

Research Article

Potential for biotic resistance from herbivores to tropical and subtropical plant invasions in aquatic ecosystems

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Abstract

Invasions of tropical and subtropical aquatic plants threaten biodiversity and cause ecological and economic impacts worldwide. An urgent question is whether native herbivores are able to inhibit the spread of these alien species thus providing biotic resistance. The potential for biotic resistance to these plants depends on plant traits that affect palatability to herbivores, i.e., plant nutritional quality and the presence of secondary metabolites related to anti-herbivory defenses. Studies across latitudinal gradients suggest that aquatic plants from lower latitudes may be less nutritious and better defended than high latitude plants. Therefore, we hypothesized that native herbivores prefer temperate plants over plants from tropical and subtropical regions which would limit the strength of biotic resistance that native temperate herbivores can provide against alien tropical and subtropical plants. Drawing upon the published literature we (1) investigated whether native temperate herbivores reduce the establishment or performance of tropical and subtropical alien plants in the field, and (2) analyzed herbivore consumption of tropical and subtropical versus temperate plants in laboratory feeding trials. In our literature survey, we found only three field studies which, in contrast to our hypothesis, all demonstrated that the native herbivores (beavers, coots or generalist insect herbivores) significantly reduced the success of invading tropical and subtropical plant species. The analysis of the feeding trials yielded mixed results. Ten out of twelve feeding trials showed that (sub)tropical and temperate plants were consumed in equal amounts by both temperate and tropical generalist ectothermic herbivores. The remaining trials showed higher consumption rate of both temperate and tropical plants by tropical snails. Although a body of evidence suggests that tropical plants are nutritionally poor and better defended (i.e., less palatable) compared to temperate plants, we conclude that in the majority of cases, herbivores would eat tropical plants as much as temperate plants. Thus, in agreement with the available field studies, evidence suggests that there is potential for biotic resistance from native generalist herbivores to tropical invasive plants in non-tropical areas.

Key words: consumption rate, feeding trial, herbivore trait, herbivory, latitudinal gradients, palatability, plant traits

Introduction

Aquatic plant invasions threaten biodiversity and cause ecological and economic impacts worldwide (Vilà et al. 2011; Hussner 2012). Invasive aquatic

plants can change community structure and composition, decrease biodiversity of aquatic communities, alter nutrient cycling and the abiotic environment, and have a negative impact on ecosystem services to humans, harming for example, fishing, navigation,

recreation activities and the esthetic value of aquatic ecosystems (Charles and Dukes 2007; Michelan et al. 2010; Vilà et al. 2011; Brundu 2015; Thomaz et al. 2015). Tropical and subtropical aquatic plants are among the world's worst invasive species (Rejmánek 2011). Notorious examples include the floating plants *Eichhornia crassipes* (Mart.) Solms, 1883, *Pistia stratiotes* L., 1753 and *Salvinia* spp., and the submerged plants *Egeria densa* Planch., 1849, *Hydrilla verticillata* (L.f.) Royle, 1839, and *Myriophyllum aquaticum* (Vell.) Verdec, 1973 (Hussner 2012; Thomaz et al. 2015).

Although freshwater ecosystems are the most threatened compared to terrestrial and marine ones (WWF 2016), and despite the prevalence of tropical invasive freshwater plant species, most invasion ecology research has been conducted in terrestrial ecosystems (Jeschke et al. 2012; Lowry et al. 2013). Moreover, the majority of studies focus on temperate species and temperate areas (Lowry et al. 2013; Evangelista et al. 2014). Therefore, the factors that may limit the success of the worst invasive freshwater plant species, which often originate from tropical and subtropical areas and are invasive elsewhere, remain largely unknown (Liu et al. 2006; Coetzee et al. 2011; Brundu 2015).

