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Biases in global effects of exotic species on local invertebrates: a systematic review

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Abstract

Historical gaps and biases in the literature may have influenced the current knowledge of the impacts of invaders on global biodiversity. We performed a systematic review and compiled the main gaps and biases in the literature and the reported negative, neutral and positive effects of exotic species on local invertebrates worldwide. We analysed the relation of these reported effects to the biogeographical origin of the exotic species, the environmental characteristics of the invaded area, the trophic level of the exotic species and of the invaded local fauna, and the elapsed time after first introduction. We analysed 1,276 publications comprising 2,984 study cases. From these, 1,786 cases included “control” situations (without exotics) and provided quantitative supporting evidence of the effects of exotic species on local invertebrates. The main gaps in the literature included tropical and arid climates, estuaries and marine ecosystems, as well as exotic species coming from Neotropical, Australian, Oriental, Ethiopian and Antarctic regions. Carnivorous and herbivorous species were underreported as exotic species and as impacted invertebrates. The considered variables were mostly unrelated to the reported effects, suggesting that the effects of exotic species on local invertebrates are heterogeneous and not unidirectional. Many impacted invertebrates were assemblages of undefined composition in terms of the native or exotic nature of the invaded organisms. Further avenues to reduce the identified biases in the current knowledge about the effects of exotic species on local invertebrates are also indicated.

Keywords: arthropods, biogeographical regions, human disturbance, insects, invader impacts, trophic groups.

I. Introduction

Exotic species introduction rates have been increasing to unprecedented levels (Lockwood *et al.* 2007; Simberloff and Rejmánek 2011; Seebens *et al.* 2017), becoming one of the main threats to biodiversity worldwide (Vitousek *et al.* 1996, 1997). Historical introductions are associated with human interest in fostering species for different purposes, and these species have accompanied humans in the colonisation of new territories (McNeely 2001). Trade, transport facilities and the creation of acclimatisation societies worldwide at the beginning of the XVIII and XIX centuries accelerated the rate of introduction of exotic species from different regions (Simberloff and Rejmánek 2011). Commercial activities have thus promoted the historical translocation of exotic species with certain biological traits that originate from preferential regions, ecosystems or climates. Such translocations may also be the target of most of the studies on invasions, resulting in geographical and taxonomical gaps and biases in the knowledge of invaders (see Pyšek *et al.* 2008). As a result, the current knowledge of biological invasions in freshwater, marine, estuary or wetland ecosystems is insufficient and biased towards empirical studies carried out in terrestrial ecosystems concerning plant invasions (Lowry *et al.* 2013; but see Gallardo *et al.* 2016). Knowledge regarding the trophic levels of exotic species is also generally unsatisfactory (but see Cameron *et al.* 2016), as well as the knowledge regarding the time elapsed after the arrival of exotic species (Strayer *et al.* 2006; de Albuquerque *et al.* 2011; Hengstum *et al.* 2014).

After surmounting geographic barriers with the aid of humans, invasion success depends on the ability of exotic species to establish self-sustained populations. Subsequent post-establishment spread may occur without direct human intervention; however, post-establishment spread may be indirectly facilitated by humans via, for example, habitat modification. During the invasion process, exotic invasive species have to withstand the new environmental conditions and the interactions with the native species (Blackburn *et al.* 2011).

A general view of an inexorable negative effect of exotic species on ecosystems has been challenged. Davis *et al.* (2011), for example, argued that in certain situations, such as those prevailing in disturbed ecosystems or old introductions, the effects of exotic species may be positive on assemblages and ecosystems. They suggested that decisions about the management of exotic species must be based on ecosystem functioning instead of species origin. In line with this argument, Schlaepfer *et al.* (2011) proposed an analysis of the negative and positive effects of exotic species before deciding on whether an intervention is necessary, which was a suggestion with strong objections (Vitule *et al.* 2012, see also the reply in Schlaepfer *et al.* 2012). To intensify this debate, Russell and Blackburn (2017a,b) recently criticised the denialism of the negative effects of invasive species. They argued that the consequences of exotic species appear slowly and are difficult to recognise during early phases after the invasion. This criticism was rebutted by authors who claimed that several studies had indicated positive effects of invasive species and not only negative ones (Briggs 2017; Davis and Chew 2017). Thus, a systematic review is needed to summarise the literature, evaluating the effects (either negative, positive or neutral) of exotic species on native assemblages, and to contribute to this debate (see Schlaepfer *et al.* 2012).

Ecosystems differ in their susceptibilities to invasions. For example, freshwater ecosystems are thought to be especially susceptible to invasion (Pyšek *et al.* 2010) and more negatively impacted by this process, showing strong decline in native biodiversity when associated with environmental changes (Sorte *et al.* 2013). Conversely, isolated and remote places, as well as areas with extreme climatic conditions, experience low invasibility (but see Chwedorzewska *et al.* 2013). This result may happen because the inaccessibility for humans reduces the propagule pressure of exotic species (Lockwood *et al.* 2005), or because only exotic species with wide niche breadths and dispersion capacities can colonise these areas (Simberloff and Rejmánek 2011). Hence, ecosystem invasibility is a consequence of the

102 characteristics of the invaded assemblages (e.g., isolation, absence of predators, competitors
103 or parasites), the environmental suitability of the invaded territories, and the attributes of the
104 exotic species (e.g., large range sizes, predator species, high reproduction rates or propagule
105 sizes). The establishment of exotic species is usually more likely in disturbed habitats,
106 probably because life-history traits of pioneer species that are typical of early successional
107 stages also facilitate invasion capacity. Thus, anthropogenic disturbance can favour invasion
108 (Byers 2002; Jauni *et al.* 2015; Florencio *et al.* 2016), sometimes relaxing competition
109 between native and exotic species and, therefore, favouring the establishment of exotic
110 species (Davis *et al.* 2000; Blumenthal 2005). Exotic species may also improve the function
111 and resilience of ecosystems in these human-altered habitats, replacing functions that would
112 otherwise be lost due to the local extinction of most intolerant native species (Schlaepfer *et*
113 *al.* 2011; Yelenik and D'Antonio 2013; Florencio *et al.* 2015). In contrast, rich assemblages
114 in pristine habitats commonly exhibit biotic resistance to invasions, hindering the
115 establishment of exotic species (*sensu* Elton 1958). However, pristine habitats could be more
116 vulnerable to detrimental effects once the invasion succeeds, reducing species diversity,
117 abundances and biomass, and even driving local extinctions (e.g., Parker *et al.* 1999; Kueffer
118 *et al.* 2007). In all of these situations, stronger impacts on biodiversity are expected with the
119 time since invasion (e.g., Olsson *et al.* 2012). The successive arrival of exotic species through
120 time, associated with the decline of native biodiversity, can increase the similarity among
121 local assemblages, leading to biotic homogenisation (McKinney and Lockwood 1999; Olden
122 and Poff 2003; Florencio *et al.* 2013). All of these singularities of the invasion process need
123 to be included in the delineation of studies aiming to estimate the impacts of exotic species.
124 Hence, the use of the characteristics of the exotic species as well as those of the recipient
125 environment are generally considered to assess species invasiveness and habitat invasibility
126 (Ricciardi and Atkinson 2004). However, the complexity of the invasion process has led to

the incorporation of new approaches, such as the study of areas where exotic species have been removed and comparisons of the evolution through time of species in invaded and non-invaded areas (Barney *et al.* 2015). Spatial and temporal comparisons between non-invaded and invaded sites are considered essential elements to reach confident conclusions about the impacts of exotic species (Thomaz *et al.* 2012).

