

1 Running head: temperature drives asymmetric competition

2

3 **Temperature drives asymmetric competition between alien and indigenous**
4 **freshwater snails (*Physa acuta* vs. *Physa fontinalis*)**

5 Denise Früh^{1,2*}, Peter Haase¹, Stefan Stoll¹

6

7 ¹Senckenberg Research Institute and Natural History Museum Frankfurt, Department of River
8 Ecology and Conservation, Clamecyst. 12, 63571 Gelnhausen, Germany.

9 ²North Rhine-Westphalia State Agency for Nature, Environment and Consumer Protection
10 (LANUV), Auf dem Draap 25, 40221 Düsseldorf, Germany.

11

12 E-Mail contacts: denise.frueh@lanuv.nrw.de, peter.haase@senckenberg.de,
13 stefan.stoll@senckenberg.de

14

15

16

17

18 **Keywords:** alien species, benthic invertebrates, species interaction, multiple stressors, climate
19 change

20 **Abstract**

21 Biological invasion represent one of the major threats to global biodiversity as alien species
22 often displace indigenous species. However, knowledge of the mechanisms behind such
23 displacements and the driving factors of the competitive superiority of the alien species still
24 remain rare. In our study we combined analysis of field data and laboratory experiments
25 examining species interactions, to investigate the impact of temperature in the case of the
26 alien freshwater snail *Physa acuta* that is held responsible for the decline of indigenous snail
27 *Physa fontinalis* in Europe. From field data, we identified higher temperature as the most
28 important difference between sites populated by alien *P. acuta* and those where indigenous
29 *P. fontinalis* occurred. Results of the species interaction experiment conducted at 15, 20, and
30 25 °C confirmed the hypothesis that the competitive superiority of *P. acuta* over *P. fontinalis*
31 increases at warmer temperatures. In single species treatments, increasing temperature
32 stimulated both species to grow faster and reach greater shell heights. Coexistence treatments
33 revealed an asymmetric competitive interaction between the two snail species. In both
34 species, the density of conspecifics did not affect snail growth; however, density of
35 heterospecifics affected the growth. At 15 °C, the presence of heterospecifics stimulated the
36 growth of both species, while at higher temperatures the presence of heterospecifics
37 stimulated the growth in *P. acuta*, but inhibited in *P. fontinalis*. Our study shows that
38 temperature can be a powerful driver of the outcomes of alien and indigenous species'
39 competition by driving asymmetric interaction. Further our results point up that the
40 environmental context cannot be disregarded when investigating the interaction between alien
41 and indigenous species, and predict alien species success and impact.

42 **Introduction**

43 Biological invasion is one of the major threats to global biodiversity (Lövei 1997, Vitousek
44 et al. 1997, Dextrase and Mandrak 2006) and invasion rates are particularly high in freshwater
45 (Sala et al. 2000). In Germany alone, to date, about 120 invertebrate species have invaded
46 freshwater systems, the largest share being molluscs and crustaceans (Strayer 2010). Negative
47 effects of alien species on indigenous species (Mack et al. 2000) may arise from a number of
48 processes leading to irreversible changes in ecosystems and to declines of indigenous species.
49 For example, alien species can alter habitat structures (e.g. Schmidlin et al. 2012), introduce
50 diseases (e.g. Bacela-Spychalska et al. 2012), exert predation pressure (e.g. van der Velden
51 et al. 2009), and compete with indigenous species for food (e.g. Morisson and Hay 2011). In
52 this context, Covich (2010) showed that alien species can change competitive dominance
53 relationships among gastropods and cause major losses of indigenous species.

54 Several factors may contribute to the success and competitive superiority of alien versus
55 indigenous species. They often have favorable life history traits such as high growth rate,
56 early maturation, and high fecundity (e.g. Grabowski et al. 2007). Moreover, aliens often have
57 more flexible diets (Boland et al. 2008), a greater ability to procure food resources (Krist and
58 Charles 2012), and to use available resources more efficiently (Morrison & Hay 2011).
59 Finally, alien species often have higher tolerances to pollution (Vermonden et al. 2010). In the
60 latter context, Früh et al. (2012a) showed that degraded freshwater habitats are more easily
61 invaded by alien species, where increases in salinity and temperature favoured invasions.
62 Verbrugge et al. (2012) showed that alien molluscs could withstand warmer temperatures than
63 indigenous molluscs and may consequently be favoured by increasing temperature. Similarly,

64 Fröh et al. (2012b) showed that crustaceans and molluscs are similarly favoured by
65 temperature increases.

66 These findings demonstrate that temperature acts as one of the key factors driving the success
67 of alien species. Consequently, increases of temperature due to climate change or other
68 anthropogenic alteration are expected to favour biological invasion. Thus with higher
69 temperatures the pool of potential invaders is enlarged, habitats are more likely to be invaded,
70 the establishment success of invaders is higher, and the outcomes of interspecific interactions
71 are shifted in the invaders favour (Rahel and Olden 2008, Walther et al. 2009). Therefore it is
72 important to analyse how increases in temperature may drive the competitive interactions
73 between alien and indigenous species.

74 The present study examines the effect of temperature on competitive interactions between the
75 acuta bladder snail, *Physa acuta* and the common bladder snail, *Physa fontinalis*. The former
76 species is an alien species able to rapidly spreading to and colonizing new areas, particularly
77 disturbed environments where it can obtain high abundance (Brackenbury and Appleton
78 1995). This alien species is of global concern because *P. acuta* has been spread worldwide via
79 navigation water ways and /or by the ornamental trade (Winterbourn 1980, Appleton 1995,
80 Kinzelbach 1995, Appleton 2003, Brackenbury et al. 2009). It is considered as one of the
81 most ubiquitous aquatic macroinvertebrates in the world (Dillon et al. 2002).

82 Specimens of *P. acuta* observed in Europe may originate from southeastern Europe (Cope and
83 Winterbourn 2004) or more likely North America (Dillon et al. 2002, Oscoz et al. 2010).