Tropical and subtropical alien plants have mainly spread due to the aquarium and ornamental trade (Martin and Coetzee 2011; Hussner 2012). Although many of these species are introduced to a new range, only a few become invasive. The failure of some alien species to either establish or spread into a new habitat is often attributed to biotic resistance (Elton 1958; Levine et al. 2004). Biotic resistance is mainly determined by ecological interactions in two layers of the food web: competition with native vegetation and consumption by native herbivores. A recent meta-analysis found that in freshwater environments biotic resistance is driven by consumption rather than competition (Alofs and Jackson 2014). However, despite the relevance of herbivory for biotic resistance (Levine et al. 2004; Alofs and Jackson 2014; Wood et al. 2017), few studies have investigated its importance in reducing the abundance of tropical and subtropical alien plant species in the field. Furthermore, most of these studies focused on biological control, i.e., the introduction of alien herbivores to reduce invading plant species (Marko et al. 2005; Coetzee et al. 2011; Tewari and Johnson 2011; Walsh and Maestro 2016). Hence, the potential of native herbivores to provide biotic resistance to tropical and subtropical alien aquatic plants is generally unexplored.

In this study, we assess whether native herbivores can provide biotic resistance to the establishment and growth of tropical and subtropical alien aquatic

plants. We consider in particular the case where tropical and subtropical plants invade non-tropical communities in which native temperate herbivores may feed on these plants and thereby prevent their establishment or reduce their performance. Biotic resistance from native herbivores will be even more effective if the herbivores prefer feeding on alien over native plants, since they will both suppress alien plants and give the native plants a competitive advantage (e.g., van Donk and Otte 1996; Parker et al. 2006). The potential for biotic resistance to alien plants depends on plant traits that affect palatability to herbivores. Here, we consider the two most important traits: plant nutritional quality (often expressed as plant C:N ratios or %N) and the presence of secondary metabolites related to anti-herbivory defenses (Cronin et al. 2002; Dorenbosch and Bakker 2011; Gross and Bakker 2012). Studies across latitudinal gradients suggest that aquatic plants at lower latitudes may be less nutritious and better defended than high latitude plants (Pennings et al. 2001, 2007; Morrison and Hay 2012). Therefore, we hypothesize that herbivores native to temperate regions prefer temperate plants over plants from tropical and subtropical regions which would limit the strength of biotic resistance that temperate native herbivores can provide against tropical and subtropical alien plants.

We draw upon the published literature to compile multiple lines of evidence to estimate the potential for biotic resistance by native temperate herbivores to tropical and subtropical aquatic plant invasions. We (1) investigated whether native temperate herbivores reduce the establishment or performance of tropical and subtropical alien plants in the field and (2) analyzed herbivore consumption of tropical and subtropical versus temperate plants in laboratory feeding trials. We summarize our findings by predicting the scope for biotic resistance to tropical and subtropical macrophyte invasions based on plant and herbivore traits, identifying research gaps and proposing future directions to test the biotic resistance hypothesis.

Methods

Literature searches

Field studies

We searched the literature for field studies that tested biotic resistance by native temperate herbivores to tropical and subtropical alien aquatic plant species. First, we searched for studies in previous meta-analyses (Parker et al. 2006; Alofs and Jackson 2014; Wood et al. 2017). In addition, we carried out a literature

search in the ISI Web of Science (1945 – April 2017) using the following combination of keywords (“biotic resistance” OR “biotic resistance hypothesis” OR “diversity-invasibility hypothesis” OR “invasion resistance”) AND (plant* OR “aquatic plant*” OR macrophyte* OR producer OR vegetation), which yielded 639 journal articles. From this set, we considered field studies that reported measurements of establishment and performance of tropical and subtropical alien aquatic plant species in the presence and absence of native herbivores.

Feeding trials

We searched the publications on no-choice feeding trials with aquatic herbivores that measured the amount of aquatic plants consumed (e.g., consumption rate: g plants consumed $\text{g}^{-1}(\text{animal weight}) \text{day}^{-1}$, animals feeding: %). We included in our analysis only studies that included both temperate and tropical or subtropical aquatic plant species.

Aquatic plants and documentation of their native distribution

The aquatic plants considered in this study are vascular aquatic photosynthetic organisms that depend on humid environments to survive, including hydrophytes and amphibious plants, but also some helophytes “whose photosynthetically active parts are permanently, or at least for several months each year, submerged or floating on the water surface” (Cook et al. 1974). They colonize a variety of running waters and wetlands, such as swamps and salt marshes, lakes, coastal lagoons and floodplains.