Invertebrates constitute the animal group with the highest global number of described species, including approximately 96 % of the total known species (Wilson 1987, Mora *et al.* 2011). Also, invertebrates are central components for ecosystem functioning (Kremen *et al.* 2007; Kremen and Chaplin-Kramer 2007). In this study, the literature on the effects of exotic species on invertebrates has been reviewed, compiling local evidences throughout the world for different aquatic and terrestrial ecosystems. Lowry *et al.* (2013) reviewed the studies that investigated biological invasions in natural systems. They recognised that numerous publications were missed in their systematic search and recommended an extension of their research to understand and correct the biases in the literature. Hence, we focus on the impacts of exotic species on local invertebrates around the world, and this study encompasses a larger number of publications than Lowry *et al.* (2013). Our study summarised the degrees of disturbance to the invaded areas for different climatic regions and trophic groups. We also evaluated these effects according to the nature of the impacted invertebrates (native or exotic), the biogeographical origin of the exotic species, and the time elapsed since the first introduction. Because the success of invasion could be mediated by the characteristics of the recipient communities, we have delineated a conceptual framework that represents the primary data necessary to estimate the effects of exotic species on native species, considering the biotic and abiotic similarities of invaded and non-invaded areas as well as their variations through time after invasion (Fig. 1). According to this framework, three main types of data are necessary to estimate the effects of exotic species: (i) environmental and biological

information about the area of origin of the exotic species, (ii) environmental and biological information on the invaded area, and (iii) information on the temporal variations in environmental and biological characteristics after the arrival of the exotic species. This study attempts to identify the gaps and biases in the knowledge of the effects of exotic species on local invertebrates by performing a systematic review and compiling the information available about these three types of data. By reviewing the available local evidence throughout the world for different aquatic and terrestrial ecosystems, our main purpose is to highlight how the current knowledge of the effects of exotic species may depend on these biases, as well as our awareness of their negative effects.

II. Methods

(1.) Systematic literature search

The ISI Web of Knowledge (Web of Science) was used to search for papers published from January 2000 to April 2015, as an appropriate and feasible time range in terms of operational effort. The systematic search included the following terms using Boolean characters and parentheses: (alien* OR exotic* OR invasiv* OR invader* OR non-native OR non native) AND ecosystem* AND (invertebrate* OR insect* OR arthropod*). We excluded publications belonging to the research fields of sociology, physics, neurosciences, neurology, general internal medicine, energy fuels, dermatology, cardiovascular systems, cardiology, geriatrics, gerontology, history, imagine science (communication science), photography technology, business economics, anthropology, palaeontology, government law, gastroenterology, hepatology, engineering, instruments and instrumentation, cultural studies, public administration, philosophy, material science, spectroscopy, medical laboratory technology, communication, cell biology and mathematical computational biology. After this procedure, a

total of 2,519 manuscripts were obtained (see Online Resource 1 for a detailed list of publications).

(2.) Inclusion and exclusion criteria

The complete texts of the selected papers were screened to ensure that only relevant literature was used in the review. Only papers written in English were considered, excluding narrative reviews, meta-analyses, prefaces and opinion articles. Papers that did not consider exotic species and did not report exotic species co-occurring with invertebrates were also excluded. Finally, seven publications were also excluded as they could not be obtained. In total, 1,276 publications were finally retained (see Fig. S1 in Online Resource 2).

(3.) Data extraction

We considered as different study cases within the same publication when they (i) reported different effects of exotic species on different groups of invertebrates (e.g., epifauna and intertidal fauna) or (ii) considered different variables to test the effects of exotic species on local invertebrates (e.g., species richness, abundance or composition). When a study separately considered the effects of different subgroups of invertebrates and, at the same time, the effects on the general group to which they belonged, the information on only the general group was retained. As a consequence, a total of 2,984 study cases were extracted from the 1,276 papers retained with the procedures described above. Study cases were classified into two groups. The first group included study cases that used “control” situations (without exotics) and provided quantitative data (e.g., statistical analyses, raw datasets or ordination plots) to estimate the effects of exotic species on local invertebrates (hereafter, evidence-based studies, $n = 1,786$). The second group included study cases that did not provide quantitative supporting evidence on these effects ($n = 1,198$). When multiple exotic

species were considered in a study from the second group, all cases were included as a single study case. Evidence-based studies were used to describe the research gaps and effects of exotic species on local invertebrate assemblages.

Based on the qualitative conclusions provided by each study, the effects of exotic species on local invertebrates were classified by means of a nominal variable indicating negative, neutral or positive effects on the different attributes of invertebrate species and assemblages (e.g., growth, survival, abundance, biomass, richness, composition; see Table S1 in Online Resource 2). Negative effects were assigned to those study cases that reported declines in a response variable, reflecting the effects of exotic species on local invertebrates (e.g., reduction in richness, changes in assemblage compositions, competitive displacement). Neutral effects were established when no effects were reported. We assigned a positive effect to those study cases that reported positive effects of exotic species on invertebrate attributes (e.g., increase in richness or diversity). This nominal variable was related to five types of explanatory variables to examine the main characteristics (if any) associated with the reported effects of exotic species: biogeographical origin of the exotic species (BIO_{EX}), environmental characteristics of the invaded area (EN_{INV}), trophic level of the exotic species (T_{EX}), trophic level of the invaded local fauna (T_{INV}) and “minimum time since introduction” of the exotic species (MTI). The purpose of this analysis is to understand how the detected gaps and biases in the literature could have influenced our current knowledge of the effects of exotic species on local invertebrates worldwide. It is important to emphasise that this analysis cannot be considered a meta-analysis, and thus, we did not estimate a summary effects of the exotic species.

BIO_{EX} is a categorical variable with nine levels: Palaearctic (Europe, Asia and North of Africa), Nearctic (North America to the Neotropical limit), Neotropical (Mexico, Central and South America), Ethiopian (central and southern Africa), Oriental (Southeast Asia,

Indonesia and Pacific islands), Australian (Australia and New Guinea, including the islands surrounding Australia and New Zealand) and Antarctic (based on Udvardy 1975). Cosmopolitan exotic species with native distribution, including multiple biogeographical regions (e.g., Oriental and Palaearctic when including the entire area east of Asia), were assigned to a level called “multiple”. An additional level, called “variety”, was assigned when a group of different exotic species with different origins was jointly considered within a study case.

The EN_{INV} variables included climate, ecosystem type and degree of human disturbance. Climate was coded according to the Köppen-Geiger classification in five levels: Mediterranean, tropical, warm-temperate, cold-temperate and arid (see Kottek *et al.* 2006). The variable representing ecosystem type has four levels: marine, estuarine, aquatic-continental (including all continental waters), and terrestrial ecosystems. The degree of human disturbance attempts to characterise the general conditions of the habitat in which the study was performed and is categorised into four levels: nearly pristine, weakly disturbed, moderately disturbed, and highly disturbed. Nearly pristine areas are those within recognised protected areas. Isolated and low-accessibility zones located in arctic regions or high-altitude mountains were also considered as nearly pristine areas. Areas subjected to low-impact activities (e.g., touristic activities), even if inside protected areas, were categorised as weakly disturbed. Moderately disturbed cases are those including areas with different levels of disturbance (ranging from nearly pristine to disturbed areas). Finally, highly disturbed cases are those including man-made environments (e.g., reservoirs, plantations, etc.), urban and rural areas.

