1    **A native herbaceous community exerts a strong allelopathic effect on the woody**

2    **range-expander *Betula fruticosa***

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13    Running title: Allelochemicals of a native herbaceous community may suppress shrub

14    encroachment

15

16 **Abstract**

17 Biological invasions by range-expanding native and alien plant species often reduce native

18 plant community diversity and productivity. Superior performance of some invasive plants

19 over native plants is due to production of allelochemicals by invaders that suppress growth of

20 native plants. Nevertheless, native plants can also produce allelopathic compounds, which

21 may provide biotic resistance against invasive plant species, in accordance with the homeland

22 security hypothesis. In support of the hypothesis, several previous studies found evidence for

23 allelopathic effects of native plant species on alien plant species. However, as most of these

24 studies tested allelopathic effects of single native plant species on invasive plant species, the

25 contribution of allelopathy to the resistance of native plant communities to invasion has

26 received considerably less attention. Here, we performed two competition experiments in a

27 greenhouse to test for potential pairwise allelopathic effects on each other of a woody

28 range-expander *Betula fruticosa* and a community of four native herbaceous species in China.

29 We tested whether *B. fruticosa* and the herbaceous community differed in their competitive

30 effects and responses, and whether these were changed by the presence of activated carbon –

31 an allelopathy neutralizer in the soil. Results show that presence of activated carbon

32 ameliorated suppressive effects of the resident herbaceous community on above-ground

33 biomass of *B. fruticosa*. By contrast, presence of activated carbon tended to aggravate

34 suppressive effects of *B. fruticosa* on the resident herbaceous community. Overall, these

35 results provide support to the homeland security hypothesis and suggest that strong biotic

36 resistance of the resident herbaceous community may limit invasion success of the woody

37 range-expander *B. fruticosa*.

**Introduction**

Biological invasions by range-expanding native and alien plant species often have detrimental ecological and socioeconomic impacts (Essl et al. 2019; Schaffner et al. 2020; Vilà and Hulme 2017). As the number of range-expanding species will likely continue to increase (Essl et al. 2019; Seebens et al. 2021), it is important to identify mechanisms that underlie establishment of plants and invasibility of the resident plant communities. Invasive plants may outperform resident plants through superior competition for resources necessary for growth such as soil moisture, nutrients, and light (Gallien and Carboni 2017; Theoharides and Dukes 2007). Studies also indicate that superior performance of some invasive plants over native plants is due to production of allelochemicals by invaders that suppress growth of native plants (Baker 1974; Callaway and Aschehoug 2000; Hickman et al. 2021; Oduor et al. 2020). In support of this idea, a recent synthesis found that majority of 524 invasive plant species that were studied produce allelochemicals with the potential to negatively affect native plant growth (Kalisz et al. 2021). The observation that many invasive plants are allelopathic led to the formulation of the novel weapons hypothesis, which posits that some alien plants are successful invaders because they produce chemical compounds that are toxic to naïve native plants (Callaway and Ridenour 2004). Numerous studies find support for the novel weapons hypothesis (e.g., Abhilasha et al. 2008; Becerra et al. 2018; Inderjit et al. 2011; Ridenour and Callaway 2001; Thorpe et al. 2009), which suggests that allelopathy might indeed play an important role in plant invasions.

Native plants can also produce allelopathic compounds, which may provide biotic resistance against invasive plant species that are naïve to allelochemicals of the natives (Rabotnov 1982; Weidenhamer and Romeo 2005), in accordance with the homeland security hypothesis (Cummings et al. 2012). Several previous studies found evidence for allelopathic effects of native plant species on alien species (Adomako et al. 2019; Christina et al. 2015;

64    Cummings et al. 2012; Hou et al. 2011; Mignoni et al. 2018; Ning et al. 2016; Weidenhamer

65    and Romeo 2005; Yuan et al. 2021). However, as most of these studies tested allelopathic

66    effects of single native plant species on invasive plant species, the contribution of allelopathy

67    to the resistance of native plant communities to invasion has received considerably less

68    attention (Yuan et al. 2022). Native plant communities may have strong allelopathic effects on

69    invaders because there may be a high likelihood that species-rich native communities harbour

70    at least one species that produces a disproportionately higher concentration of potent

71    allelochemicals or there could be synergistic effects of different allelochemicals from different

72    species within the community (Yuan et al. 2022). This prediction has received little empirical

73    test (but see Adomako et al. 2019; Ning et al. 2016; Yuan et al. 2022).