We documented the native latitudinal range of the plants used in the selected feeding trials based on the literature (Stuckey 1974; Orchard 1979; Hussner 2012; Redekop et al. 2016; Grutters et al. 2017) and online databases (Agricultural Research Service – Germplasm Resources Information Network (ARS-GRIN, <https://npgsweb.ars-grin.gov>), eFloras, International Union for Conservation of Nature’s Red List of Threatened Species (IUCN Red List, <http://www.iucnredlist.org>), Global Biodiversity Information Facility (GBIF, <http://www.gbif.org>), New Zealand Plant Conservation Network (NZPCN, <http://www.nzpcn.org.nz>) and United States Department of Agriculture (USDA, <http://plants.usda.gov>) – Natural Resources Conservation Service). We classified the latitudinal range of species based on whether their native distribution mainly lies in frost-free (tropical and subtropical, hereafter referred to as “Tropical”) or mainly in frost-prone (hereafter referred to as “Temperate”) regions (Supplementary material: Table S1).

Data analysis

We re-analyzed the results of the studies that performed feeding trials to specifically test whether herbivore consumption rates differed on tropical versus temperate plants. For each study, we classified the plant species used according to their native distribution. Species whose latitudinal range could not be established owing to their wide native distribution, as well as macro-algae species, were excluded from the analyses. We defined a feeding trial as a separate experiment in which the consumption of multiple temperate and tropical plant species by a single herbivore species was measured. One study could therefore include more than one feeding trial: for example, Parker and Hay (2005) performed three feeding trials, testing consumption rates by three different species of herbivores. Each feeding trial was analyzed separately because the consumption rate measurements were not directly comparable on a single axis due to the different parameters measured in the studies. Thus, for each feeding trial, we tested differences between means of consumption of tropical and temperate plant species groups using a non-parametric Wilcoxon Rank-Sum test. The mean group consumption of tropical versus temperate plant species was calculated by extracting the mean consumption of each plant species from the original papers and averaging these over the number of tropical plant species and the number of temperate plant species used in the respective feeding trial. When the same plant species was measured multiple times in the same feeding trial, we averaged their mean consumption rate to determine a single value per species. The mean consumption rate per plant species could be extracted directly from papers when they were given in Tables, or using DataThief software when they appeared in graphs or figures. Statistical analyses were performed in R version 3.3.2. Data are available in Supplementary material Table S3, S4 and S5.

Results

Field studies testing biotic resistance to tropical plants

We found only three studies that addressed the effect of native herbivores on tropical invasive plant species in the field. All three found evidence that native herbivores may contribute to reducing invasion success.

Parker et al. (2007) excluded the native North American beaver (*Castor canadensis* (Kuhl, 1820)) from two wetlands near Atlanta, Georgia, USA (33°54'N; 84°26'W) over 2 years. Total aquatic plant biomass was reduced by 60% through beaver herbivory compared to the enclosures, which also resulted

in severely altered plant species composition. Beavers demonstrated feeding selectivity as they reduced the abundance of the South-American alien plant species *M. aquaticum* in particular by nearly 90%. This species was 7.9 fold more abundant in exclosures compared to beaver foraging areas.

Another exclosure study demonstrated that herbivory by American coots (*Fulica americana* (Gmelin, 1789)) had negative impacts on the invasive Eurasian *H. verticillata* in Lake Fairfield, Texas, USA (31°47'N; 96°03'W) during periods of high wetland bird activity (Esler 1989). After six months, *H. verticillata* biomass was over three-fold greater in exclosures compared to plots accessible by coots.

In China, generalist native insect herbivores were found to disproportionately reduce the abundance of the invasive South-American *Alternanthera philoxeroides* (Mart.) Griseb relative to native wetland plant vegetation (Fan et al. 2016). Exclosure studies on islands in Liangzi Lake (30°16'N; 114°34'E) revealed that shoot biomass of *A. philoxeroides* was almost twice as high after five months compared to plots open to native insect herbivores. *Alternanthera philoxeroides* is consumed by the native insect *Atractomorpha sinensis* (Bolívar, 1905), the larvae of *Cassida nebulosi* (Linnaeus, 1758), *Spoladea recurvalis* (Fabricius, 1775), *Pieris rapae* (Linnaeus, 1758) and some aphids and spiders (Fan et al. 2016). The higher consumption of *A. philoxeroides* compared to the native plant species was positively correlated with its higher leaf nitrogen concentration.