The T_{EX} variable represents the trophic level of the exotic species, while T_{INV} indicates the trophic levels of the local invertebrates present in the invaded areas. The trophic category was divided into four levels: carnivorous, herbivorous, omnivorous and autotrophs..

For simplicity, parasites and scavengers were included as carnivorous species, while grazers, shredders, frugivorous, plant suckers, plant parasites or cellulose eaters were considered herbivorous species. Omnivorous species included decomposers and predators if these predators prey on only a few of the species that compose their usual diet spectrum.

We defined the “minimum time since introduction” (MTI) as the time elapsed, in years, from the first reported observation of each exotic species to the study year. In the absence of this information in the retained publications of the systematic review, we estimated the MTI for the study region or the study country (or states in the USA) carefully reviewing peer-review scientific literature about each exotic species using Scholar Google. In many cases, we did not find data on time of the first introduction of the exotic species even at the country level, or the same study case considered a variety of different exotic species; thus, these cases were discarded from the statistical analyses.

Local invertebrate species or assemblages were classified into four categories according to their compositional origin (C_{OR}): native, exotic, assemblages composed of both native and exotic species (native/exotic), and unknown when the authors did not provide any information regarding the origin of the invaded assemblages. When no information was provided in the publications, we estimated the BIO_{EX} , EN_{INV} , T_{EX} , T_{INV} and MTI by consulting websites and specific literature about the exotic species, the impacted invertebrates and the invaded areas. Next, we examined the groups of variables BIO_{EX} , EN_{INV} , T_{EX} and T_{INV} and selected the categories within each one containing a higher number of study cases than expected for an equitable probability. We then combined the selected categories in a pairwise manner to indicate well-represented situations in the literature (hereafter referred to as well-represented situations).

(4.) Statistical analyses

We obtained information on the MTI (number of years) using the data from 1,241 study cases. We tested whether the effects of recent or ancient exotic species introductions on local invertebrates have been more frequently studied. To do so, we performed a Spearman rank correlation between MTI values and the number of study cases ($n = 150$).

Multinomial logistic regressions were used to relate the nominal response variable representing the effects of exotic species on local invertebrates to the five aforementioned groups of explanatory variables. These analyses were repeated using only the formerly mentioned well-represented situations. The general purpose of these analyses was to estimate the explanatory capacity of each group of variables and to assess whether reported effects were associated with any of the considered characteristics. To do so, we constructed a *full model* (saturated) using the “multinom” command implemented in the “nnet” R package (Venables and Ripley 2002). As these effects may differ depending on the compositional origin of the native assemblages, the C_{OR} variable was included in each *full model* (i.e., testing the hypothesis that the effects of exotic species differed in local invertebrate assemblages composed solely of native species, exotic species or a mixture of exotic and native species). All explanatory variables included in the models were categorical with the exception of MTI, which was included as a continuous predictor. The explanatory capacity (%) of each *full model* was estimated using the reduction in deviance from an intercept-only model in which no predictor was considered (Dobson 1999). The importance of the C_{OR} variable was assessed by comparing the *full model* with a simplified model (reduced model) that included only each group of variables (i.e., BIO_{EX} , EN_{INV} , T_{EX} , T_{IN} and MTI), leaving out the C_{OR} variable and using likelihood ratio tests (LRT) (Pinheiro and Bates 2000). In all these analyses, the study cases without information of any explanatory variable or those including a “variety” of categories of each explanatory variable were removed. Consequently, the

reported effects of exotic species on local invertebrates were statistically analysed using a different number of study cases per group of explanatory variables: $n = 1,013$ for BIO_{EX} , $n = 1,180$ for EN_{INV} , $n = 1,215$ for T_{EX} , $n = 738$ for T_{INV} , and $n = 836$ for MTI. All analyses were performed in R software version 3.4.0. (R Core Team 2017).

III. Results

(1.) Geographical and environmental gaps and biases

(a.) Invaded areas

Most studies ($n = 681$) came from the United States, encompassing 38.2 % of the study cases (Fig. 2). The next country with most study cases was Australia (165 study cases, 9.3 %), while the remaining countries did not exceed 4 % of study cases ($n = 71$). Only 3.4 % of the studies (60 cases) were performed in two or three countries, while no studies had a global scope. Three study cases did not specify the study country.

Studies were also not homogeneously distributed among the different climatic regions, ecosystem types and degrees of human disturbance. Study cases are notably underrepresented in the arid (3.8 %, only 68 study cases) and tropical zones (11.4 %) (Fig. 3a). In contrast, most of the study cases were conducted in warm-temperate (45.7 %, 816 cases), Mediterranean (18.6 %) and cold-temperate (18.3 %) climate regions. Estuaries (9.4 %) and marine (16.9 %) ecosystems were also considered to be underrepresented in comparison with terrestrial (39.9 %) and aquatic-continental (33.8 %) ecosystems. There was a paucity of studies in the nearly pristine category (18.2 %) in comparison with those in highly (30.7 %), moderately (25.8 %) and weakly (23.0 %) disturbed categories (Table S2, in Online Resource 2).

(b.) Origin areas of exotic species

Most of the studied exotic species were native to the Palaearctic region (33.8 %, 604 study cases), but a high number of studies also reported the effects of cosmopolitan exotic species originating from multiple biogeographical regions (13.4 %). The exotic species with Nearctic origins represented 12.7 % of the study cases, while the numbers of studies focusing on exotic species from Neotropical, Australian, Oriental, Ethiopian or Antarctic origins were very low (7.3 %, 5.4 %, 5.2 %, 2.5 % and 0 %, respectively, Fig. 3b). (Table S2, in Online Resource 2).

(c.) Trophic level of the exotic species

The number of study cases focusing on the different trophic groups of exotic species also differed. The numbers of studies carried out on autotroph (44.2 %, 790 study cases) and omnivorous exotic species (32.9 %) were higher than those carried out on carnivorous (14.8 %) or herbivorous exotics (6.7 %, 119 cases, Table S2, in Online Resource 2).

(d.) Trophic levels of invaded invertebrates

The number of study cases differed among the different trophic groups of the invaded local invertebrates, as carnivorous (9.0 %, 160 study cases) and herbivorous (16.2 %) invertebrates were studied less than omnivorous invertebrates (23.2 %). However, the highest number of study cases (915, 51.2 %) reported the effects of exotic species on invertebrate assemblages composed of different trophic levels (Table S2, in Online Resource 2).

(e.) Minimum time since introduction

Although 90% of the exotic species have been introduced during the last 149 years, the median of the MTI was 33 years (upper quartile = 86.5; lower quartile = 12). The number of

study cases reporting effects of exotic species significantly decreased with the MTI ($n = 150$, Spearman's $r = -0.63$, $P < 0.001$; see Fig. 4).

