1 **Impacts of an invasive plant on primary production: testing a functional trait-based**

2 **framework with a greenhouse experiment**

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Abstract

Questions: Predicting when invasive species will affect ecosystem functioning remains problematic, with strong contingency upon both the invasive species and the recipient community's identities. Adopting a functional trait-based approach might overcome this context-dependence. As an early exploration of this approach, we used a greenhouse experiment to assess the potential invasion effects on community trait composition and biomass production.

Location: We introduced seeds of the invasive plant *Impatiens glandulifera* from three distant European origins, namely northern France (50.1 °N 2.0 °E), southern Sweden (55.9 °N 12.9 °E) and central Norway (63.5 °N 10.9 °E) to transplanted vegetation turves from the Trondheim area in central Norway.

Methods: At the end of the greenhouse experiment, we measured three functional traits: plant height, specific leaf area (SLA) and leaf dry matter content (LDMC), and standing biomass of both the invasive plant and the turf communities. With this data we evaluated invasion effects on community trait composition and standing biomass (as a first test of ecosystem function effects), including its dependence on invasive species origin and recipient community composition.

Results: Invasion by *I. glandulifera* introduced divergent trait values (high plant height and SLA, low LDMC) to the recipient community. The trait set of both the invader and, to a lesser extent, the community were altered following invasion, seemingly driven by increased competition. Competitive and graminoid-dominated communities showed stronger changes in LDMC following invasion. Functional traits of both the communities and the invasive species helped explain the increase in standing biomass. Southern invader plants more strongly affected the recipient community than their northern counterparts, resulting in stronger biomass reduction of the recipient community.

45 **Conclusions:** This study forms an example of the potential of a functional trait-based approach

46 to predict invasive species effects on productivity, and by extension potentially other ecosystem

47 functions.

48

49 **Nomenclature**

50 The Plant List (2013) Version 1.1. for plants, published on the Internet;

51 http://www.theplantlist.org

52

53 **Key words**

54 Competition; *Impatiens glandulifera*; latitudinal gradient; plant height; productivity; specific

55 leaf area; species origin; leaf dry matter content.

56

57 **Abbreviations**

58 A = grown alone; C = grown in competition; CWM = community weighted mean; IMP =

59 *Impatiens glandulifera*; LDMC = leaf dry matter content; SLA = specific leaf area

60

61 **Running head:**

62 Functional trait mediated invader impacts

63

64 **Introduction**

65 Invasive alien species are increasingly affecting biodiversity and ecosystems across the globe

66 (Vilà et al. 2011; van Kleunen et al. 2015). Certain plant species invasions have even been

67 observed to cause great changes in ecosystem functioning (e.g. Dassonville et al. 2008; Vilà et

68 al. 2011; Pyšek et al. 2012). Despite considerable research effort, predicting when invasive

69 plant species will cause such ecosystem changes, and which processes trigger them, has

70   remained problematic (Strayer 2012; Kumschick et al. 2015; Bernard-Verdier & Hulme 2015).

71   Research so far suggests that ecosystem effects are highly contingent upon both the invasive

72   species identity and the composition of the recipient community, and thus strongly context-

73   dependent (Mason & French 2008; Pyšek et al. 2012; Ricciardi et al. 2013).

74   One potential way to overcome this context-dependence is adopting a functional trait-

75   based approach (Levine et al. 2003; Drenovsky et al. 2012; Strayer 2012; Kumschick et al.

76   2015). Ecosystem functions are believed to be directly mediated by the functional trait set of

77   the plant species present in these ecosystems. Most studies so far, however, have focused on

78   traits that affect invasiveness, rather than on traits that impact ecosystem functioning directly

79   (McIntyre et al. 2005; van Kleunen et al. 2010; Ordonez et al. 2010).

80   Theoretically, the invaded plant communities' trait set, and thus ecosystem functioning

81   can be strongly altered by invasive species through two, non-exclusive pathways (Strayer

82   2012). First, if the invasive species exhibits trait values that are very distinct from those of the

83   native species pool, they are likely to cause pronounced changes in ecosystem functioning

84   (Vitousek 1990; Ehrenfeld 2010). Research has indeed shown that invasive plants are often

85   more likely to successfully invade communities if they exhibit trait values that differ from those

86   of the native species (Tecco et al. 2010; Hejda & de Bello 2013), with many invasive plants

87   characterized by trait values linked to fast growth and resource acquisition (Wright et al. 2004;

88   van Kleunen et al. 2010). Second, species invasion can cause shifts in the identity and

89   abundance of the native species, in this way triggering changes in ecosystem functioning,

90   through effects on native species' traits (Lavorel et al. 1997; Mack et al. 2001; Strayer 2012).

91   Several studies have observed shifts in species diversity and community composition after

92   establishment of invasive species (Levine et al. 2003; Vilà et al. 2011; Pyšek et al. 2012). This

93   shift was, at least in some studies, associated with competition-driven changes in the functional

94   trait diversity and composition of those communities (Michelan et al. 2010; Hejda & de Bello

95   2013; Case et al. 2016). Some early exploration of the theoretical functional trait-based

96   framework to assess ecosystem functioning changes has proven successful. A recent study

97   illustrated that invasive species cause larger effects on ecosystem properties when they exhibit

98   different trait values than those of the recipient community, but not when they share similar

99   trait values (Scharfy et al. 2011; however see Castro-Díez et al. 2016).