Feeding trials

We found nine studies, containing twelve feeding trials that included both temperate and tropical plants that determined aquatic herbivore consumption rates on aquatic plants. We found that herbivores generally seemed not to consume more temperate than tropical aquatic plants (Figure 1). This was valid across a range of herbivores varying from invertebrates, such as four species of snail (*Pomacea insularum* (d'Orbigny, 1839), *Pomacea canaliculata* (Lamarck, 1822), *Radix swinhoei* (Adams, 1866), *Lymnaea stagnalis* (Linnaeus, 1758)), two species of crayfish (*Procambarus spiculifer* (LeConte, 1856), *Procambarus acutus* (Girard, 1852)), and two species of insects (*Paraponyx stratiotata* (Linnaeus, 1758), *Hygraula nitens* (Butler, 1880)); and one vertebrate species (grass carp *Ctenopharyngodon idella* (Valenciennes, 1844)). These studies were conducted at a variety of latitudes (e.g. from temperate North America to tropical Asia) and with very different selections of plant species. Across all twelve feeding trials presented in Figure 1, in only one was the mean consumption rate on temperate

plants significantly higher than that of tropical plants, by the tropical herbivorous snail *P. canaliculata* ($n_{\text{temperate}} = 23$, $n_{\text{tropical}} = 15$, $W = 248$, $P = 0.02$, Figure 1 panel 3). However, another feeding trial showed the opposite pattern in that the consumption rate of the tropical snail *P. insularum* was higher on tropical than on temperate plants ($n_{\text{temperate}} = 3$, $n_{\text{tropical}} = 8$, $W = 8$, $P = 0.04$) (Figure 1, panel 2). In the other ten feeding trials, there was no difference between temperate and tropical plant consumption rates (Figure 1 all other panels), regardless of whether the herbivores themselves were predominantly tropical or temperate (Table 1).

Discussion

Herbivory is an important biotic process in aquatic ecosystems because it regulates plant abundance and may limit the invasion success of aquatic plants (Alofs and Jackson 2014; Bakker et al. 2016; Wood et al. 2017). We found that field studies that tested whether consumption by native herbivores can limit or decrease the establishment and growth of tropical alien aquatic plants are scarce as most studies focus on temperate species (Alofs and Jackson 2014; Evangelista et al. 2014). Even though our very broad search yielded 639 hits, only 3 provided field tests including native herbivores and tropical aquatic plant species. In contrast to our hypothesis, these studies found that native beavers, coots or insects significantly reduced the success of invading plant species. The analysis of laboratory feeding trials showed that tropical and temperate plants were consumed in similar amounts in ten out of twelve trials. In one study, tropical plants were consumed more than temperate plants while another showed herbivores consumed more temperate plants. We conclude that in the majority of cases herbivores would eat tropical plants as much as temperate plants, and thus may be able to provide biotic resistance to tropical plant invasions, which is also in contrast to our hypothesis.

Plant perspective

Herbivore consumption rate and preference depends on plant palatability which is determined by multiple plant traits and their interactions (Agrawal 2011; Grutters et al. 2017). The main traits that determine aquatic plant palatability are plant nutritional value and the presence of anti-herbivore defenses (Cronin et al. 2002; Sotka et al. 2009). Plants with higher nutritional quality tend to support higher consumption rates (Wong et al. 2010; Dorenbosch and Bakker 2011; Bakker and Nolet 2014) and better herbivore performance, such as faster growth, longer survival