(2.) Effects of exotic species on local invertebrates

Among the discarded literature that did not meet the requirements for the systematic review, 482 publications were narrative reviews. We found 449 study cases (15 %) that made inferences about the effects of exotic species on local invertebrates without any quantitative supporting evidence, while approximately 60 % of the study cases can be regarded as evidence-based studies. From these, 924 cases (51.7 %) reported the effects of exotic species on specific native invertebrates. In contrast, 544 cases (30.5 %) reported these effects on undefined local invertebrates, 192 cases (10.7 %) reported on assemblages composed of both native and exotic invertebrate species, and 126 cases (7.1 %) reported on exotic invertebrates. Excluding the seven cases in which no conclusions about the effects of exotic species were provided, a total of 831 cases (46.7%) reported negative effects, which is more than the number of cases reporting positive (388 cases, 21.8 %) and neutral effects (560 cases, 31.5 %).

No group of variables explained more than 3 % of the total variability in the reported effects of exotic species on local invertebrates (Table 1; see also Table S4 in the Online Resource 2). These analyses were repeated considering the eleven well-represented situations. In these analyses, the inclusion of compositional origin (C_{OR}) increased the explanatory capacity of the different variables in warm-temperate climates and terrestrial ecosystems (Table 1). However, the explanatory capacity of the five groups of variables did not increase substantially in the other situations. The BIO_{EX} , EN_{INV} , T_{EX} and T_{INV} variables accounted for more than 10 % of the total variability when the C_{OR} variable was considered in terrestrial and aquatic ecosystems, and moderately disturbed areas subjected to warm-

temperate climates (Table 1). In these three situations, roughly half of study cases reported negative effects (Table 2). These negative effects mainly reported changes in assemblage compositions and declines in abundance, richness, diversity, biomass, survival, physiological conditions and rates of visitations of the local invertebrates. The reported positive effects of exotic species mainly referred to increases in abundance, richness and the novel use of resources provided by the exotic species (Table 2).

IV. Discussion

(1.) How representative are published data on invasion effects?

In this study, we identified four main sources that may interfere and result in a misleading interpretation of the effects of exotic species on local invertebrates. First, 482 publications were narrative reviews that received high numbers of citations according to Web of Science (69 citations on average, February 2017). This high citation rate seems to indicate the large influence that narrative reviews could have on the current knowledge of the impact of exotic species, as these reviews summarise the conclusions of multiple research articles but do not provide a primary empirical base. Second, we observed the recurrent selection of some exotic invasive species in the evidence-based studies; the molluscs *Dreissena polymorpha* (64 study cases), *Crassostrea gigas* (46), and *Corbicula fluminea* (31), the algae *Caulerpa taxifolia* (42) or the ant *Solenopsis invicta* (28) are some examples, which could have influenced the number of negative effects reported in the literature (Pysek *et al.* 2008; Song *et al.* 2013; Guerin *et al.* 2018). We also cannot discard that those results contradicting the assumed idea that exotic/invasive species are harmful could have been less prone to be published (see Koricheva 2003), thus diminishing the rate of publications of positive and/or neutral effects (Charlebois and Sargent 2017). Third, our study also indicates that recent introductions were studied more often than older introductions; very few studies attempt to examine the effects

of exotic species that appeared more than 33 years ago. This result could be associated with cultural aspects: as a society, we progressively accept these invaders and thus ignore the research on their possible long-term impacts, and even accept some exotic species as targets of conservation initiatives (Clavero 2014). Although these species could contribute to the functions of the invaded ecosystems, it is also true that some introductions require long times before showing evident damages to the invaded areas (Simberloff and Rejmánek 2011). For example, the exotic Asian lady beetle *Harmonia axyridis* was introduced to North America for biocontrol in 1916. However, it was after only a long time that their devastating effects on native invertebrates began to be evident during the eighties in the United States and Europe (Brown *et al.* 2008). Fourth, our study also highlighted that most pristine areas have remained quite unexplored in comparison to the high number of studies that have focused on disturbed ecosystems. Exotic species can easily establish in anthropogenically disturbed ecosystems, even more so when the original native assemblages have already been extirpated (Jauni *et al.* 2015). However, confounding effects between habitat disturbance (e.g., fragmentation, land-use transformation) and the invasion process can also lead to erroneous conclusions about the impacts of exotic species on biodiversity loss, which could be a consequence of the anthropogenic perturbation itself (Mollot *et al.* 2017).

(2.) Main gaps in the literature of invasion

Our results demonstrate that the existing information about the effects of exotic species on local invertebrates is incomplete and biased. The USA was by far the most studied country. In addition to a well-established research community, this may be because the Great Lakes, San Francisco Bay, Chesapeake Bay, and notably Hawaii are some of the areas with the most accelerated rates of invasions in the world (Simberloff and Rejmánek 2011). Hence, most studies were conducted in these areas, even including underrepresented marine and estuarine ecosystems (e.g., Chesapeake Bay). After the USA, Australia was largely

represented. Australia has a well-known history of invasions, including several recognised exotic invasive species worldwide that affect local invertebrates (e.g., *Cyprinus carpio*, *Bufo marinus*, *Crassostrea gigas*, *Caulerpa taxifolia*). The study case with the most ancient introduction in Australia (> 175 years ago) reported negative effects of camels on the abundance and richness of macroinvertebrates, as well as changes in their assemblage compositions because of faecal eutrophication (McBurnie *et al.* 2015). However, we did not detect studies that assessed the effects of exotic birds on invertebrates despite the large number of introductions reported in Australia (see Simberloff and Rejmánek 2011). In comparison with the USA and Australia, other countries can be considered largely understudied.

The most represented study regions worldwide, as well as the underrepresentation of tropical climatic regions, are in concordance with the general gaps detected in the literature on invasions (see Lowry *et al.* 2013). However, the fact that arid climates are poorly investigated is especially relevant. Arid and undisturbed regions may represent low-invaded and inhospitable areas (see Burgess *et al.* 1991; Hunter 1991), from deserts in Arizona and Utah to cold steppes along South African coasts. In these arid regions, freshwater ecosystems play a fundamental role to maintain the local biodiversity. Among the scarce number of study cases, aquatic macroinvertebrates were often used to analyse changes in biodiversity, e.g., reducing their species richness and abundance in response to the Ethiopian predator fish *Tilapia* sp. in Mexico (Bogan *et al.* 2014) or without noticing any effect in the case of the Palearctic plant *Tamarix chinensis* in Arizona (Pomeroy *et al.* 2000). In addition to the underrepresented tropical continental countries, many tropical islands around the world such as Hawaii, Mauritius, and Seychelles provided quantitative supporting evidence about the effects of exotic species on local invertebrates. Many of the insular exotic species were autotrophs that severely decreased the abundances of native invertebrates, such as the native

crayfish *Ocypode cordimana* in Seychelles (Brook *et al.* 2009) or the native butterflies in Mauritius (Florens *et al.* 2010). Exotic predators were also important worldwide, such as *Gambusia affinis*, which modified the diel activity of an endemic Hawaiian crustacean *Halocaridina rubra* (Capps *et al.* 2009).