100   Although functional traits are often treated as fixed at the species level by community

101   ecologists, research has repeatedly shown that most functional traits show relatively high

102   intraspecific trait variation (Siefert et al. 2015). This trait variation is often more substantial for

103   invasive species, and has been interpreted as one of the potential reasons of a species' invasion

104   success (Davidson et al. 2011; Drenovsky et al. 2012). Consequently, invasive species might

105   have different effects on ecosystem functioning across their invaded range, because of

106   substantial intraspecific trait variation (Godoy et al. 2011). Competition is expected to increase

107   under environmentally favorable conditions at the southern end of the invaded range (cf. the

108   stress gradient hypothesis, Bertness and Callaway 1994), which can result in shifts towards

109   invader trait values associated with high competitiveness and resource acquisition.

110   Additionally, invasive species might strongly alter the recipient community's trait set towards

111   more competitive traits merely through effects on its intraspecific trait variation, even when

112   community composition and diversity remains unaffected (Strayer 2012).

113   The impact of invasive species on the recipient communities may also vary with the

114   community's species diversity. Both invasibility and trait change of the recipient community

115   are expected to be reduced in species rich communities. Invasibility is expected to be reduced

116   due to increased competition related to high saturation of the niche space (Elton 1958; Bennett

117   et al. 2016), while trait change is likely to be buffered by the higher functional diversity and

118   redundancy in species rich communities (Walker 1992).

119   Here, we explore how functional trait values of both the recipient community and the

120   invasive species interact during invasion of the non-native *Impatiens glandulifera* and how

121   these traits subsequently affect productivity. We explore the potential use of a functional trait

122   framework for more elaborate ecosystem functioning research to assess invasive species

123   impact. This species usually has very limited effects on species diversity and composition of

124   invaded communities in Europe (Hejda & Pyšek 2006; Hulme & Bremner 2006). Even so,

125   invasion of this species is known to affect several ecosystem functions, including nutrient

126   cycling (Dassonville et al. 2008) and soil erosion (Greenwood & Kuhn 2014). Furthermore,

127   the high trait variation in *I. glandulifera* along its invaded range in Europe (Kollmann &

128   Bañuelos 2004; Acharya 2014), makes it an ideal study species to study effects of invasion on

129   functional trait shifts across both a gradient in *I. glandulifera* origin and a gradient in recipient

130   community diversity and composition of the invaded vegetation. Indeed, previous research on

131   *I. glandulifera* has elucidated that its performance, and thus potential ecosystem impact, also

132   depends on community composition, with reduced performance in graminoid-dominated and

133   competitive communities (Mujuni et al. unpubl.).

134   In a greenhouse experiment, we introduced *I. glandulifera* seeds originating from three

135   different locations along its invaded European gradient to transplanted natural riparian

136   vegetation turves of different species diversity and composition. We recorded three functional

137   traits (plant height, specific leaf area and leaf dry matter content) and standing biomass of both

138   the vegetation and *I. glandulifera* plants of invaded and uninvaded turves. These traits were

139   selected because of their expected link with (community level) productivity. Plant height has

140   been shown to relate to both a plant's competitive ability and species level biomass, whereas

141   both selected leaf traits express variation along the independent leaf economics trait variation

142   axis, and are linked to competiveness, resource acquisition strategies and both species and

143   community level productivity (high SLA, low LDMC) (Westoby 1998; Garnier et al. 2004;

144 Wright et al. 2004). Using this greenhouse setup, we can minimize effects of abiotic factors,

145 allowing us to assess the following hypotheses:

146

147   1. The invader trait values reflect higher competitiveness (higher plant height and SLA,

148   lower LDMC) than those of the recipient community.

149   2. The invader shows more competitive trait values for plants grown in competition as

150   compared to grown alone and for the environmentally more favorable (southernmost)

151   location due to increased competitive interactions.

152   3. Invasion shifts the trait set of the recipient community towards more competitive trait

153   values.

154   4. The strength of this community trait set shift is proportional to the competitive strength

155   of the invader. Consequently, we expect stronger shifts when invaders have high

156   biomass, when invaders originate from the southernmost location and when species

157   diversity of the recipient community is low and characterized by low percentages of

158   grasses and competitive species.

159   5. Both invader traits and changes in recipient community traits (higher plant height and

160   SLA, lower LDMC) can help explain increases in standing biomass of the vegetation.

161

162 **Methods**

163 *Study species*

164 *Impatiens glandulifera* Royle (*Balsaminaceae*) originates from the western Himalaya, but has

165 become strongly invasive across Europe, North America and New Zealand (Beerling & Perrins

166 1993; GBIF 2017). The species mainly grows in riparian habitats in its invaded range and is a

167 competitive annual of up to 2.5 m high which produces up to 2500 seeds per individual per

168 year. These seeds are dispersed through both ballistochory and hydrochory, resulting in very

169   fast colonization of unoccupied habitats (Beerling & Perrins 1993; Greenwood & Kuhn 2014).