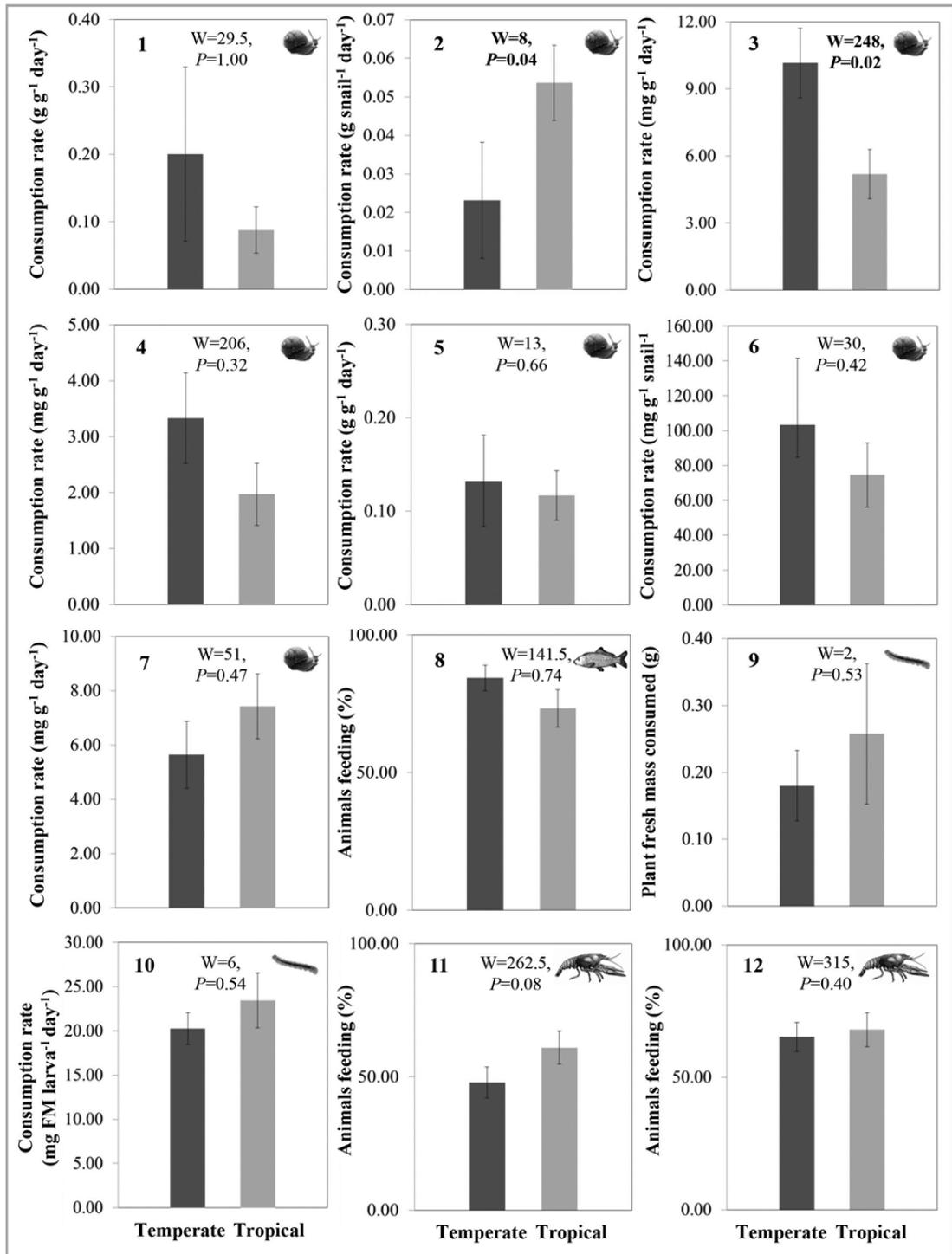


Figure 1. Summary of no-choice feeding trials showing average consumption rates (mean ± SE) on aquatic plants from temperate (dark grey bars) and tropical (including subtropical) latitudinal range, here referred to as tropical (light grey bars). Each graph corresponds to one feeding trial (see Table 1 for the number of temperate and tropical plant species included in each feeding trial). Animal symbols indicate the functional group of plant consumers used in the feeding trials, but they do not reflect the individual species. See Table 1 for details of the individual feeding trials. A non-parametric Wilcoxon Rank-Sum test was used to test for differences in consumption between temperate and tropical plant species in each panel. Data are available in Supplementary material Table S3, S4 and S5.