84 Impacts on indigenous species have been reported for example in South Africa, New Zealand
85 and Australia (Winterbourn 1980, Brackenbury and Appleton 1995, Zukowski and Walker
86 2009). In this context, studies from Italy and France showed that the expansion of *P. acuta*

87 was related to a decline of the indigenous species *P. fontinalis* (Manganelli et al. 2000,
88 Mouthon and Daufresne 2010). In parts of its distribution range, *P. fontinalis* has already been
89 included in Red Lists (Frank and Reischütz 1994, Turner et al. 1994, Beran et al. 2005,
90 Jungbluth and von Knorre 2009). However, as is the case in most displacements of indigenous
91 by alien species, knowledge of the interaction mechanisms between *P. acuta* and *P. fontinalis*
92 and factors which influence this interaction is still lacking.

93 Therefore, using a two-step approach consisting of analysis of field data on the occurrence of
94 both species in regard to different physico-chemical variables and subsequent species
95 interaction experiments in the laboratory we tested following hypotheses.

96 (1) Temperature is one of the most important environmental variables determining the
97 occurrence of *P. acuta* vs. *P. fontinalis*.

98 (2) Consequently changes in temperature modify the competitive interaction between *P. acuta*
99 and *P. fontinalis*.

100 (3) Increasing temperature drives the competitive superiority of *P. acuta* against *P. fontianlis*.

101 **Methods**

102 **Field data**

103 To pinpoint the most important environmental variables that determine the occurrence of
104 *P. acuta*, *P. fontinalis*, and both species in coexistence we analyzed field data on species
105 occurrence in dependence of eight physico-chemical variables, pH, temperature, ammonium,
106 chloride, phosphate, nitrite, total organic carbon (TOC), and oxygen. We derived exclusive
107 occurrence points of *P. acuta* (n = 25) and *P. fontinalis* (n = 51) as well as occurrence points
108 of both species in coexistence (n = 6) from a database (unpublished data from State Agency
109 for Nature, Environment and Consumer protection North Rhine Westphalia). This database
110 contains benthic invertebrate monitoring data from the years 2000 to 2011 in North Rhine
111 Westphalia, Germany, using the German standard multi-habitat benthic invertebrate sampling
112 method developed by Haase et al. (2004). We selected only sites where physico-chemical
113 water measurements existed in the same database. As a minimum requirement, physico-
114 chemical measurements had to be conducted at least 10 times at even intervals throughout the
115 year. For the analysis, we used the annual averages of each physico-chemical variable.

116 For statistical analysis of the field data, we categorized species occurrence points as either
117 *P. acuta*-presence-sites (*P. fontinalis*-absence-sites), *P. fontinalis*-presence-sites (*P. acuta*-
118 absence-sites) or coexistence sites. To identify the most predictive physico-chemical variables
119 for occurrence of *P. acuta*, *P. fontinalis*, and coexistence of both species we calculated a
120 canonical correspondence analysis (CCA). Significance of environmental variables was tested
121 using a forward selection and 999 Monte Carlo permutations under full model conditions. We
122 down-weighted rare site-categories, as their number was unequal. In the model, species
123 occurrence data served as dependent variables with physico-chemical variables acting as

124 predictor variables. For statistical analysis, we log (x+1)-transformed the measures of
125 ammonium, chloride, phosphate, nitrite, TOC, and oxygen. The CCA was calculated with
126 Canoco 4.5 (Wageningen UR - University & Research centre, Netherland).

127

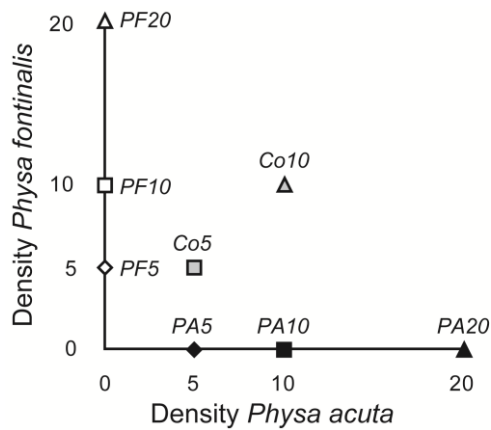
128 **Species interaction experiment**

129 We established the cultures of both snail species. Specimens of *P. acuta* were collected in the
130 Fulda River and specimens of *P. fontinalis* in the Eder River, Germany. In the laboratory, we
131 maintained the snails in 12-liter aquaria with aerated tap water in a controlled environmental
132 room (20 °C, 16:8 light:dark cycle). The cultures were fed ad libitum with commercial fish
133 flakes 3 times a week and we renewed the water of the aquariums once a week.

134 For the experiment, we used neonate snails of both snail species. Neonates were obtained
135 from 10 adults cultured in 500 ml of aerated tap water in 1-liter jars. We also fed these snails
136 ad libitum with commercial fish flakes and renewed the water once a week. We checked these
137 jars every day for egg masses which were removed and incubated in separate jars. Further we
138 checked egg masses daily for neonates. Shell heights of the neonates were measured under the
139 stereomicroscope (Olympus SZX 12; Olympus, Hamburg, Germany) and the neonates were
140 allocated randomly to experimental jars (again, 1-liter jars filled with 500 ml aerated tap
141 water) according to the experimental design (Fig. 1).

142 This design comprised single-species treatments with different densities as well as
143 coexistence treatments with different densities of both species. Densities of single-species
144 treatments were 5, 10, and 20 snails per jar (hereafter called *PA5*, *PA10*, *PA20* for treatments
145 using *P. acuta* and *PF5*, *PF10*, *PF20* for treatments using *P. fontinalis*). For the coexistence

146 treatment two different density combinations were used: 5:5 and 10:10 snails of both species,
147 hereafter called *Co5* and *Co10*. Each treatment was replicated 6 times and tested at 3 different
148 temperatures, 15, 20, and 25 °C; however 2 replicates of *Co10* at 15°C failed during the
149 experiment und were therefore excluded from the analysis.



150

151 **Figure 1** Different density treatments used in the species competition experiment. Single species treatments with
152 only *Physa acuta* or *Physa fontinalis* are marked with *PA* and *PF*, respectively, coexistence treatments are
153 marked with *Co*. All treatments were replicated six times at three temperature levels, 15, 20, and 25 °C.