170   For this study we used *I. glandulifera* individuals originating from three different locations

171   along a European latitudinal gradient; namely northern France (50.1 °N 2.0 °E), southern

172   Sweden (55.9 °N 12.9 °E) and central Norway (63.5 °N 10.9 °E).

173

174   *Experimental setup*

175   We transferred intact cylindrical vegetation turves (20 cm diameter, 20 cm depth) from

176   streamside locations to the greenhouse. Turves were collected from riparian plant communities

177   within a 50×50 m^2 area in the Stjørdal-Trondheim area (central Norway, 63.5 °N 10.9 °E), in

178   close proximity of known *I. glandulifera* populations during Nov 2015 and are expected to

179   have comparable soil characteristics. Turves were sampled in groups of four, resulting in 88

180   individual turves originating from 22 separate sampling sites (turf clusters), covering a gradient

181   ranging from herb-dominated to grass-dominated vegetation and a representative range in

182   species richness (three to 16 species) for *I. glandulifera* invasion-prone communities. The

183   vegetation turves were subsequently transferred to the greenhouse and embedded in plastic pots

184   (37 cm diameter, 20 l volume) filled for 70% with standard potting soil. For all turves, litter

185   was removed and resident vegetation was clipped until 1.5 cm above the ground level after

186   embedding.

187   For each of the three latitudinal origins of *I. glandulifera*, five seeds were sown in the

188   turves in each of the 22 pots, resulting in a total of 66 pots. The remaining 22 pots functioned

189   as community control treatment. This set-up resulted in one pot for each of the four treatments

190   per sampling site (turf cluster) (fully replicated design). For each latitudinal origin, five *I.*

191   *glandulifera* seeds were sown in three additional pots filled with only potting soil, resulting in

192   nine '*Impatiens* alone pots'. After germination, one *I. glandulifera* plant was retained per pot.

193   For two pots no seeds of *I. glandulifera* (originating from northern France) germinated and

194   were hence excluded from the data analysis.

195

196   *Trait, biomass and diversity measurements*

197   At the end of the experiment, plant height was measured for up to 15 individual ramets of each

198   species in each pot. Up to 15 leaf samples were additionally sampled of up to the ten most

199   abundant species in the pot (5.5 species on average per pot, totalling up to minimum 80% of

200   the total abundance of the vegetation) and *I. glandulifera*. Leaf samples were used to calculate

201   specific leaf area (SLA) and leaf dry matter content (LDMC) according to standardized

202   protocols (Cornelissen et al. 2003). The standing biomass was sorted by species and oven-dried

203   at 60°C for 72 h and subsequently weighed separately per plant species for each pot (0.01g

204   accuracy).

205   Community, standing biomass weighted, mean trait values (CWM) were calculated per

206   pot for plant height, SLA and LDMC, based on the measured trait values of all species,

207   excluding *I. glandulifera*. Next, we calculated three differentiation measures for each of the

208   three measured functional traits. First, we calculated the difference between the CWM trait

209   value of each pot growing in competition with *I. glandulifera* (CWM_C) and the trait value of

210   the *I. glandulifera* in that same pot (IMP_C) (community-invader trait difference). Second, we

211   calculated the difference between IMP_C and the *I. glandulifera* trait values of *I. glandulifera*

212   plants growing alone (IMP_A) (invader trait difference). Note that IMP_A trait values were

213   calculated separately for the three *I. glandulifera* origins, as the average trait value of the three

214   '*Impatiens* alone pots' for each *I. glandulifera* origin. Third, we calculated the 'community

215   trait difference' as the difference between CWM_C and the CWM trait value of the community

216   control pot (without *I. glandulifera* plant) (CWM_A). A different CWM_A value was obtained for

217   each of the 22 sampling sites (turf clusters). Note that the subscripts 'C' and 'A' stand for

218   'grown in competition' and 'grown alone', respectively.

219   Regarding species diversity, we calculated the species richness and the Simpson

220   evenness for each pot. For species composition, we calculated the mean standing biomass

221   weighted 'functional competition signature' (C-signature) based on the C-S-R plant functional

222   type system (Grime 1977), following the method of Hunt et al. (2004). The C-signature variable

223   varies from 0 (no competitive species) to 1 (community completely composed of competitive

224   species). We additionally calculated the community biomass weighted mean percentage per

225   pot of species belonging to *Cyperaceae*, *Juncaceae* or *Poaceae* (% graminoids) (Appendices

226   S1 & S2).

227

228   *Data analysis*

229   We performed three separate sets of simple intercept linear mixed models (LMM) to establish

230   whether average trait differences were larger than zero for the 'community-invader trait

231   difference', the 'invader trait difference' and the 'community trait difference', to respectively

232   test hypotheses 1, 2 and 3. These three intercept LMM were run for each functional trait (height,

233   SLA and LDMC) separately, with turf cluster as random factor. To assess *I. glandulifera* trait

234   differences between the three plant origins (to test hypothesis 2), additional LMM were run for

235   each *I. glandulifera* trait value and each 'invader trait difference' with *I. glandulifera* origin as

236   a fixed factor and turf cluster as a random factor. To explore the trait differences between

237   invaded and non-invaded communities in more detail (to test hypothesis 4), we also performed

238   more elaborate LMM on community trait difference for each functional trait. These models

239   included turf cluster as a random factor, *I. glandulifera* origin as a fixed factor and *I.*

240   *glandulifera* biomass, invader trait difference, species richness, evenness, C-signature and %

241   graminoids as fixed covariates. The interaction term between *I. glandulifera* origin and biomass

242 was also included. Potential effects of the turf species diversity and composition on *I.*

243 *glandulifera*'s performance (biomass) was assessed using a similar LMM with species

244 richness, evenness, C-signature and % graminoids as fixed covariates and turf cluster as a

245 random factor, to address hypothesis 4.