Table 1. Summary of the data presented in Figure 1, indicating the feeding trial studies from which the data were extracted, names of herbivore species, their native distribution and number of temperate and tropical plant species included in the analysis. The native distribution of individual plants species is given in Supplementary material Table S1 and S2.

Graph number	Feeding trial studies	Herbivore species	Native distribution of herbivore	Number of temperate plant species included	Number of tropical plant species included*
1	Baker et al. (2010)	<i>Pomacea insularum</i>	Tropical and subtropical America	5	12
2	Burlakova et al. (2009)	<i>Pomacea insularum</i>	Tropical and subtropical America	3	8
3	Grutters et al. (2017)	<i>Pomacea caniculata</i>	South America	23	15
4	Grutters et al. (2017)	<i>Lymnaea stagnalis</i>	Europe and Asia	23	15
5	Qiu and Kwong (2009)	<i>Pomacea caniculata</i>	South America	3	7
6	Wong et al. (2010)	<i>Pomacea caniculata</i>	South America	3	15
7	Xiong et al. (2008)	<i>Radix swinhoei</i>	Asia	9	14
8	Parker and Hay (2005)	<i>Ctenopharyngodon idella</i>	Asia	12	22
9	Grutters et al. (2016)	<i>Parapoynx stratiotata</i>	Europe	6	3
10	Redekop et al. (2016)	<i>Hygraula nitens</i>	Australasia	2	4
11	Parker and Hay (2005)	<i>Procambarus spiculifer</i>	North America	28	26
12	Parker and Hay (2005)	<i>Procambarus acutus</i>	North America	28	26

*: including subtropical species (see methods).

and higher fecundity (Grutters et al. 2016; Lach et al. 2000; Ho and Pennings 2013). Similarly, the higher consumption of the alien *A. philoxeroides* by native insects coincided with its higher leaf nitrogen concentration (Fan et al. 2016).

Plant nutrient concentration and defenses differ systematically along a latitudinal gradient. Tropical aquatic plants are exposed to high temperatures, which directly influences the length of the growing season and the plant's physiology. This usually results in a low nutritional content (Reich and Oleksyn 2004), which may make the plants less attractive for herbivores. Accordingly, two crayfish species strongly preferred high latitude over low latitude plants after the plants' structural characteristics were removed by grinding them (Morrison and Hay 2012). Similarly, herbivores significantly preferred plant material from higher latitudes in 27 (59%) of 48 studies analyzed (Moles et al. 2011).

Whereas several studies that we analyzed used feeding trails to investigate whether herbivores prefer native or exotic non-native plants (Lach et al. 2000; Xiong et al. 2008; Burlakova et al. 2009; Qiu and Kwong 2009; Baker et al. 2010), only one study was designed to investigate whether herbivores prefer temperate or tropical plants (Grutters et al. 2017). In this study, both generalist herbivores consumed more temperate than tropical plants, which was positively related to plant nitrogen content and negatively to total phenolic compounds (Grutters et al. 2017).

Hence, the general patterns in plant traits suggest lower palatability of tropical plants relative to temperate plants (Table 2). However, overall, we

found that herbivores seem to consume temperate and tropical aquatic plants mostly in equal amounts. Given that none of the studies, except Grutters et al. (2017), aimed to test the consumption rates on tropical versus temperate plants, variation in the data due to unequal and sometimes small sample sizes for temperate and tropical plants could possibly explain the lack of consistent patterns. The field studies demonstrated strong consumption of tropical plants by temperate herbivores, but here only one tropical species per study was available to the herbivores. Furthermore, the herbivores were different among the field studies and differed from those used in the feeding trials. The traits of the herbivores may also play a role in their potential to provide biotic resistance.