154

155 We choose these three temperature regimes to represent the water temperature in the snail's
156 habitats during a cool (15 °C) and a hot (20 °C) summer today and during a hot summer day
157 in the future (25 °C). Temperature in each jar was maintained with heating or chilling rods
158 and temperature was controlled every day using a digital hand thermometer. The maximum
159 deviation recorded was ± 1 °C. We conducted the experiment under controlled light
160 conditions (16:8 hours light:dark regime). Throughout the experiment, we measured the shell
161 height weekly under the stereomicroscope and recorded mortality. We replaced dead snails by
162 individuals of the same species, size and age that were marked with nail polish. At the end of
163 the experiment, marked snails were not taken into account within analyses. The experiment
164 was terminated after 5 weeks. The snails in the experiment were fed with a constant food

165 concentration of 1 mg commercial fish flakes per snails per day. The water within the
166 experimental jars was renewed weekly after measuring the snail's shell heights.

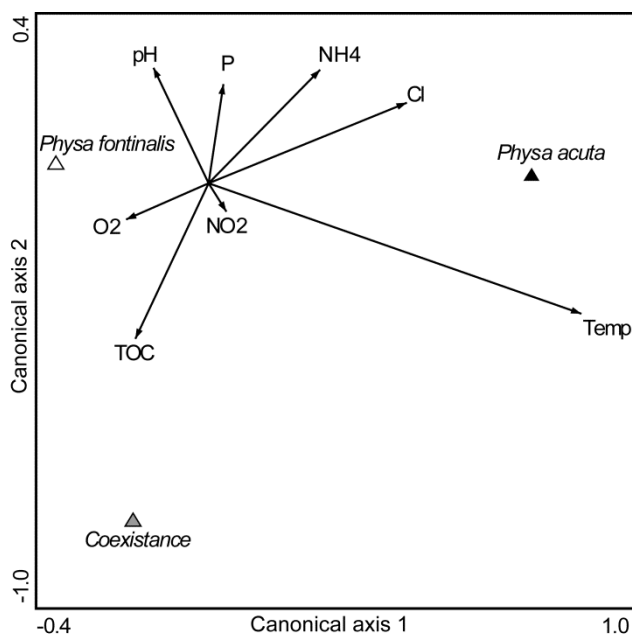
167 For statistical analysis, we $\log(x+1)$ -transformed the lengths of snails were. To analyze the
168 effect of temperature on species growth rates we used repeated measures analysis of variance
169 (rm-ANOVA) with densities of conspecifics and heterospecifics as additional predictor
170 variables. Rm-AVOVAs were calculated for both species separately. We performed these
171 analyses with STATISTICA 8 (StatSoft, Inc., Tulsa, Oklahoma, USA). To examine the effect
172 of interspecific interaction in relation to temperature, we compared the average final shell
173 heights (day 35) of *P. acuta* vs. *P. fontinalis* in single-species (PA10, PF10, PA20, PF20) and
174 coexistence treatments (Co5, Co10) at the three experimental temperatures 15, 20, and 25 °C.
175 To this end, we calculated the differences in the average shell height between *P. acuta* and
176 *P. fontinalis* for all replicate combinations within each of the corresponding treatment of the
177 two species (PA10 vs. PF10, PA20 vs. PF20, *P. acuta* of Co5 vs. *P. fontinalis* of Co5,
178 *P. acuta* of Co10 vs. *P. fontinalis* of Co10, at each of the three temperatures, respectively).

179 From this pairwise comparison of replicates, we further calculated the mean differences and
180 standard errors for each of the corresponding treatments.

181 **Results**

182 **Field data**

183 Analysis of physico-chemical variables at occurrence sites of *P. acuta* and *P. fontinalis*
184 showed that temperature was by far the most important variable differentiating between
185 *P. acuta*, *P. fontinalis* and coexistence sites (Fig. 2, Table 1.). Sites where *P. acuta* occurred
186 were significantly warmer (annual mean temperature about 14 °C) compared to sites where
187 *P. fontinalis* (annual mean temperature about 12.5 °C) were found. Annual mean temperature
188 of coexistence sites were at an intermediate value of about 13 °C.



190

191 **Figure 2** Canonical correspondence analyses (CCAs) biplot of the occurrence of *Physa acuta*, *Physa fontinalis*,
192 and coexistence of both species. Environmental variables were: pH, temperature (Temp), ammonium (NH₄),
193 chloride (Cl), phosphate (P), nitrite (NO₂), total organic carbon (TOC), and oxygen (O₂).

194

195

196 **Table 1** Results of canonical correspondence analysis (CCA) and conditional effects in forward selection. The
 197 eigenvalues of the first two canonical axis (CA) and explained variance by the CAs and the order of the
 198 environmental variables determining the occurrence of *Physa acuta*, *Physa fontinalis*, and coexistence of both
 199 species are given. Environmental variables were: pH, temperature (Temp), ammonium (NH₄) chloride (Cl),
 200 phosphate (P), nitrite (NO₂), total organic carbon (TOC), and oxygen (O₂).

	CA	
	Axis 1	Axis 2
Eigenvalues	0.259	0.029
Variance (%)	13.0	14.4

Variable	λ_a	p	F
Temp	0.20	0.001	8.76
TOC	0.03	0.318	1.24
P	0.00	0.630	0.43
NH ₄	0.02	0.629	0.50
NO ₂	0.02	0.349	0.91
Cl	0.01	0.578	0.56
pH	0.00	0.821	0.21
O ₂	0.01	0.851	0.17

201

202 **Species interaction experiment**

203 The rm-ANOVA showed for both species a significant effect of temperature (Time*Temp) on
 204 their shell height (Table 2). Both species were stimulated by increasing temperature, growing
 205 faster and reaching bigger shell heights until the end of the experiment (Fig. 3). Depending on
 206 density treatment, *P. acuta* reached a mean shell heights of about 2200 - 4000 μm until the
 207 end of the experiment at 15 °C, while at 25 °C the mean shell heights were about 6000 – 7500
 208 μm (Figs 3 A-F). Compared to *P. acuta*, *P. fontinalis* grew less and final mean shell height
 209 was depending on treatment about 1700 to 2600 μm at 15 °C and 3200 to 4600 μm at 25 °C
 210 (Figs 3 G-L).