246   To assess differences in standing biomass production between invaded and non-invaded

247 pots as a proxy for the ecosystem function productivity, we calculated the difference between

248 standing biomass of an invaded pot and the standing biomass of the community control pot

249 (without *I. glandulifera* plant). This difference was calculated once including the *I. glandulifera*

250 biomass (biomass$_{diff,incl.IMP}$), and once excluding *I. glandulifera* biomass (biomass$_{diff,excl.IMP}$) to

251 explore hypothesis 5. Subsequently, we performed two LMM, one on biomass$_{diff,incl.IMP}$ and one

252 on biomass$_{diff,excl.IMP}$, both with turf cluster as a random factor and *I. glandulifera* biomass as a

253 fixed covariate. Variation in the standing biomass difference including *I. glandulifera* biomass

254 (biomass$_{diff,incl.IMP}$) was further explored using an extended LMM model which included turf

255 cluster as a random factor, *I. glandulifera* origin as a fixed factor and *I. glandulifera* (IMP)

256 plant height, IMP SLA, IMP LDMC, CWM plant height, CWM SLA and CWM LDMC as

257 fixed covariates. Semi-partial R^2_{beta} coefficients were calculated for each covariate using the

258 method of Edwards et al. (2008), and quantify the contribution of the fixed effect predictor to

259 the dependent variable. See Appendix S3 for the extended methods section.

260

261 **Results**

262 *I. glandulifera* showed a significantly higher plant height and SLA, and significantly lower

263 LDMC than the CWM trait values of the invaded plant communities (Table 1, Fig. 1). *I.*

264 *glandulifera* plants grown in competition had, as predicted, higher SLA and lower LDMC

265 values, but tended to be, contrary to expectations, shorter as compared to *I. glandulifera* plants

266 grown alone (Table 1, Fig. 1). Trait values did not significantly differ between *I. glandulifera*

267 plants originating from France, Sweden and Norway, except that Norwegian plants showed a

268 significantly larger reduction in LDMC compared to their French and Swedish counterparts

269 when grown in competition with the turf communities (Appendix S4).

270   Significant changes in CWM trait values were only observed for plant height, with a

271 reduction in CWM plant height after introducing *I. glandulifera* in the vegetation (Table 1, Fig.

272 1a). Note that *I. glandulifera* trait values were not included in the CWM_C calculation. The

273 absence of a clear community trait difference for LDMC, and for a lesser extent SLA, is partly

274 caused by the relatively high variability in these trait differences, rather than by their absence,

275 further elucidated in the extended models (Fig. 1b & 1c). For LDMC, community trait

276 differences became positive (higher LDMC for invaded communities) when *I. glandulifera*

277 biomass was high, and plant communities were characterized by a competitive and/or grass-

278 dominated species composition (Table 2). Community LDMC differences were furthermore

279 positively related to invader LDMC differences (Table 2). Community SLA differences, on the

280 other hand, were higher for invaded communities with high evenness (Table 2). For plant

281 height, community trait differences became more negative (decreased CWM plant height) with

282 increasing *I. glandulifera* biomass. This pattern was, however, dependent on plant origin, with

283 the strongest/weakest change for plants originating from France and Norway, respectively

284 (Table 2). Low evenness of the community furthermore resulted in smaller reduction in CWM

285 plant height after invasion (Table 2). *I. glandulifera* performance (biomass) was only

286 significantly affected (reduced) by the percentage of graminoid species (Appendix S5).

287   Total invaded community standing biomass became increasingly larger than that of

288 uninvaded communities, with increasing *I. glandulifera* biomass ($biomass_{diff,incl.IMP}$ LMM

289 results: intercept $F = 0.08$, $P = 0.78$, *beta* = -1.83; IMP biomass $F = 60.2$, $P < 0.001$, *beta* =

290 0.78, $R^2_{beta} = 0.488$; $N = 64$) (Fig. 2). The standing biomass of the recipient community

291 (excluding *I. glandulifera* biomass) became increasingly smaller when *I. glandulifera* biomass

292   increased (biomass$_{\text{diff,excl.IMP}}$ LMM results: intercept $F = 0.08$, $P = 0.79$, *beta* = -1.81; IMP

293   biomass $F = 4.9$, $P = 0.03$, *beta* = -0.22, $R^2_{beta} = 0.072$; $N = 64$) (Fig 2). Changes in total

294   standing biomass following invasion (biomass$_{\text{diff,incl.IMP}}$) responded to characteristics of both

295   the invasive species and the recipient community composition. Communities invaded by *I.*

296   *glandulifera* plants originating from France had slightly lower standing biomass than those

297   invaded by *I. glandulifera* plants from Sweden or Norway (lower intercept, Table 3). Plant

298   height of the *I. glandulifera*, but not of the recipient community, was furthermore strongly

299   related to standing biomass change (Table 3, Fig. 3a). For LDMC, however, CWM values of

300   the recipient community was a better predictor of standing biomass change than the

301   corresponding values of the invasive species (Table 3, Fig. 3b).