Herbivore perspective

Latitudinal pattern of herbivory

Biotic interactions, such as predation, competition and herbivory are widely assumed to be more intense and specialized in tropical regions due to the lack of freezing winters and the favorable and predictable climate (Dobzhansky 1950; Schemske et al. 2009). Studies in a wide range of ecosystems have shown that herbivore consumption pressure increases toward the equator (Coley and Aide 1991; Bolser and Hay 1996; Coley and Barone 1996; Pennings et al. 2007, 2009), though others argue that further investigation is needed (Moles and Ollerton 2016). Despite the debate, the majority of studies suggest that herbivore grazing pressure is less in temperate than tropical areas, which would reduce

Table 2. Properties of plants and herbivores and their influence on the potential for biotic resistance by native temperate herbivores to tropical and subtropical plant invasion.

Property	Contribution to potential for biotic resistance at high latitude	Mechanism	References
Plant palatability	Negative	Tropical plants have lower nutritional quality (i.e., low C:N, %N); are better defended, and have lower herbivore consumption rates than temperate plants	Lach et al. (2000); Xiong et al. (2008); Burlakova et al. (2009); Qiu and Kwong (2009); Baker et al. (2010); Morrison and Hay (2012)
Herbivore pressure (i.e., herbivore abundance and grazing damage)	Negative	At higher latitudes there are lower herbivory rates resulting in lesser top-down control than at lower latitudes	Pennings et al. (2009); Gonzalez-Bergonzoni et al. (2012)
Herbivore thermoregulation	Negative	Ectothermic herbivores feed less or become inactive in cold environments	Seals et al. (1997); He and Silliman (2016)
Herbivore body size	Positive	Animals in colder environments are larger; larger animals can live of a diet of plant material	Clements et al. (2009); Wood et al. (2012)
Herbivore diet breadth	Negative	Lower amount of plants in the diet of omnivores at higher latitudes	Jeppesen et al. (2010); Gonzalez-Bergonzoni et al. (2012)

the potential for temperate herbivores to provide sufficient biotic resistance to invasions of tropical plants (Table 2).

Herbivore traits

Herbivore consumption of aquatic plants is generally determined by the density of herbivores and their traits including taxonomic identity, body size and diet breadth (Bakker et al. 2016; Wood et al. 2017).

Higher herbivore density leads to a stronger reduction of plant biomass (Kelkar et al. 2013; Wood et al. 2017). Herbivore taxa differ in their effect on plant abundance: echinoderms, mollusks and fish have a relatively large impact compared to insects and birds (Wood et al. 2017). A recent meta-analysis on consumer control of vegetation in coastal wetlands suggested that animal thermoregulation also plays a role: top-down control by ectothermic rather than endothermic herbivores increases with increasing annual mean temperature, resulting in weaker top-down control at higher latitudes (He and Silliman 2016). Ectothermic herbivores feed less or become inactive in cold environments reducing overall grazing pressure (Seals et al. 1997; Vejříková et al. 2016). As a result, the potential for biotic resistance from herbivores may be lower at higher latitudes (Table 2), unless endotherms become more influential.

Most aquatic plant consumers are omnivorous animals and their body size is a strong predictor of the degree of plant consumption (Bakker et al. 2016).

In water birds, the bigger the animal, the more plant biomass is included in the diet, relative to animal prey. The smallest water birds include a lot of animal prey in their diet, the larger ones eat animal prey and seeds and the largest consume mostly plants, with a lot of green leafy material (Wood et al. 2012). Similarly, in fish, larger fish consume more plant material. This can be seen both in fish ontogeny, where only the older, and thus larger, fish consume plant material, as well as between species, where especially in cold water conditions, only large fish species can live of a diet of plant material (Clements et al. 2009). The positive relationship between body size and the ability to live on green plant material can be explained by the length of the digestive tract. Larger animals have longer digestive tracts, allowing them more time to break down plant cell walls and extract their nutrients (Demment and Van Soest 1985). As animals tend to be bigger at higher latitudes, this would favor their impact on aquatic plants and their potential for providing biotic resistance (Table 2).

Specialist herbivores are rare in aquatic systems (Lodge et al. 1998; Shurin et al. 2006) hence introduced aquatic plant species are less likely to benefit from natural enemy release (Keane and Crawley 2002; Xiong et al. 2008). Instead, with most aquatic herbivores being generalists, they may provide biotic resistance through non selective feeding, thus consuming most plant species, including alien plants (Table 2). As generalist herbivores can consume significant amounts of aquatic plants their potential to provide biotic resistance can be high (Cyr and

Pace 1993; Bakker et al. 2016; Wood et al. 2017). This is in line with the field studies that we analyzed, where generalist herbivores reduced the abundance of alien tropical plants.