211 Beside the temperature effect, we found that the growth of both snails species was influenced
 212 by the presence of the other snail species (Term in the rm-ANOVA for *P. acuta*: Time*PF;
 213 for *P. fontinalis*: Time*PA, Table 2, Fig. 3), while density of conspecifics did not affect

214 growth (Term in the rm-ANOVA for *P. acuta*: *Time*PA*; for *P. fontinalis*: *Time*PF*, Table 2,
 215 Fig. 3).

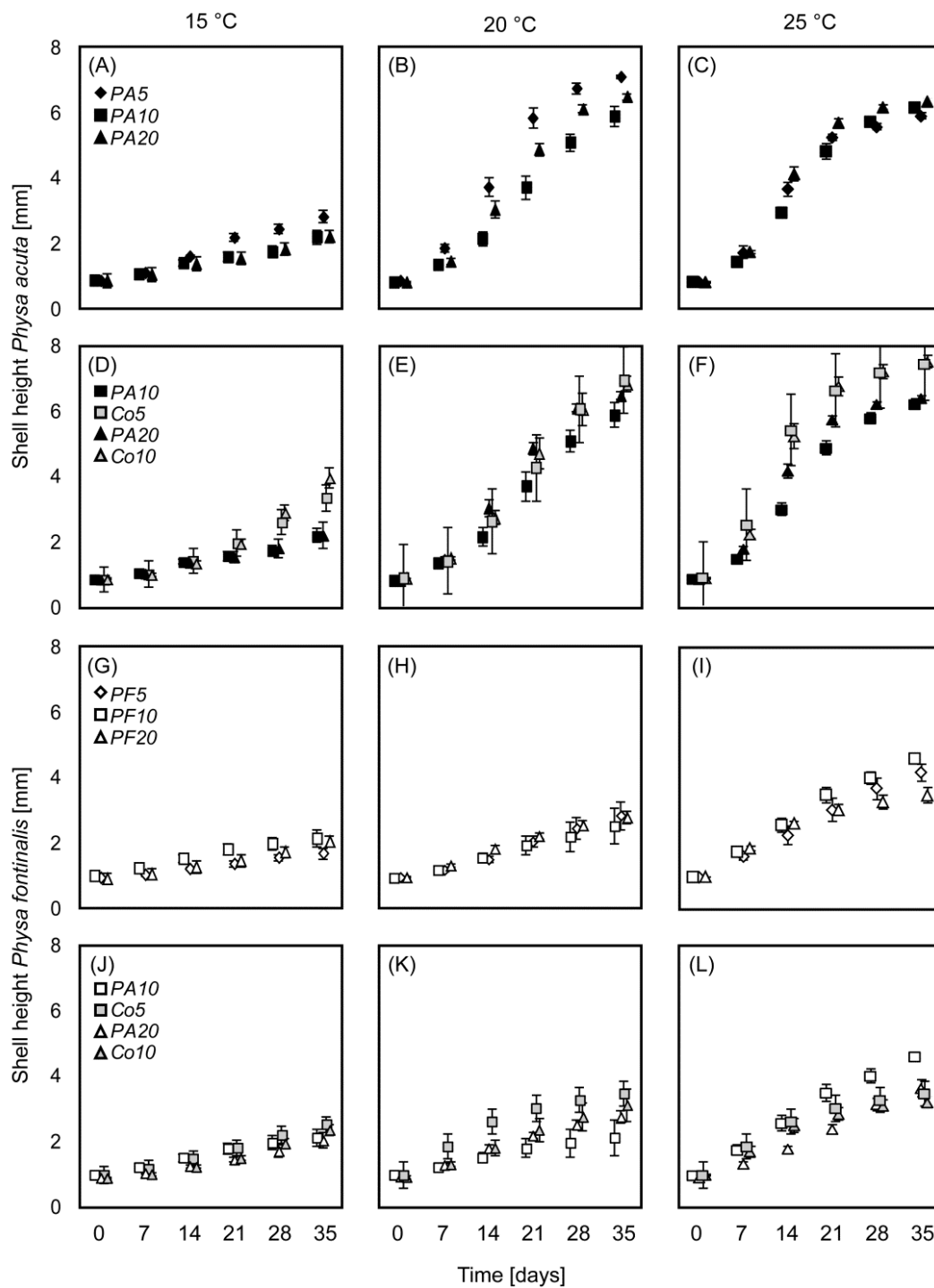
216 **Table 2** Results of the repeated measures analysis of variance (rm-ANOVA). Rm-ANOVA was calculated for
 217 the shell heights of *Physa acuta* (A) and *Physa fontinalis* (B) during the species interaction experiment in
 218 dependence of species density of *P. acuta* (*PA*) and *P. fontinalis* (*PF*) and temperature (Temp).

Dependent variable	Effect	SS	df	F	p
(A) Shell height of <i>Physa acuta</i>	Intercept	33.68	1	916.68	< 0.001
	Temp	1.25	1	34.08	< 0.001
	<i>PA</i>	0.10	1	2.63	0.108
	<i>PF</i>	0.01	1	0.27	0.603
	Temp* <i>PA</i>	0.07	1	1.96	0.165
	Temp* <i>PF</i>	0.05	1	1.40	0.239
	Error	3.67	100		
	Time	0.03	5	1.28	0.273
	Time*Temp	0.36	5	13.78	< 0.001
	Time* <i>PA</i>	0.05	5	1.96	0.084
	Time* <i>PF</i>	0.31	5	11.80	< 0.001
	Time*Temp* <i>PA</i>	0.05	5	1.75	0.121
	Time*Temp* <i>PF</i>	0.28	5	10.79	< 0.001
	Error	2.63	500		
	(B) Shell height of <i>Physa fontinalis</i>	Intercept	31.40	1	810.45
Temp		1.12	1	28.89	< 0.001
<i>PA</i>		0.04	1	1.10	0.298
<i>PF</i>		0.02	1	0.53	0.470
Temp* <i>PA</i>		0.03	1	0.88	0.350
Temp* <i>PF</i>		0.03	1	0.88	0.350
Error		3.87	100		
Time		0.05	5	3.15	0.008
Time*Temp		0.29	5	17.10	< 0.001
Time* <i>PA</i>		0.21	5	12.10	< 0.001
Time* <i>PF</i>		0.01	5	0.57	0.724
Time*Temp* <i>PA</i>		0.21	5	12.19	< 0.001
Time*Temp* <i>PF</i>		0.01	5	0.61	0.685
Error		1.70	500		