302

303   **Discussion**

304   I. glandulifera *trait values*

305   Understanding how and predicting when invasive plant species affect community composition

306   and ecosystem functioning is crucially important in a time of global biotic homogenization. In

307   our study, all measured *I. glandulifera* trait values differed significantly from the average

308   community trait values (CWM). Therefore, this species could potentially affect ecosystem

309   functioning directly by introducing trait values differing from the community means into the

310   system (Vitousek 1990; Ehrenfeld 2010). These trait differences, i.e. high plant height and

311   SLA, and low LDMC confirmed our first hypothesis and have been observed in several

312   successful invading species, suggesting their close link to invasion success (Leishman et al.

313   2007; van Kleunen et al. 2010). Large plant height is generally associated with increased

314   competitive ability for light (van Kleunen et al. 2010). High SLA and low LDMC, on the other

315   hand, are characteristic of the acquisitive resource strategy, in turn associated with fast

316   growing, highly competitive species (Wright et al. 2004; Leishman et al. 2007).

317   *I. glandulifera* trait values change significantly when grown in competition with the

318   native communities, as compared to grown alone. This change follows the theoretically

319   expected pattern under increased competition for light (increased SLA), and competition for

320   nutrients (reduced plant height and LDMC) (Andrews et al. 2009; Hodgson et al. 2011), thus

321   (partly) confirming our second hypothesis. These trait value shifts illustrate the context-

322   dependence of a plant's trait set due to intraspecific trait variation, and the importance of using

323   system-specific trait values (Davidson et al. 2011; Drenovsky et al. 2012; Siefert et al. 2015).

324   Our results even suggest that the significantly higher SLA for *I. glandulifera* plants compared

325   to the community's SLA only occurs for *I. glandulifera* plants grown in competition (Fig. 1b).

326   unlike postulated in the second hypothesis, we observed no clear differences in trait values for

327   *I. glandulifera* plants originating from France, Sweden and Norway (Kollmann & Bañuelos

328   2004; Acharya 2014). Notwithstanding, LDMC decreased more strongly for plants originating

329   from Norway, which could suggest that Norwegian *I. glandulifera* plants are more susceptible

330   to the community nutrient competition. Note that differences in *I. glandulifera* trait values

331   between competition pots (with native vegetation) and *Impatiens* alone pots (without native

332   vegetation) can also be partly caused by soil differences (presence or absence of turves of native

333   vegetation). To rule out turf soil impact on these patterns, these results should ideally be

334   verified by assessing community competition effects on *I. glandulifera* traits under

335   standardized soil conditions.

336

337   *Community trait values*

338   Although CWM plant height was the only trait that showed a significant change for invaded

339   communities compared to uninvaded communities (hypothesis 3), more detailed analyses of

340   community trait differences showed a more nuanced picture. Changes in both plant height and

341   LDMC of the community, but not in SLA, were affected by the invasive species presence.

342 Following hypothesis 4, our results suggest that these trait effects are mainly driven by

343 competition, with much stronger CWM trait changes when *I. glandulifera* biomass is high

344 (Hodgson et al. 2011). For CWM plant height, this biomass mediated competition effect was,

345 as postulated, much stronger for French *I. glandulifera* plants, with an almost absent

346 competition effect of Norwegian *I. glandulifera* plants. Previous research has shown that

347 southern European *I. glandulifera* plants grow relatively tall, with larger leaf area and little

348 branching, while more northern European plants tend to remain shorter with smaller leaves,

349 but heavily branched, when grown under greenhouse conditions (Acharya 2014). In agreement

350 with hypothesis 4, these differences might result in stronger shading and thus higher

351 competition for light by southern *I. glandulifera* plants (Bertness & Callaway 1994), even

352 though the *I. glandulifera* traits measured in this study did not differ strongly among the three

353 plant origins.

354   For LDMC, the observed CWM trait change was opposite to expectations following

355 increased competition (hypothesis 4) (Andrews et al. 2009; Hodgson et al. 2011). Our results

356 show that the increase in LDMC after invasion is likely caused by strong effects of invasion

357 (competitive displacement) on competitive (high C-sign.) and graminoid species. This pathway

358 is further supported by the significantly lower abundance of competitive species (C-sign.) in

359 invaded pots compared to non-invaded pots, when looking at invaded pots with *I. glandulifera*

360 biomass > 10 g (LMM results with cluster as random factor: $F = 4.2$, $P = 0.048$, $beta_{non\text{-}invaded}$ =

361 1.68, $beta_{invaded}$ = 1.61). Similarly, invaded pots with high graminoid abundance had lower *I.*

362 *glandulifera* biomass, again illustrating strong competition effects between graminoid species

363 and *I. glandulifera*, although in this case graminoids seemed to affect *I. glandulifera*

364 performance too, which is in agreement with previous studies (Tickner et al. 2001; Scharfy et

365 al. 2011). Alternatively, increased competition for nutrients in invaded pots could potentially

366 induce a more resource conservation strategy, thus favouring species with high LDMC. The

367 positive correlation between community trait change and invader trait change suggests that *I.*

368 *glandulifera* LDMC is less affected (reduced) in communities where it reaches high biomass,

369 and subsequently strongly affect CWM LDMC (increased).