Most of the study cases analysed the effects of exotic species coming from the Palaearctic region, including many exotic species coming from Asia, which were mainly from China and Japan. Some examples are the worldwide exotic invasive species *Harmonia axyridis* or *Rattus norvegicus*, with the latter invading even remote, near-pristine places such as the Alaskan islands (Kurle *et al.* 2008). Many other Palaearctic exotic species have a Ponto-Caspian native distribution, as many aquatic species are recognised as important exotic invasive species around the world (e.g., *Dreissena polymorpha*, *D. rostriformis bugensis*, *Dikerogammarus villosus*). We found relatively few studies in pristine areas. This result can be explained by an effect of availability (disturbed areas are more common than pristine ones) and possibly by the low invasiveness of these ecosystems, as species-rich and well-preserved protected areas around the world have been recently revealed as resistant to invasions (Gallardo *et al.* 2017). However, we cannot discard that the impacts of exotic species on local invertebrates may be underappreciated in these pristine areas, which might be related to the difficulty in obtaining permissions and funding to sample in protected areas (see Geldmann *et al.* 2018). Some examples of studies performed in pristine ecosystems include wetlands recognised as UNESCO sites in South Africa (Miranda and Perissinotto 2014) and macroinvertebrate assemblages of the Tijuana River National Estuarine Research Reserve, in San Diego, USA (Whitcraft *et al.* 2008).

Better understanding of the effects of exotic species on local invertebrates would require reducing the gaps. Increasing experimental/modelling studies (Lowry *et al.* 2013) and adopting reliable designs (Charlebois and Sargent 2017), at different spatial scales (Shea and

Chesson 2002), are important steps to overcome these gaps. Moreover, improvements in the measurement of propagule pressure (Cassey *et al.* 2005) and anthropogenic impacts (Pysek *et al.* 2010), and additional research efforts in insular ecosystems, which are considered especially prone to invasions (but see Sol 2000; Vilà *et al.* 2010), are necessary for a better understanding of the effects of exotic species. Our results also indicate that more research effort should be devoted to the impacts of exotic species that have long been introduced.

(3.) Are the effects of exotic species generally harmful to invertebrates?

Our results suggest that the reported effects of exotic species on local invertebrates are heterogeneous. This result is in line with the pattern observed for the effects of exotic plants on animals and plants around the world (Vilà *et al.* 2011). Specifically, we observed that the number of study cases that did not report negative effects of exotic species on local invertebrates was even higher (948 study cases reporting positive or neutral effects) than those reporting negative effects (831). Thus, our results indicate the validity of the debate about invasive species being drivers of both negative and non-negative effects on biodiversity. The definition of invasive species of Russell and Blackburn (2017a,b) is based on negative impacts, so for them harmful effects are intrinsic to invasive species. However, we emphasise that this result cannot be used as support to deny the effects of exotic species on local communities of invertebrates because we are not summarising the primary literature on that topic. A key contribution to this debate requires a formal (i.e., inverse-variance weighting) meta-analysis (Gurevitch *et al.* 2018; but see Simberloff 2006). We did not attempt to conduct a meta-analysis because most studies lacked a control area (without the effects of exotic species) or did not provide any information about the origin of the invaded invertebrates, sometimes omitting the number of sampling units or any measurement of

statistical error. Better reporting practices are essential to improve the design of studies for the posterior inclusion of data in possible meta-analyses (see Gerstner *et al.* 2017).

Neutral and positive effects seem to be related to exotic species that increased the habitat complexity of the invaded areas and exotic species that provided limiting resources or reduced natural enemies such as parasites and predators (Davis 2009). Some examples of the former included exotic plants that improved the performance of spider webs, and consequently, the fitness of native spiders in terrestrial ecosystems (Smith *et al.* 2016), or many examples of exotic dreissenid mussels that result in improvements to the habitat complexity for native epifauna in aquatic-continental ecosystems (Ward and Ricciardi 2007). However, positive and negative effects could be strongly dependent on the response variable (see Davis 2009). For example, in freshwater ecosystems, a meta-analysis revealed that the common carp and the red swamp crayfish have strong negative effects on macroinvertebrates but indirect positive effects on zooplankton species (Shin-ichiro *et al.* 2009). Moreover, these effects seem to be dependent on the trophic group of the exotic species and the studied ecosystem type (Gallardo *et al.* 2016; Mollot *et al.* 2017). For example, positive effects in species richness were generally observed when the exotic species were detritivores in aquatic ecosystems (e.g., Schmidlin *et al.* 2012). Moreover, herbivorous exotic species usually promote non-obvious indirect effects on ecological processes and interactions that ultimately can reduce native biodiversity (Gandhi and Herms 2010). This could be the case of the mud-snail *Potamopyrgus antipodarum*, with both positive and negative effects on local macroinvertebrates (Múrria *et al.* 2008). Many local invertebrates can also utilise exotic plants as resources, which are commonly used as a food supply for herbivorous invertebrates (e.g., Lankau *et al.* 2004, Pedersen *et al.* 2005). In the understudied arid zones, exotic species also provided limiting resources for herbivorous and carnivorous invertebrates that inhabit such environments (e.g., Hinnert and Hjelmroos-Koski 2009; Dumont *et al.* 2011). Few study

cases reported positive effects of exotic species due to the reduction of natural enemies. For example, the Asian mongoose *Herpestes javanicus* indirectly increased the abundance of native insects, which was probably associated with the reduction of their native predators through top-down cascades (Watari *et al.* 2008). Furthermore, those invaded ecosystems where native species are phylogenetically poorly related to potential exotic species could favour invasions and the displacement of native species. These ecosystems would share few enemies with the native areas of invaders to regulate and limit their abundances and impacts (Ricciardi and Atkinson 2004).

We need to consider that the current knowledge of the negative and non-negative effects of exotic species on local invertebrates could be associated with the gaps and biases highlighted in this study. However, when we used the best-represented situations in the literature to minimise the effects of these biases, we did not observe any variable that was able to explain the reported effects of exotic species on local invertebrates. Therefore, negative and non-negative effects of exotic species on local invertebrates seem to be idiosyncratic and non-easily predictable. This finding suggests that the effects of exotic species are not unidirectional, revealing complex and context-dependent effects. Notably, we observed that the composition of the invaded assemblages could partially modulate the reported effects of exotic species. Thus, positive effects can be more frequent when these assemblages are dominated by exotic invertebrates, while negative effects can be more frequent when the assemblages are dominated by native invertebrates. For example, it is well-known that exotic species can facilitate the arrival of other exotic species (Simberloff and Von Holle 1999), even amplifying their negative effects; this process of invasional meltdown has been demonstrated using native and exotic invertebrates (Green *et al.* 2011). However, a high number of studies in the literature (n = 544) omitted the information necessary to define

the origin of the invaded invertebrates (native or exotic), which could have a profound influence on the current knowledge of the impacts of exotic species.

Exotic species with a broad geographic range are considered to have a high potential for invasion (Duncan *et al.* 2001; Cadotte *et al.* 2006). In our study, many study cases included exotic species with multiple origins, for which the reported effects ranged from negative to positive. An example is the algae *Caulerpa taxifolia* (tropical and subtropical distribution), which was associated with the decline in the abundance of macroinvertebrates in an Australian estuary and the increase in invertebrate richness (Bishop and Kelaher 2013).

The time elapsed since invasion is also considered an important variable that can modulate the effects of exotic species (Iacarella *et al.* 2015). Ecological and evolutionary adjustments of exotic species can occur after long periods of time, and new characteristics can also appear in invaded species and ecosystems after long periods of introductions (Strayer *et al.* 2006). However, in our study, the frequencies of positive, negative or neutral reported effects did not seem to be related to the time elapsed since invasion. Hengstum *et al.* (2014) also found that the time since the introduction of exotic plants did not explain the effects of exotic species on local arthropod communities worldwide. They suggested that the spectrum of time considered in their meta-analysis (mostly < 150 years) could be too short to go through the different stages of the invasion and, thus, to affect local arthropods. Although we cannot discard this possibility in our study, we emphasise that this result could be a consequence of the geographical scale of observation for the MTI. The lack of spatial concordance between the location of the study areas and the first introduction of exotic species could have diminished the real influence of the MTI on the reported effects. We thus suggest that further studies should make an effort to consider the time elapsed since the first introduction at the most local spatial scale possible.