219

220

221

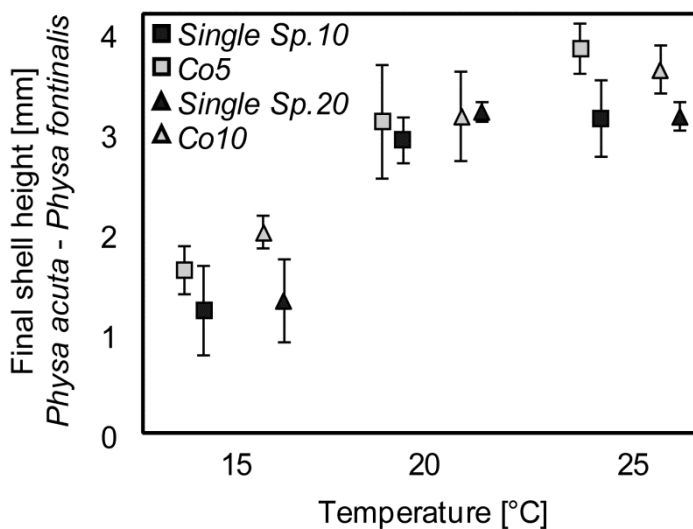


222

223 **Figure 3** Mean shell height (\pm SE) of *Physa acuta* (A-F) and *Physa fontinalis* (G-L) during the species
 224 interaction experiment. Intraspecific interaction in single-species treatments with 5, 10, and 20 snails of *P. acuta*
 225 (*PA5*, *PA10*, *PA20*; a-c) and *P. fontinalis* (*PF5*, *PF10*, *PF20*; g-i). Interspecific interaction between *P. acuta* and
 226 *P. fontinalis* in coexistence treatments under density combinations *CO5* and *CO10* compared to the single-
 227 species-treatments *PA10*, *PA20* (d-f) and *PF10*, *PF20* (j-l), respectively. All treatments were conducted at three
 228 temperatures, 15, 20, and 25 °C.

13

229 An asymmetric competitive interaction between the two species was observed influenced by
 230 temperature (Term in the rm-ANOVA for *P. acuta*: Time*Temp*PF; for *P. fontinalis*:
 231 Time*Temp*PA, Table 2, Fig. 3). At all temperatures, alien *P. acuta* was stimulated by the
 232 presence of indigenous *P. fontinalis*. At 15 °C and 20 °C, the indigenous snail *P. fontinalis*
 233 was also stimulated by the presence of alien *P. acuta*. However, these effects switched at
 234 25 °C. Here the growth of *P. fontinalis* was inhibited in the coexistence-treatments. Especially
 235 at 25 °C specimens of *P. acuta* in the coexistent-treatments (CO5, CO10) grew significantly
 236 faster and were up to 1500 µm longer compared to the snails in single-species-treatments
 237 (PA5, PA10, PA20). In contrast, *P. fontinalis* were up to 1400 µm smaller in the coexistent-
 238 treatments (CO5, CO10) at 25 °C compared to the single-species-treatments (PF5, PF10,
 239 PF20). As a result, in the coexistence treatments, the differences in final shell heights between
 240 both species increased with increasing temperatures (Fig. 4).



241
 242 **Figure 4** Mean differences (\pm SE) between the final shell heights (day 35) of the species *Physa acuta* (PA) and
 243 *Physa fontinalis* (PA) in the species interaction experiments in dependence of temperature (15, 20, and 25 °C).
 244 Differences of the final shell height are shown for snails in the single-species treatments with 10 snail (PA10
 245 vs. PF10 referred to *Single Sp.10*) and 20 snails (PA20 vs. PF20 referred to *Single Sp.20*) and for snails in
 246 coexistence-treatments with 5 (Co5) and 10 (Co10) snails of each species.

247 **Discussion**

248 Knowledge on the mechanism behind displacements of indigenous species by alien species
249 and the driving factors of the competitive superiority of the alien species is still rare. Even
250 though it is often assumed that temperature may be a driving factor in this context, concrete
251 demonstrations of this hypothesis and the underlying mechanism are few. However linking
252 interspecific interaction between alien and indigenous species with environmental conditions
253 as potential driving factors of invasion success is important to predict invasions and the
254 impact of alien on indigenous species assemblage. Therefore in our study we chose a two-step
255 approach combining analysis of field data and species interaction experiments on the species
256 pair *P. acuta* and *P. fontinalis*.

257 Using field data we identified temperature as most important differences between the sites
258 where the alien snail *P. acuta* occurred compared to sites where the indigenous snail
259 *P. fontinalis* occurred. Sampling sites where *P. acuta* was found were warmer compared to
260 sites where the indigenous snail *P. fontinalis* was found and coexistence sites where
261 intermediate, slightly shifted to *P. fontinalis* sites. This pattern reflects the high tolerance of
262 *P. acuta* to increased temperature (Zukowski and Walker 2009, Höckendorff et al. accepted).
263 Furthermore, our findings corroborates the results of previous studies suggesting that
264 temperature is one of the best predictors of the sensitivity of freshwater habitats to alien
265 invertebrate species (Früh et al. 2012a, 2012b, Verbrugge et al. 2012). This leads to the
266 assumption that changes in temperature modify the competitive interaction between *P. acuta*
267 and *P. fontinalis* and that *P. acuta* may be able to outcompete indigenous snail species, in this
268 case *P. fontinalis*, especially at warmer temperatures. This assumption is supported by the
269 findings of our species interaction experiment.