370 The absence of species richness effects on CWM trait changes, suggests that, at least at

371 the studied small spatial scale, the theoretically expected buffering effect of species richness

372 on community trait change through functional redundancy does not occur in this system

373 (hypothesis 4) (Walker 1992; Castro-Díez et al. 2016). A decrease in CWM plant height and

374 an increase in CWM SLA was furthermore mainly observed for communities with high

375 Simpson evenness. One can expect that in communities with low evenness, the dominant

376 species have a similar shading effect on the community trait set as the invasive species has,

377 resulting in no further change in trait set for these communities. Note that the observed lower

378 abundance of competitive species in invaded pots indicates that, at least part of the CWM trait

379 changes is driven by shifts in species abundances. However, more research is needed to

380 quantify how much of the CWM trait changes are driven directly by intraspecific trait variation

381 as opposed to community composition shifts. Similarly, small differences in species

382 composition occurred among turf clusters, likely resulting in additional unexplained variation

383 in CWM trait changes. The use of fully replicated, artificial communities could resolve this

384 issue and verify our results.

385

386 *Standing biomass (productivity)*

387 Corresponding to earlier studies, the invasion by *I. glandulifera* significantly affected

388 productivity, with higher standing biomass in invaded communities (Dassonville et al. 2008).

389 Although *I. glandulifera* presence suppressed biomass production of the recipient community

390 (up to 95% biomass reduction in our study, Fig. 2b), this reduction was more than compensated

391 by the biomass produced by the invasive plant, with up to a 360% increase in biomass in our

392   study (Fig. 2b). The amount of biomass increase depended partly on *I. glandulifera* origin, with

393   lower standing biomass for communities invaded by French *I. glandulifera* plants. This

394   difference is likely caused by the previously discussed tendency of French *I. glandulifera* plants

395   to strongly shade out competitors, with comparatively less biomass (Acharya 2014).

396   In agreement with hypothesis 5, both *I. glandulifera* trait values (plant height) and

397   average community trait values (LDMC) were good predictors of changes in standing biomass.

398   This suggests that both the introduction of new trait values by the invasive species (Vitousek

399   1990; Ehrenfeld 2010; Scharfy et al. 2011) and changes in the trait set of the recipient

400   community (Lavorel et al. 1997; Mack et al. 2001; Strayer 2012) are important in governing

401   productivity (standing biomass) in this system. The absence of a strong SLA effect in our study

402   is in line with the recent study of Smart et al. (2017), which showed that community level

403   LDMC is a superior predictor of above-ground net primary production compared to SLA. The

404   community level LDMC relationship was opposite to the expectations however, suggesting

405   that caution should be taken in extrapolation theoretical species level links between functional

406   traits and productivity to invasive species impacts at the community level.

407

408   *Conclusions*

409   We observed that during invasion, *I. glandulifera* introduces trait values that strongly differ

410   from the native community mean trait values. We furthermore show that the trait set of both

411   the invader and the recipient community are significantly altered during invasion, illustrating

412   the importance of intraspecific trait variation (Davidson et al. 2011; Drenovsky et al. 2012;

413   Siefert et al. 2015). These trait changes in the invader, and to a lesser extent the community,

414   were seemingly driven by increased competition for nutrients and light, resulting in reduced

415   invader plant height and LDMC and increased SLA (Wright et al. 2004; Hodgson et al. 2011).

416   We also observed different effects on both invader and community trait changes between the

southern French populations and the northern Norwegian populations, again illustrating the importance of working with site-specific functional trait values (Davidson et al. 2011; Drenovsky et al. 2012; Acharya 2014). Community composition also mediated invasive plant effects, with stronger trait changes in competitive and graminoid dominated communities.

When evaluating changes in standing biomass, our results suggest that the introduced trait set of the invader alone is not sufficient to explain variation in productivity. Indeed, the additional change in the co-occurring species trait set also helped predicting changes in biomass production. We believe that these results form a first illustration of how both pathways of trait change can together shape changes in productivity (Lavorel et al. 1997; Ehrenfeld 2010), adding to the early exploration of the potential of adopting a functional trait-based approach to assess ecosystem functioning changes during species invasion (Scharfy et al. 2011; Castro-Díez et al. 2016). We suggest that future research should assess their validity for other, more complex ecosystem functions in both this system and other invader-community systems.

Acknowledgements

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593

Tables

Table 1. Parameter estimates of the performed intercept linear mixed models on trait differences. Models based on trait differences between 1) *I. glandulifera* and the invaded community (community-invader trait difference) 2) *I. glandulifera* grown in competition and *I. glandulifera* grown alone (invader trait difference) and 3) invaded and non-invaded communities (community trait difference). Models run for plant height, specific leaf area (SLA) and leaf dry matter content (LDMC) separately. Beta coefficient ($beta_0$, intercept), test statistic (F) and semi-partial R^2_{beta} given for each intercept. $N = 64$

	plant height			SLA			LDMC		
	$beta_0$	F	R^2_{beta}	$beta_0$	F	R^2_{beta}	$beta_0$	F	R^2_{beta}
community-invader trait difference	-76.28	69.5***	0.764	-4.42	3.5[(*)]	0.142	66.04	96.1***	0.825
invader trait difference	-65.16	64.1***	0.749	6.41	15.8**	0.425	-14.92	12.9**	0.383
community trait difference	-10.22	4.1*	0.161	-1.81	1.2	0.054	7.92	1.0	0.047

Significance: [(*)]: $0.10 \geq P$-value > 0.05; [*]: $0.05 \geq P$-value > 0.01; [**]: $0.01 \geq P$-value > 0.001; [***]: $0.001 \geq P$-value.