V. Conclusions

- 1) We found few studies examining the effects of exotic species that were introduced a long time (> 33 years) ago. Thus, more research effort should be directed to evaluate the effects of old invaders, ideally considering local invertebrates with both ancient and recent introductions of the exotic species.
- 2) Tropical and arid regions, as well as the effects of exotic species from Neotropical, Australian, Oriental and Ethiopian areas, are poorly investigated, and more information is required from these regions to understand the effects of exotic species in these climates. Studies focusing on the effects of exotic species in arid climates are particularly relevant to fill a “climatic” gap.
- 3) Estuaries and marine ecosystems are poorly studied and, according to our search criteria, we did not find studies in Antarctica.
- 4) The impacts of exotic species on local invertebrates are mainly assessed in anthropogenically disturbed habitats. Well-preserved protected areas, and low-disturbed ecosystems should be more studied.
- 5) The time elapsed after the first introduction should be estimated at the local study area. The compilation of historical records at a local scale could help to better understand the negative or positive effects of exotic species.
- 6) Regarding the biological characteristics of the exotic species and the impacted invertebrates, the existing knowledge is focused on autotroph exotic species affecting omnivorous invertebrates. In contrast, exotic carnivores and mainly exotic herbivores, as well as carnivorous and herbivorous invertebrates, are underreported. Exotic herbivorous typically cause indirect effects. Increasing the knowledge about the magnitude and direction of these indirect effects would improve our understanding about the impacts of exotic species.

- 7) Many studies did not provide information about the trophic groups and the native or exotic nature of the invaded invertebrate assemblages. Further studies should clearly define the original composition of the invaded areas providing taxonomic lists and indicating the exotic origin of resident species, to avoid possible biases in the knowledge of the impacts of exotic species.
- 8) Global studies are also scarce, and global patterns have been practically assessed by only meta-analyses, while more empirical studies comparing exotic effects in multiple regions and climates are necessary. A more global understanding of the impacts of exotic species might include simultaneous local experiments in different countries.
- 9) Robust conclusions about the effects of exotic species on local invertebrates require more and better data from primary studies. Better practices in the design of such studies are essential to obtain proper data to perform a formal meta-analysis that summarises the effects of exotic species on local invertebrates. Ideal data should cover environmental and biological information about the origin of the exotic species and the invaded areas, as well as about the temporal variation of the native assemblages after the arrival of exotic species.

VI. References

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Table 1: Multinomial logistic model results showing the explanatory capacity (in %) of each group of explanatory variables on the nominal response variable that was classified as negative, neutral or positive effects of exotic species on local invertebrates. This classification was performed according with the qualitative conclusions reported by each retained study in the systematic review. Well-represented data are those combinations of the considered variables that represented the highest number of study cases. Well-represented data include only native invertebrates (marked with #) or invertebrate assemblages with different compositional origins (C_{OR} , indicated without #). In the latter, the C_{OR} variable was included as a co-variable, and the importance of this variable was estimated by comparing a *full model* including the two types of variables (e.g., C_{OR} and BIO_{EX}) to a simplified model (reduced model) that excluded the C_{OR} variable by using likelihood ratio tests (LRT) (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, n.s. = non-significant). Therefore, percentage values are the explanatory capacity of each group of variables, and P values indicate if the reduced model (excluding the C_{OR} variable) was significantly different from the *full model*. The number of study cases and the proportions of cases that represented these situations out of the 1,786 total study cases (in %) are indicated. BIO_{EX} is the biogeographical origin of exotic species, EN_{INV} is the environmental characteristics of the invaded area, T_{EX} is the trophic level of the exotic species, T_{INV} is the trophic level of the invaded local fauna, and MTI is the “minimum time since introduction” of the exotic species (see Table S3 in the Online Resource 2 for the detailed number of study cases per group of variables). The partial effects of the considered variables were also calculated (see Table S4, in the Online Resource 2).

	Study cases	Proportion (%)	BIO _{EX}	EN _{INV}	T _{EX}	T _{INV}	MTI
<i>All data</i>			1.2 _{n.s.}	1.2**	1.8*	2.3*	0.7 _{n.s.}
<i>Well-represented data</i>							
Warm-temperate climate and terrestrial ecosystems	314	17.6	8.9**	10.0***	9.2***	10.7***	7.9*
Warm-temperate climate and aquatic-continental ecosystems	275	15.4	8.5 _{n.s.}	4.8 _{n.s.}	5.0 _{n.s.}	12.1 _{n.s.}	4.7 _{n.s.}
Warm-temperate climate and highly disturbed areas	249	13.9	6.6 _{n.s.}	3.2 _{n.s.}	4.4*	4.0 _{n.s.}	2.0 _{n.s.}
Warm-temperate climate and moderately disturbed areas	240	13.4	15.4 _{n.s.}	4.2 _{n.s.}	11.5 _{n.s.}	13.6*	5.4*
Warm-temperate climate and native invertebrates#	442	24.8	2.2	1.3	0.8	2.5	0.3
Highly disturbed areas and native invertebrates#	299	16.7	4.2	3.2	3.9	2.3	0.8
Moderately disturbed areas and native invertebrates#	215	12.0	6.1	6.1	5.5	8.4	0.9
Palaeartic origin of exotics affecting native invertebrates#	323	18.1	—	4.4	6.5	4.2	0.4
Omnivorous exotic species affecting native invertebrates#	344	19.3	3.6	4.7	—	4.9	0.3
Autotroph exotic species affecting native invertebrates#	330	18.5	5.8	4.9	—	2.4	0.9
Exotics affecting omnivorous native invertebrates#	293	16.4	2.9	4.9	1.2	—	0.2

933 **Table 2:** Values of the proportions (%) and numbers of study cases reporting negative, neutral and positive effects of exotic species on local
934 invertebrates in two well-represented situations, (1) in warm-temperate climates and terrestrial ecosystems, (2) in warm-temperate climates and
935 moderately disturbed areas, and (3) in warm-temperate climates and aquatic-continental ecosystems. Values are indicated for the different
936 attributes of local invertebrates used to determine the exotic effects when their contribution to the total number of study cases was greater than
937 1.25 % (see Table S1 in Online Resource 2 for a detailed explanation of these attributes).