270 *P. acuta* showed higher growth gains as a result of higher temperatures. Furthermore, we
271 demonstrated that the competitive interaction between the two species is asymmetric.
272 Especially at high temperatures, heterospecifics had a stimulating effect on growth of
273 *P. acuta*, while contrary heterospecifics had an inhibitory effect on growth of *P. fontinalis*.
274 This asymmetric competitive interaction between the two model species may be caused by
275 several, potentially overlapping mechanisms. The effect of the presence of heterospecifics
276 might be mediated through chemical cues as suggested by Kawata and Ishigami (1992),
277 working on *P. acuta* and *Lymnaea columella*. Furthermore, direct interaction with
278 heterospecifics may change an organism's behavior, resulting in a decrease in foraging and
279 feeding, as for example Brenneis et al. (2010) showed for the snail *Potamopyrgus*
280 *antipodarum* and the isopod *Gnorimosphaeroma insulare*. Also a higher efficiency to use and
281 convert resources of alien compared to indigenous snails (e.g. Byers 2000a, Nunez 2010,
282 Morrison and Hay 2011) may cause asymmetric interactions; however, in our case no
283 resource limitation was intended in the experiment, as all snails were fed with food aliquots
284 equivalent to the total snail density in the treatment.

285 The superiority in growth of *P. acuta* coexisting with *P. fontinalis* at high temperatures may,
286 in turn, result in an increase in reproduction. It is already known that *P. acuta* not only grows
287 faster but also has a higher reproduction output at warmer water temperatures (Brackenbury
288 and Appleton, 1991). Consequently the superiority of *P. acuta* may not only be due to
289 limitations of the growth of the coexisting species, but also from enhanced feeding, higher
290 conversion efficiencies resulting in increased rates of growth and reproduction. Our findings
291 suggest that *P. acuta* have an advantage against *P. fontinalis*, when coexisting especially at
292 relatively warm temperatures. Consequently rising water temperatures induced by

293 anthropogenic action and predicted in the context of climate change may exacerbate the
294 impact of *P. acuta* and consequently the problem of decreasing populations of *P. fontinalis*.

295 Here we focus on the impact of changing environmental conditions on the interaction between
296 alien and indigenous species. This study shows that temperature can be a powerful driver of
297 the outcomes of species competition. We assume that the mechanism we found for our two
298 model species is more broadly applicable to interactions between other alien and indigenous
299 species, since alien species are a non random set of species, overrepresented by mollusks and
300 crustaceans (Karatayev et al. 2009, Strayer 2010). Furthermore, alien species are often
301 characterized by similar life history traits such as early maturation, large brood size, high
302 partial fecundity, and a high number of generations per year (e.g. Grabowski et al. 2007).

303 Beside these traits, different alien species are favored in a similar manner by higher tolerance
304 to structural habitat degradation (Havel et al. 2005, Johnson et al. 2008), chemical degradation
305 (MacNeil et al. 2000, Byers 2000b, Grabowski et al. 2009), and temperature increase (e.g.
306 Wijnhoven et al. 2003, Werner and Rothhaupt 2008, Weitere et al. 2009, Zukowski and
307 Walker 2009, Sargent et al. 2011, Verbrugge et al. 2012). In this context Früh et al. (2012a, b)
308 already showed that freshwater habitats with increased temperature are more prone to
309 invasion, suggesting that alien species are a non random set of species (Strayer 2010), due to
310 similar selection pressure when reaching a new habitat by the same vectors such as within
311 tank ballast water. Based on this findings we assume that further increases in temperature may
312 generally contribute to the superiority of alien species against indigenous species by
313 strengthen the asymmetric interaction between alien and indigenous species. Furthermore the
314 higher tolerance level of many alien species towards a whole array of environmental stressors
315 compared to indigenous species (e.g. Zukowski and Walker 2009, Früh et al. 2012a, Früh
316 et al. 2012b, Verbrugge et al. 2012), will commonly result to competitive superiority of alien

317 species at anthropogenically degraded sites or under the effect of climate change. Thus when
318 investigating the interaction between alien and indigenous species, the environmental context
319 cannot be disregarded (Höckendorff et al. accepted, Stoll et al. 2013). Consequently our
320 results further underline the importance to link biotic interactions and environmental variables
321 when predicting and assessing alien species distribution and success or potential impacts on
322 indigenous systems. Thus for example when predicting further distribution of alien species
323 using tools like species distribution models, beside environmental predictors the impact of
324 biotic interaction have to be take into account.

325 **Acknowledgements**

326 We are grateful to State Agency for Nature, Environment and Consumer protection North
327 Rhine Westphalia for kindly providing the species and physico-chemical data. The present
328 study was funded by the research funding program “LOEWE - Landes-Offensive zur
329 Entwicklung Wissenschaftlich-ökonomischer Exzellenz” of Hesse’s Ministry of Higher
330 Education, Research, and the Arts.

331

332

333 **References**

- 334 Appleton, C. C. 2003. Alien and invasive fresh water Gastropoda in South Africa. African
335 Journal of Aquatic Science 28:69-81.
- 336 Bacela-Spychalska, K., R. A. Wattier, C. Genton, and T. Rigaud. 2012. Microsporidian
337 disease of the invasive amphipod *Dikerogammarus villosus* and the potential for its
338 transfer to local invertebrate fauna. Biological Invasions 14:1831-1842.
- 339 Beran, L., L. Juříčková, and M. Horsák. 2005. Mollusca. Pages 69-74 in J. Farkač, D. Král,
340 and M. Škorpík (editors). Red list of threatened species in the Czech Republic,
341 Invertebrates. AOPK ČR, Prague, Czech Republic.
- 342 Boland, B. B., M. Meerhoff, C. Fosalba, N. Mazzeo, M. A. Barnes, and R. L. Burks. 2008.
343 Juvenile snails, adult appetites: Contrasting resource consumption between two species
344 of applesnails (Pomacea). Journal of Molluscan Studies 74:47-54.
- 345 Brackenbury, T. D., and C. C. Appleton. 1991. Effect of controlled temperatures on
346 gametogenesis in the gastropods *Physa acuta* (Physidae) and *Bulinus tropicus*
347 (Planorbidae). Journal of Molluscan Studies 57:461-469.
- 348 Brackenbury, T. D., and C. C. Appleton. 1995. Recolonization of the Umsindusi River, Natal,
349 South Africa, by the invasive gastropod, *Physa acuta* (Basommatophora, Physidae).
350 Journal of Medical and Applied Malacology 5:39-44.
- 351 Brenneis, V. E. F., A. Sih, and C. E. de Rivera. 2010. Coexistence in the intertidal:
352 interactions between the nonindigenous New Zealand mud snail *Potamopyrgus*
353 *antipodarum* and the native estuarine isopod *Gnorimosphaeroma insulare*. Oikos
354 119:1755-1764.
- 355 Byers, J. E. 2000a. Competition between two estuarine snails: Implications for invasions of
356 exotic species. Ecology 81:1225-1239.