Table 2. Parameter estimates of the performed linear mixed models on trait differences between invaded and non-invaded communities (community trait difference). Models run for plant height, specific leaf area (SLA) and leaf dry matter content (LDMC) separately. Beta coefficient (slope), test statistic (F) and semi-partial R^2_{beta} given for each retained predictor after model reduction. C-signature = mean biomass weighted functional competition signature, FR = France, IMP = *Impatiens glandulifera*, NO = Norway, SE = Sweden, % graminoids = biomass weighted mean percentage of graminoid species. $N = 64$

	plant height			SLA			LDMC		
	beta	F	R^2_{beta}	beta	F	R^2_{beta}	beta	F	R^2_{beta}
Invasive species									
IMP origin	$beta_{FR}$ 32.35 $beta_{SE}$ 13.33 $beta_{NO}$ 14.59	2.2	0.051						
IMP biomass	-0.06	6.9*	0.109				0.33	4.8*	0.078
IMP origin*biomass	$beta_{FR}$ -0.57 $beta_{SE}$ -0.16 $beta_{NO}$ -0.06	2.6(*)	0.055						
invader trait difference							0.45	7.8**	0.142
Community									
evenness	-37.75	4.6*	0.080	13.89	11.6***	0.197			
C-signature[a]							117.01	9.2**	0.140
% graminoids							0.70	9.7**	0.141

Significance: (*): $0.10 \geq P$-value > 0.05; *: $0.05 \geq P$-value > 0.01; **: $0.01 \geq P$-value > 0.001; ***: $0.001 \geq P$-value. [a] = logarithm transformation.

617　**Table 3.** Parameter estimates of the performed linear mixed models on standing biomass

618　difference between invaded and non-invaded communities. Beta-coefficient (slope) and test

619　statistic (*F*) and semi-partial R^2_{beta} given for each retained predictor after model reduction. C-

620　signature = mean biomass weighted functional competition signature, FR = France, IMP =

621　*Impatiens glandulifera*, LDMC = leaf dry matter content, NO = Norway, SE = Sweden. *N* =

622　64

623

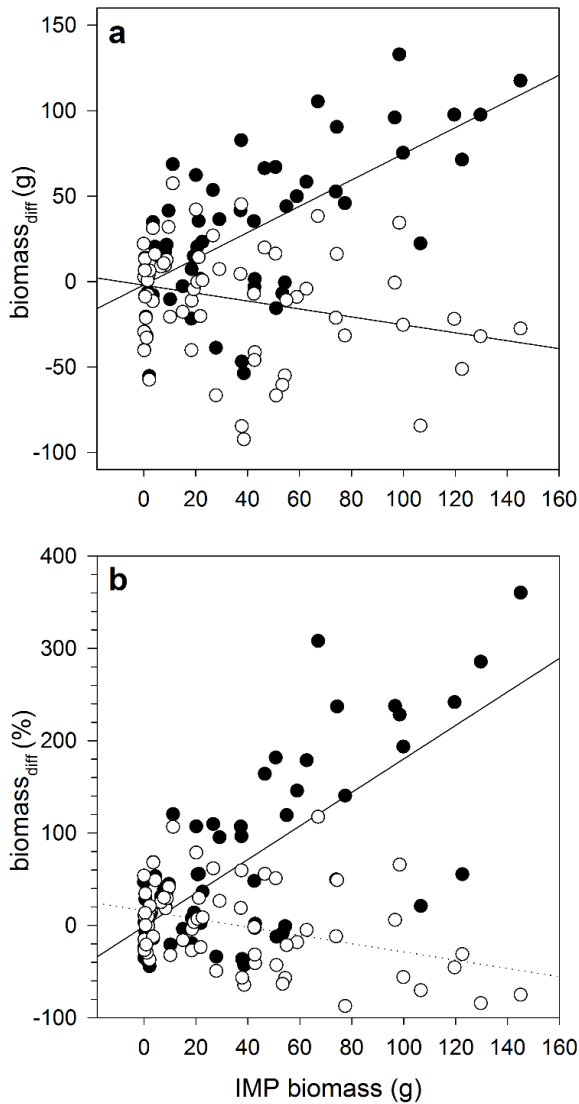|	Standing biomass change		
	beta	*F*	R^2_{beta}
Invasive species			
IMP origin	$beta_{FR}$ -30.44	4.2[*]	0.098
	$beta_{SE}$ -16.13		
	$beta_{NO}$ -6.19		
IMP plant height	0.29	13.1[**]	0.196
Community			
CWM LDMC	0.29	10.7[**]	0.162

