the amphipod *Dikerogammarus villosus*. In the past decades, it spread through most of the continent and displaced nearly all native amphipods in waterways (e.g. Bij de Vaate et al., 2002; van der Velde et al., 2000; van Riel et al., 2006). In the Rhine River it has even outcompeted *Gammarus tigrinus*, which originated in North America and had displaced many European amphipods years before (Haas et al., 2002). Several behavioral and physiological features make *D. villosus* a "perfect invader" (Rewicz et al., 2014). Compared with other gammarids, it displays a high fecundity, early maturity, fast growth and cooccurrence of up to 14 cohorts at a time (Pöckl, 2007; Pöckl, 2009; Wijnhoven et al., 2003), low metabolic rates and high glycogen reserves (Becker et al., 2016; Maazouzi et al., 2011), an energy-efficient and temperature-adapted preying strategy (Pellan et al., 2015), high salinity tolerance (Piscart et al., 2011) and excellent spreading mechanisms (Bacela-Spychalska et al., 2013). The main displacement mechanism, however, seems to be intraguild predation on other amphipods, as described by Dick et al. (2002). Due to this high invasional potential *D. villosus* can be regarded as a global threat, e.g., for North American freshwater ecosystems such as the Great Lakes system (Bruijs et al., 2001). *D. villosus* is a less performant shredder than native amphipods such as *G. fossarum* or *G. roeselii*, thus a complete replacement of the native amphipods may have negative impacts on the organic matter budgets of lake ecosystems, whereas under coexistence, leaf litter breakdown rates could remain reasonably high (Little and Altermatt, 2018).

D. villosus was first recorded in Lake Constance in 2003 (Mürle et al., 2004) and quickly spread throughout the lake (Hesselschwerdt et al., 2008). Lake Constance is the second largest prealpine lake. Large parts of its water arrive from the alpine Rhine catchment, and it flows into the Rhine River further downstream (Uehlinger et al., 2009). Due to the Rhine fall at Schaffhausen, there is no navigable connection between the water bodies, thus Lake Constance (bordered by Germany, Switzerland, and Austria) lacks many of the invasive species that inhabit the river, however, some invasive species have found their way into the lake, such as *Dreissena polymorpha, Corbicula fluminea* and diverse benthic-pelagic shrimp species (Gergs and Rothhaupt, 2015; Hanselmann et al., 2013; Mörtl and Rothhaupt, 2003; Rothhaupt et al., 2014; Werner et al., 2005; Werner and Rothhaupt, 2007).

Before the arrival of *D. villosus* in Lake Constance, its amphipod communities had already undergone changes. The earliest recorded recent species are *Gammarus fossarum*, *G. lacustris* and *G. pulex* (Muckle, 1942; Schellenberg, 1942). Later, *Gammarus roeselii* (Gervais) appeared in Lake Constance. This species, originating from the Balkans (Jazdzewski, 1980), was first recorded in Central Europe near Paris (Gervais, 1835), however it is not considered a strong competitor to the native invertebrate fauna (Josens et al., 2005). In the past decades, fostered by the eutrophic phase of Lake Constance (1960s to 1980s), *G. roeselii* was dominating, but its densities strongly declined after the invasion of *D. villosus* (Mörtl et al., 2005), most likely due to direct predation by *D. villosus* (Hesselschwerdt et al., 2009; Kinzler and Maier, 2003), or source competition (Rothhaupt et al., 2014). Currently, the density of *D. villosus* determines 26% of the variability of benthic invertebrate assemblages in Lake Constance (Gergs and Rothhaupt, 2015).

In spite of these findings, both amphipod species coexisted in plant parts of the macroalga *Chara* sp. and in winter, and *G. roeselii* even dominated parts of the littoral (Hesselschwerdt et al., 2008). In order to test hypotheses for this coexistence, different laboratory studies were made. We could show that *G. roeselii* was able to smell and avoid the scent of *D. villosus* (Hesselschwerdt et al., 2009), moreover, slightly different substrate preferences exist (Hesselschwerdt et al., 2008). Further studies tested tolerance against ammonia (Gergs et al., 2013) or pesticides (Bundschuh et al., 2013), both with limited results. Another study had shown that *D. villosus* is able to drive native gammarid species out of