- 357 Byers, J. E. 2000b. Differential susceptibility to hypoxia aids estuarine invasion. *Marine*
358 *Ecology Progress Series* 203:123-132.
- 359 Cope, N. J., and M. J. Winterbourn. 2004. Competitive interactions between two successful
360 molluscan invaders of freshwaters: an experimental study. *Aquatic Ecology* 38:83-91.
- 361 Covich, A. P. 2010. Winning the biodiversity arms race among freshwater gastropods:
362 competition and coexistence through shell variability and predator avoidance.
363 *Hydrobiologia* 653:191-215.
- 364 Dextrase, A. J., and N. E. Mandrak. 2006. Impacts of alien invasive species on freshwater
365 fauna at risk in Canada. *Biological Invasions* 8:13-24.
- 366 Dillon, R. T., A. R. Wethington, J. M. Rhatt, and T. P. Smith. 2002. Populations of the
367 European freshwater pulmonate *Physa acuta* are not reproductively isolated from
368 American *Physa heterostropha* or *Physa integra*. *Invertebrate Biology* 121:226-234.
- 369 Frank, C., and P. L. Reischütz. 1994. Rote Liste gefährdeter Weichtiere Österreichs
370 (Mollusca: Gastropoda und Bivalvia). Pages 1-355 in J. Gepp (editor). Rote Listen
371 gefährdeter Tiere Österreichs. Grüne Reihe des Bundesministeriums für Umwelt,
372 Jugend und Familie, Graz.
- 373 Früh, D., S. Stoll, and P. Haase. 2012a. Physicochemical and morphological degradation of
374 stream and river habitats increases invasion risk. *Biological Invasions* 14:2243-2253.
- 375 Früh, D., S. Stoll, and P. Haase. 2012b. Physico-chemical variables determining the invasion
376 risk of freshwater habitats by alien mollusks and crustaceans. *Ecology and Evolution*
377 2:2843-2853.
- 378 Grabowski, M., K. Bacela, and A. Konopacka, 2007. How to be an invasive gammarid
379 (Amphipoda: Gammaroidea) - comparison of life history traits. *Hydrobiologia* 590:75-
380 84.

381 Grabowski, M., K. Bacela, A. Konopacka, and K. Jazdzewski. 2009. Salinity-related
382 distribution of alien amphipods in rivers provides refugia for native species. *Biological*
383 *Invasions* 11:2107-2117.

384 Guo, Y. H., C. C. Hwang, and H. X. He. 2009. Expansion of an invasive freshwater snail
385 *Physa acuta* (Gastropoda: Physidae) in China. *Molluscan Research* 29:174-178.

386 Haase, P., S. Lohse, S. Pauls, K. Schindehütte, A. Sundermann, P. Rolauffs, and D. Hering.
387 (2004) Assessing streams in Germany with benthic invertebrates: development of a
388 practical standardised protocol for macro invertebrate sampling and sorting.
389 *Limnologica* 34:349-365.

390 Havel, J. E., C. E. Lee, and M. J. van der Zanden. 2005. Do reservoirs facilitate invasions into
391 landscapes? *Bioscience* 55:518-525.

392 Höckendorff, S., D. Früh, N. Hormel, P. Haase, and S. Stoll. Accepted. Biotic interactions
393 under climate warming: temperature-dependent and species-specific effects of the
394 oligochaete *Chaetogaster limnaei* on snails. *Freshwater Science*.

395 Johnson, P. T. J., J. D. Olden, and M. J. van der Zanden. 2008. Dam invaders: impoundments
396 facilitate biological invasions into freshwaters. *Frontiers in Ecology and the*
397 *Environment* 6:359-365.

398 Jungbluth, J. H., and D. von Knorre. 2009. Rote Liste der Binnenmollusken [Schnecken
399 (Gastropoda) und Muscheln (Bivalvia)] in Deutschland. 6. revidierte und erweiterte
400 Fassung 2008. *Mitteilung der Deutschen Malakozoologischen Gesellschaft* 81:1-28.

401 Karatayev, A. Y., L. E. Burlakova, D. K. Padilla, S. E. Mastitsky, and S. Olenin. 2009.
402 Invaders are not a random selection of species. *Biological Invasions* 11:2009-2019.

403 Kawata, M., and H. Ishigami. 1992. The growth of juvenile snails in water conditioned by
404 snails of a different species. *Oecologia* 91:245-248.

PeerJ PrePrints

405 Kinzelbach, R. 1995. Neozoans in european waters - Exemplifying the worldwide process of
406 invasion and species mixing. *Experientia* 51:526-538.

407 Krist, A. C., and C. C. Charles. 2012. The invasive New Zealand mudsnail, *Potamopyrgus*
408 *antipodarum*, is an effective grazer of algae and altered the assemblage of diatoms more
409 than native grazers. *Hydrobiologia* 694:143-151.

410 Lövei, G. L. 1997. Biodiversity - Global change through invasion. *Nature* 388:627-628.

411 Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. (2000)
412 Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological*
413 *Applications* 10:689-710.

414 MacNeil, C., P. Boets, K. Lock, and P. L. M. Goethals. 2013. Potential effects of the invasive
415 'killer shrimp' (*Dikerogammarus villosus*) on macroinvertebrate assemblages and
416 biomonitoring indices. *Freshwater Biology* 58:171-182.

417 MacNeil, C., J. T. A. Dick, and R.W. Elwood. 2000. Differential physico-chemical tolerances
418 of amphipod species revealed by field transplantations. *Oecologia* 124:1-7.

419 Manganelli, G., M. Bodon, S. Cianfanelli, L. Favilli, and F. Giusti. 2000. [Knowledge and
420 conservation of Italian non-marine mollusks: The status of the research]. *Bollettino*
421 *Malacologico* 36:5-42.