624

625　Significance: [*]: $0.05 \geq P$-value > 0.01; [**]: $0.01 \geq P$-value > 0.001; [***]: $0.001 \geq P$-value.

626　**Figures**
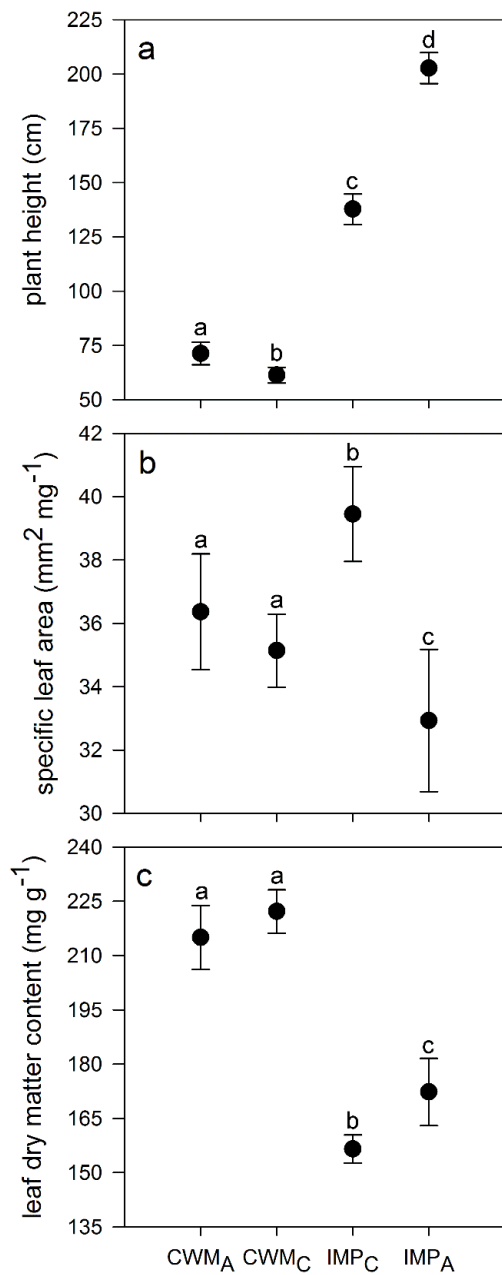
627

628　**Figure 1.** Mean and standard error trait values for uninvaded communities (CWM$_A$), invaded

629　communities (CWM$_C$), *I. glandulifera* growing in competition (IMP$_C$) and *I. glandulifera*

630　growing alone (IMP$_A$). Separate graphs for a) plant height, b) specific leaf area (SLA) and c)

631　leaf dry matter content (LDMC). Significantly different mean values are indicated with

632　different letters.

Figure 2. The relationships between *I. glandulifera* biomass and the total standing biomass difference between invaded and non-invaded communities (biomass$_{diff}$), both including *I. glandulifera* biomass (full circles, continuous line) and excluding *I. glandulifera* biomass (open circles, dotted line). Relationships visualized for a) absolute values of biomass$_{diff}$ and b) percentage values of biomass$_{diff}$ compared to community control pot biomass.
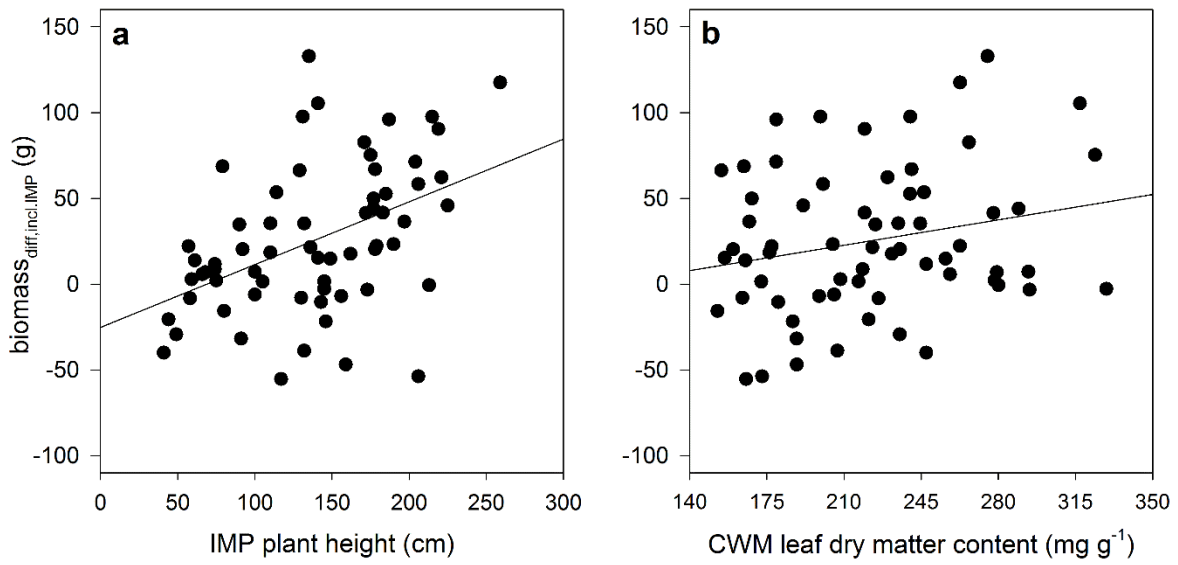
Figure 3. The relationships between the total standing biomass (including *I. glandulifera* biomass) difference between invaded and non-invaded communities (biomass$_{diff,incl\ IMP}$) and a) *I. glandulifera* plant height and b) community biomass weighted mean leaf dry matter content (LMDC).

Electronic appendices

Appendix S1. Species list for the full study. C-S-R plant functional type (Grime 1977) and graminoid identity given for each species.

Appendix S2. Overview of pot-level trait values and biotic factors.

Appendix S3. Extended methods section

Appendix S4. Parameter estimates of the performed linear mixed models on invader trait values and invader trait differences to test for *I. glandulifera* origin differences.

Appendix S5. Parameter estimates of the performed linear mixed models on invader performance (biomass).