	Negative (%)	Number of cases	Neutral (%)	Number of cases	Positive (%)	Number of cases
(1) Warm-temperate climate and terrestrial ecosystems	45.2	142	36.3	114	18.5	58
Composition	75.0	30	25.0	10	0	0
Abundance	40.2	49	35.2	43	24.6	30
Richness	38.7	24	48.4	30	12.9	8
Diversity	40.0	10	48.0	12	12.0	3
Biomass	75.0	6	25.0	2	0	0
Survival	46.1	6	30.8	4	23.1	3
Physiology	62.5	5	25.0	2	12.5	1
Resource utilization	31.2	5	25.0	4	43.8	7
Visits	42.8	3	28.6	2	28.6	2

(2) Warm-temperate climate and moderately						
disturbed areas	47.1	113	31.2	75	21.7	52
Composition	10.0	24	4.2	10	0	0
Abundance	15.4	37	12.5	30	10.4	25
Richness	6.7	16	5.4	13	4.2	10
Diversity	4.6	11	1.7	4	0	0
Biomass	2.5	6	1.7	4	0	0
Survival	1.7	4	0	0	0	0
Physiology	1.3	3	0	0	0	0
Resource utilization	0	0	2.1	5	2.1	5
(3) Warm-temperate climate and aquatic-continental						
ecosystems	48.2	132	33.6	92	18.2	50
Composition	8.4	23	3.6	10	0	0
Abundance	18.2	50	11.7	32	8.8	24
Richness	5.1	14	4.7	13	4.0	11
Diversity	3.3	9	3.6	10	0	0
Biomass	3.3	9	1.8	5	0	0
Survival	2.2	6	1.8	5	0	0
Physiology	2.9	8	2.6	7	0	0

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List of figures:

Fig. 1 Conceptual diagram showing the three main types of data necessary to estimate the effects of exotic species. These types of data consider the invasiveness of the exotic species, (i) environmental and biological information (e.g., conspecific competition, natural enemies, or trophic groups) about the origin area of the exotic species, as well as the invasibility of local areas, (ii) environmental and biological information (e.g., phylogenetical relationships, enemy release, or trophic cascades) on the invaded area. Also, it is worth to consider (iii) information on the temporal variations in environmental and biological characteristics after the arrival of exotic species; exotic species can transform the invaded environments and/or facilitate the arrival of other exotic species, which may delay the impacts on native biodiversity. The use of potential areas subjected to invasion (“potential invaded areas”) and the monitoring after the arrival of exotic species would warn about possible impacts on the native assemblages. These data are thus essential to calculate the measurements of similarity that reveal different degrees of invasibility, using potential ($t = 0$) and current invaded areas ($t = 1$) and regarding the period after the arrival of the exotic species ($t = n+1$).

Fig. 2 World map showing the number of studies performed in each country from the total of 1,786 evidence-based study cases retained in the systematic review.

Fig. 3 Gaps in the literature (bright red colour) summarised in the systematic review, considering only those evidence-based study cases for the effect of exotic species on local invertebrates worldwide. A) Gaps in the literature relative to the invaded area according to the Köppen-Geiger climate classification (see Kottek *et al.* 2006), i.e., arid (BW, BS) and tropical (Af, Am, As, Aw) climates. Climate classifications have been performed using the data available for GIS software that were observed between 1975 and 2000 (Rubel and

Kottek 2010), and categorised as Mediterranean, tropical, warm-temperate, cold-temperate and arid. B) Gaps in the literature relative to the original area of the exotic species, i.e., the Australian, Ethiopian, Oriental, Neotropical and Antarctic regions. Palearctic and Nearctic regions are also indicated. Biogeographical regions have been depicted according to the Terrestrial Ecoregions of the World (Olson *et al.* 2001) (see Table S2 in the Online Resource 2 for the number of study cases considered for each level of the climatic regions and the biogeographical origins of the exotic species).

Fig. 4 Negative relation between the number of study cases and the log (X+1) transformed minimum time since introduction [Log(MTI+1)].

Online Resource 1 List of publications included in our Systematic search in the literature

Online Resource 2 Different attributes of the local invertebrates used to classify the effects

of exotic species on local invertebrates (Table S1); flowchart following the preferred

reporting items for systematic review (Fig. S1); number of study cases and proportion of the

study cases of each category calculated per each type of explanatory variables (Table S2);

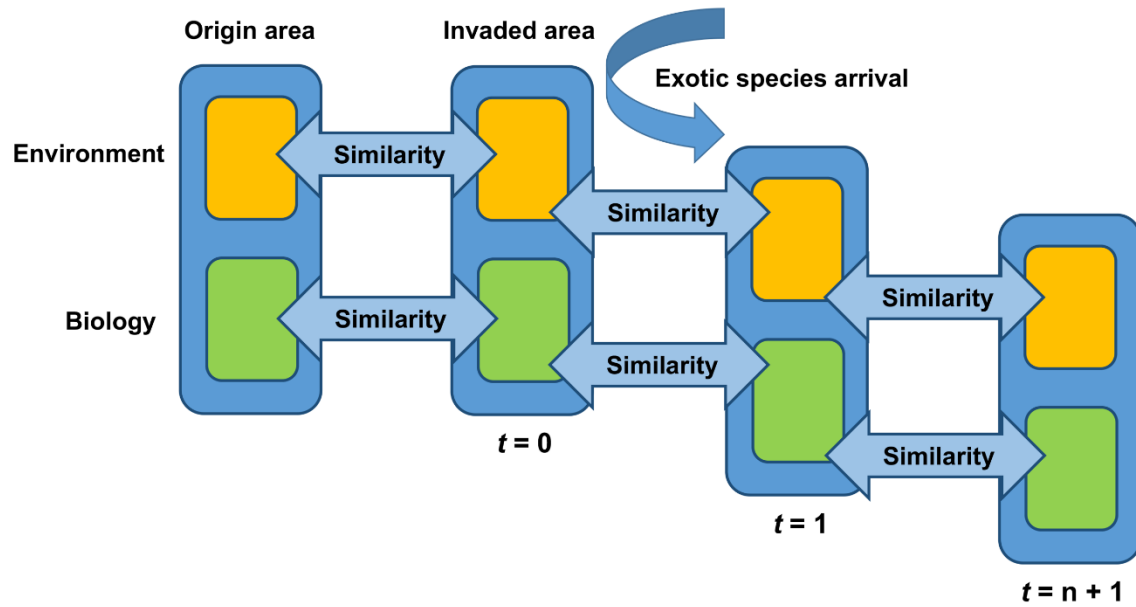
number of study cases included in each situation to test the explanatory capacity of the

different groups of variables for the well-represented situations in Table 1 (Table S3); partial

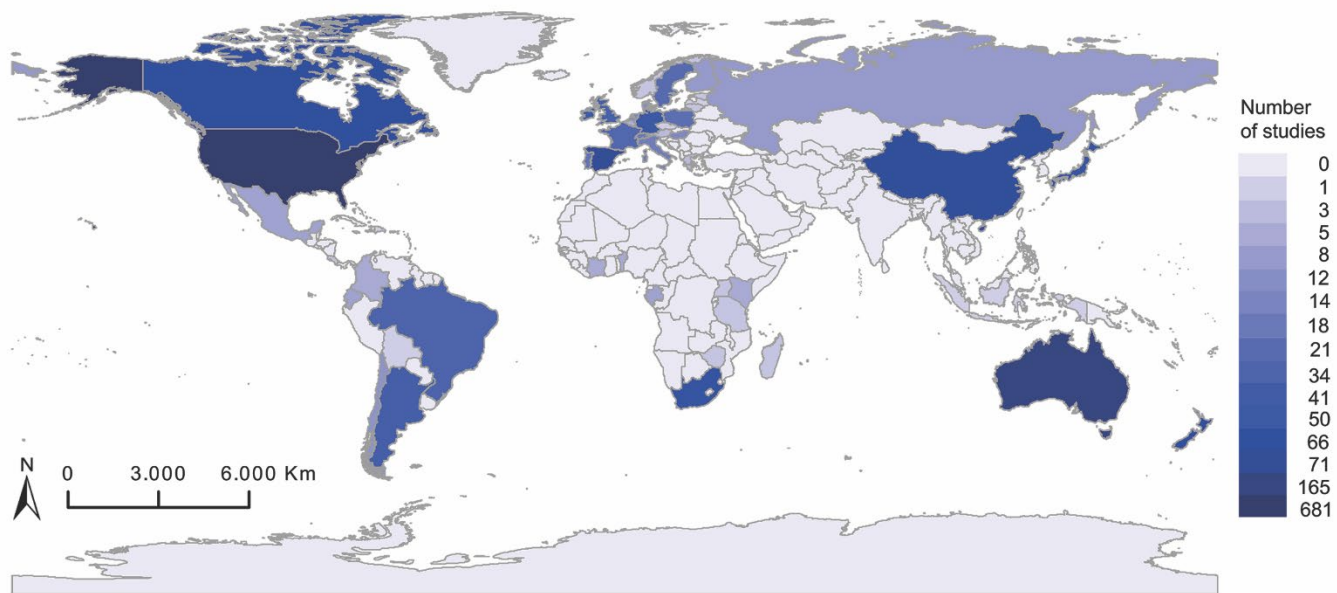
effects of each variable (excluding MTI) after a multinomial logistic model, using as nominal