422 Morrison, W. E., and M. E. Hay. 2011. Feeding and growth of native, invasive and non-
423 invasive alien apple snails (Ampullariidae) in the United States: Invasives eat more and
424 grow more. *Biological Invasions* 13:945-955.

425 Mouthon, J., and M. Daufresne. 2010. Long-term changes in mollusc communities of the
426 Ognon river (France) over a 30-year period. *Fundamental and Applied Limnology*
427 178:67-79.

- 428 Nunez, V. 2010. Differences on allocation of available resources, in growth, reproduction,
429 and survival, in an exotic gastropod of Physidae compared to an endemic one. *Iheringia*
430 *Serie Zoologia* 100:275-279.
- 431 Oscoz, J., P. Tomas, and C. Duran. 2010. Review and new records of non-indigenous
432 freshwater invertebrates in the Ebro River basin (Northeast Spain). *Aquatic Invasions*
433 5:263-284.
- 434 Rahel, F. J., and J. D. Olden. 2008. Assessing the effects of climate change on aquatic
435 invasive species. *Conservation Biology* 22:521-533.
- 436 Riley, L. A., M. F. Dybdahl, and R. O. Hall. 2008. Invasive species impact: asymmetric
437 interactions between invasive and endemic freshwater snails. *Journal of the North*
438 *American Benthological Society* 27:509-520.
- 439 Sala, O.E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-
440 Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A.
441 Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H.
442 Wall. 2000. Biodiversity - Global biodiversity scenarios for the year 2100. *Science*
443 287:1770-1774.
- 444 Sargent, L.W., S. W. Dolladay, A. P. Civich, and S. P. Opsahl. 2011. Physicochemical habitat
445 association of a native and non-native crayfish in the Lower Flint river, Georgia:
446 implications for invasion success. *Biological Invasions* 13:499-511.
- 447 Schmidlin, S., D. Schmera, and B. Baur. 2012. Alien molluscs affect the composition and
448 diversity of native macroinvertebrates in a sandy flat of Lake Neuchâtel, Switzerland.
449 *Hydrobiologia* 679:233-249.
- 450 Strayer, D.L. 2010. Alien species in fresh waters: ecological effects, interactions with other
451 stressors, and prospects for the future. *Freshwater Biology* 55:152-174.

452 Stoll, S., D. Früh, B. Westerwald, N. Hormel, and P. Haase. 2013. Density-dependent
453 relationship between *Chaetogaster limnaei limnaei* (Oligochaeta) and the freshwater
454 snail *Physa acuta* (Pulmonata). *Freshwater Science* 32:642–649.

455 R Development Core Team. 2012. R: A language and environment for statistical computing.
456 R Foundation for Statistical Computing, Vienna, Austria.

457 Turner, H., M. Wüthrich, and J. Rüetschi. 1994. Rote Liste der gefährdeten Weichtiere der
458 Schweiz. Page 97 in P. Duelli (editor). *Rote Listen der gefährdeten Tierarten der*
459 *Schweiz*. Bundesamt für Umwelt, Wald und Landschaft, EDMZ, Bern.

460 Van der Velde, G., R. Leuven, D. Platvoet, K. Bacela, M. A. J. Huijbregts, H. W. M.
461 Hendriks, and D. Kruijt. 2009. Environmental and morphological factors influencing
462 predatory behaviour by invasive non-indigenous gammaridean species. *Biological*
463 *Invasions* 11:2043-2054.

464 Verbrugge, L. N. H., A. M. Schipper, M. A. J. Huijbregts, G. van der Velde, and R. Leuven.
465 2012. Sensitivity of native and non-native mollusc species to changing river water
466 temperature and salinity. *Biological Invasions* 14:1187-1199.

467 Vermonden, K., R. Leuven, and G. van der Velde. 2010. Environmental factors determining
468 invasibility of urban waters for exotic macroinvertebrates. *Diversity and Distributions*
469 16:1009-1021.

470 Vitousek, P. M., C. M. Dantonio, L. L. Loope, M. Rejmanek, and R. Westbrooks. 1997.
471 Introduced species: A significant component of human-caused global change. *New*
472 *Zealand Journal of Ecology* 21:1-16.

473 Walther, G.-R., A. Roques, P. E. Hulme, M. T. Sykes, P. Pysek, I. Kuhn, M. Zobel, S.
474 Bacher, Z. Botta-Dukat, H. Bugmann, B. Czucz, J. Dauber, T. Hickler, V. Jarosik, M.
475 Kenis, S. Klotz, D. Minchin, M. Moora, W. Nentwig, J. Ott, V. E. Panov, B. Reineking,

PeerJ PrePrints

476 C. Robinet, V. Semenchenko, W. Solarz, W. Thuiller, M. Vila, K. Vohland, and J.
477 Settele. 2009. Alien species in a warmer world: risks and opportunities. Trends in
478 Ecology and Evolution 24:686-693.

479 Weitere, M., A. Vohmann, N. Schulz, C. Linn, D. Dietrich, and H. Arndt. 2009. Linking
480 environmental warming to the fitness of the invasive clam *Corbicula fluminea*. Global
481 Change Biology 15:2838-2851.

482 Werner, S., and K. O. Rothhaupt. 2008. Mass mortality of the invasive bivalve *Corbicula*
483 *fluminea* induced by a severe low-water event and associated low water temperatures.
484 Hydrobiologia 613:143-150.

485 Wijnhoven, S., M. C. van Riel, and G. van der Velde. 2003. Exotic and indigenous freshwater
486 gammarid species: physiological tolerance to water temperature in relation to ionic
487 content of the water. Aquatic Ecology 37:151-158.

488 Winterbourn, M.J. 1980. The Distribution and Biology of the Fresh Water Gastropods *Physa*
489 and *Physastra* in New-Zealand. Journal of the Malacological Society of Australia 4:233-
490 234.

491 Zukowski, S., and K. F. Walker. 2009. Freshwater snails in competition: alien *Physa acuta*
492 (*Physidae*) and native *Glyptophysa gibbosa* (*Planorbidae*) in the River Murray, South
493 Australia. Marine and Freshwater Research 60:999-1005.