As most aquatic plant consumers are omnivorous, to predict grazing pressure across latitude it is very important to consider the distribution of feeding modes. At lower latitudes, there is higher richness and abundance of herbivorous and omnivorous fish, whereas carnivorous fish are more abundant towards the poles (Gonzalez-Bergonzoni et al. 2012; Jeppesen et al. 2010). These patterns are observed both at the level of fish communities and within a single species, such as the marine *Girella nigricans* (Ayres, 1860), which includes more plants in its diet at lower compared to higher latitudes (Behrens and Lafferty 2012). This distribution of feeding modes suggests lower plant consumption at higher latitudes, reducing the potential for biotic resistance (Table 2).

Predicting the scope for biotic resistance to tropical plant invasions

Macro-ecological latitudinal patterns suggest that tropical plants have lower nutrient concentrations and higher defenses, and are less palatable than temperate plants (Table 2). Furthermore, herbivore abundance is lower at higher latitudes, more animals are carnivorous and ectotherms in general eat less at colder temperatures, all resulting in lower grazing pressure on plants. Together this suggests that temperate herbivores have less potential to provide biotic resistance to tropical plants, as they consume limited amounts of plants and would not select these plant species. Only the generally larger body size of temperate plant consumers would favor their potential to provide biotic resistance.

Whereas these macro-ecological patterns are well-established, interestingly, our analysis of empirical data does not support the general idea that the potential for biotic resistance by native temperate herbivores would be low. Instead, we found that native herbivores can provide strong biotic resistance to tropical plants, particularly in the field studies. Also, in the feeding trials herbivores were rather unselective, and thus would have the potential to provide biotic resistance, or at least to inhibit the spread of alien tropical plants to a certain extent.

Knowledge gaps and future research

Our current understanding of biotic resistance by native herbivores to tropical invasive aquatic plants is constrained by a lack of empirical studies. Current gaps in this regard are the lack of appropriate experimental designs to compare herbivory on tropical versus

temperate macrophytes. Furthermore, most studies are exclusively temperate. A solution is to design experiments including plant species from both latitudes in a balanced design, i.e. with equal amounts of temperate and tropical plant species to allow statistical testing of the results. In addition, the lack of field studies strongly limits our ability to judge the quantitative strength of herbivore impact on tropical plant invasions in aquatic systems and hence their potential as a natural defense system. Plant-species interactions are always context dependent. In this respect, the role of endotherm herbivores should be further investigated: in temperate areas especially, endotherms such as water birds and mammals, particularly large species, may have the strongest potential to provide biotic resistance. Moreover, to reach firm conclusions on the role of herbivory on invasiveness of macrophytes, experiments should be conducted in both their native and introduced ranges. For example, to conclude that invasion success is explained by enemy release, it is necessary to show that the growth of macrophytes in the absence of herbivores is higher in their invasive than in their native range (see Prior et al. 2015). In this case, experiments should measure plant traits related to invasion success for the same plant species, in the native and invasive range, and in the presence and absence of herbivores (Prior et al. 2015). This could be achieved by international collaborations employing similar protocols in different regions, such as described for feeding trials (Elger and Barrat-Segretain 2002; Burlakova et al. 2009). Experiments designed to investigate the joint effects of herbivory and abiotic conditions on invasiveness of macrophytes is also recommended, since these factors interact (e.g., Coetzee and Hill 2012). In summary, future studies on the role of native herbivores providing biotic resistance to plant invasions are urgently needed. Our study provides the relevant parameters to measure as well as hypotheses that can easily be tested in feeding trials or field studies.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Metadata of the plant species used in the no-choice feeding trial studies included in our analysis.

Table S2. Sources of information for Table S1.

Table S3. Explanatory notes for Table S5.

Table S4. Plant identification code for Table S5.

Table S5. Data extracted from the no-choice feeding trial studies included in our analysis.

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