response variable the negative, neutral or positive effects of the exotic species on local

invertebrates (Table S4)



1004 **Fig. 2**



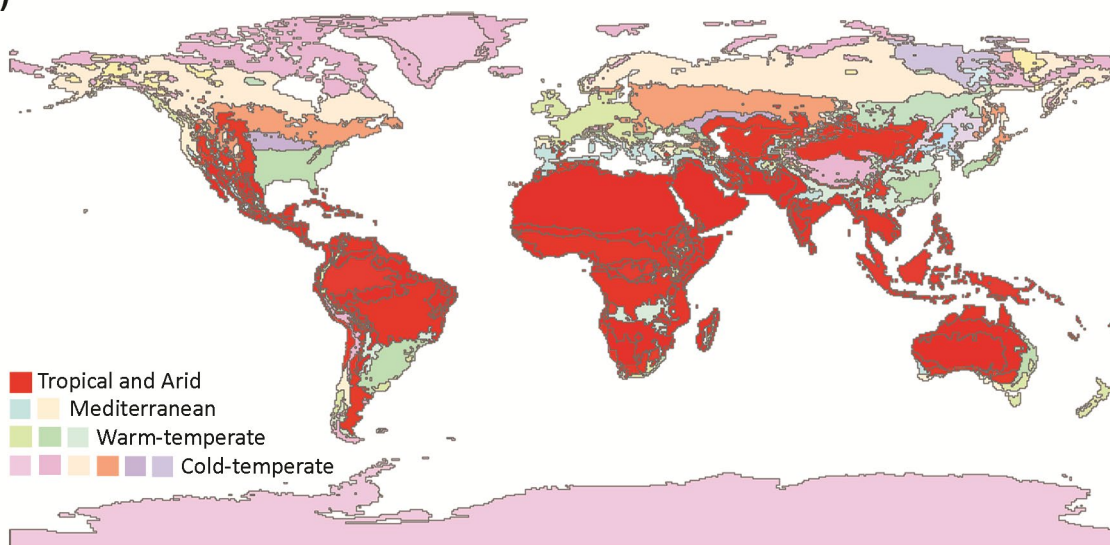
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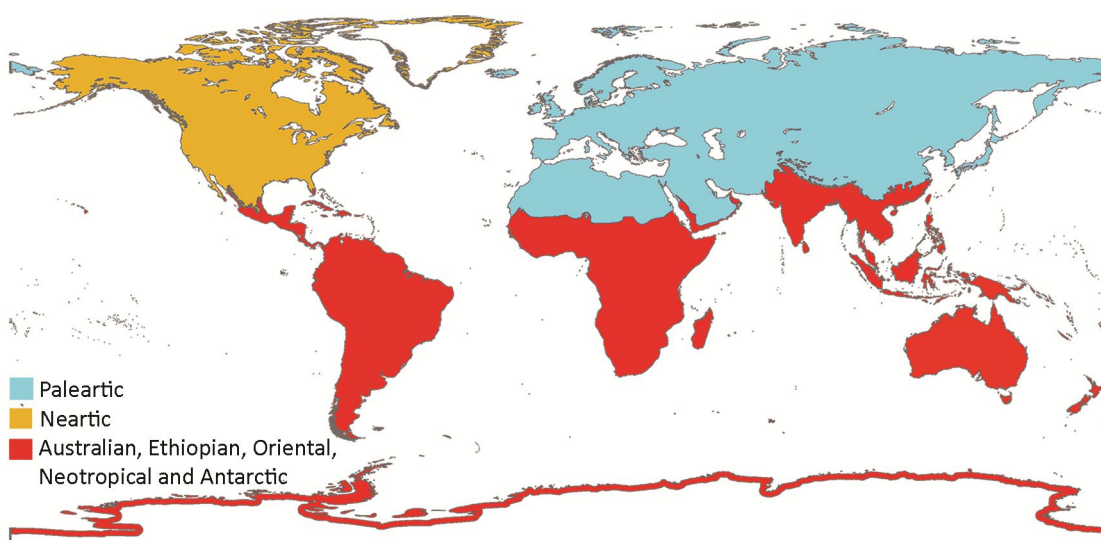
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1008 **Fig. 3**

(a)



(b)



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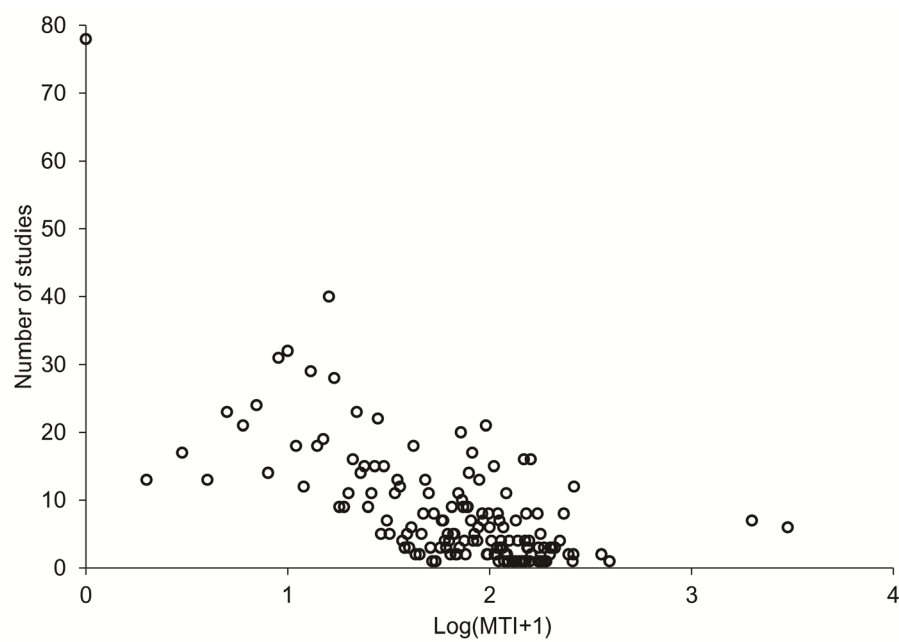
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1017 **Fig. 4**



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