74        Temperate herbaceous wetlands of China have been experiencing encroachment by

75    various range-expanding shrub species in recent decades, as a consequence of global

76    warming and anthropogenic disturbances (Lee et al. 2017; Lett and Dorrepaal 2018; Vuorinen

77    et al. 2017). Because of the fundamental differences in functional traits between the

78    range-expanding shrubs and native herbaceous species (Zhang et al. 2021a), shrub

79    encroachment may threaten native plant community diversities. *Betula fruticosa* is one of the

80    prominent range-expanding shrub species within the herbaceous wetlands (Zhang et al.

81    2021a). The species is distributed in Inner Mongolia and northern Heilongjiang

82    (http://www.iplant.cn) where it grows at 600-1100 meters above sea level, and flowers and

83    fruits between June and August. It has been expanding and gradually occupying a dominant

84    position in the herb-dominated wetland habitats of the Sanjiang Plain in Northeast China

85    (Zhang et al. 2021a). However, whether allelopathy mediates interaction between *B. fruticosa*

86    and resident herbaceous communities remains unclear.

87        In this study, we performed a greenhouse experiment to test a prediction of the homeland

88    security hypothesis that native plant communities may resist invasion by the range-expander

89   *B. fruticosa* through inhibitory allelopathic effects. We addressed two questions: (1) Do *B.*

90   *fruticosa* and the community have mutual allelopathic effects on each other? (2) Are the

91   allelopathic effects of the community on *B. fruticosa* stronger than those of *B. fruticosa* on

92   the community?

93

94   **Material and Methods**

95   **Study species and cultivation**

96   All the study species used for the experiment co-occur naturally in the Sanjiang Plain of

97   northeast China, and their seeds were collected from wild populations (**Table 1**). On 3

98   January 2021, we sowed seeds of *B. fruticosa* into plastic trays (19.5 cm × 14.6 cm × 6.5 cm)

99   that had been filled with a sterilized growth medium that comprised a mixture of sand and

100  fine vermiculite (Pindstrup Plus, Pindstrup Mosebrug A/S, Denmark; pH: 6; 120.0 mg/L N;

101  12.0 mg/L P; 400.0 mg/L K; 28.0 mg/L Mg; 0.4 mg/L B; 2.0 mg/L Mo; 1.7 mg/L Cu; 2.9

102  mg/L Mn; 0.9 mg/L Zn; 8.4 mg/L Fe) 25%, 25%, 50%) in a ratio of 1:1 (v/v). The growth

103  medium had been sterilized with a dose of 25 kGy of $60CO\gamma$ irradiation for four days (at the

104  Harbin Guangya Radiation New Technology Co., Ltd.,Harbin, China) to eliminate the

105  potential influence of live soil organisms. One month later (i.e. 3 February 2021), we

106  transplanted 200 similar-sized *B. fruticosa* individuals into a seedling tray, one individual in

107  each tray hole. Between 19 February and 23 March, we fertilized the seedlings with 1g/L of

108  Peters Professional® liquid fertilizer once every week for a total of five weeks. The fertilizer

109  contained the following nutrients: 20% nitrogen, 20% potassium oxide ($K_2O$), 0.02% Boron,

110  0.015% Cooper, 0.12% Iron, 0.06% Manganese, 0.010% Molybdenum, and 0.08% Zinc. On

111  15 February, we sowed approximately 200 seeds for each of the four wetland herb species in

112  trays that had been filled with the same sterilized growth medium as above. We placed all

113      trays with seeds in a greenhouse under natural light conditions, with a temperature between

114      15 and 25 ℃.

115

116      **Experimental set-up and measurement**

117      To assess whether allelopathy mediates competitive interactions between *B. fruticosa* and the

118      resident native herbaceous community, we performed two separate greenhouse experiments.

119      The first experiment aimed to test allelopathic effect of the woody plant *B. fruticosa* on the

120      herbaceous community of native species (Experiment-1), while the second experiment tested

121      allelopathic effect of the herbaceous community on *B. fruticosa* (Experiment-2) (**Figure S1**).

122      Both experiments employed a fully-crossed factorial design. In Experiment 1, we grew the

123      native community with vs. without *B. fruticosa* and in the presence vs. absence of activated

124      carbon (**Figure S1**). In Experiment 2, we grew the woody plant *B. fruticosa* with vs. without

125      the native community and in the presence vs. absence of activated carbon (**Figure S1**).

126      Activated carbon is widely used in ecological studies to adsorb and neutralize potential

127      allelochemicals produced by experimental plants (Kabouw et al. 2010; Zhang et al. 2021b).

128      To set up the experiments, we filled 160 circular 2.5-L plastic pots (top diameter × bottom

129      diameter × height: 18.5 cm × 12.5 cm × 15 cm) with a sterilized growth medium that had

130      been prepared as described above. In each pot, we homogenized the growth medium with 5 g

131      of a slow-release fertilizer (Osmocote Exact Standard; 15.00% N + 9.00% phosphorus

132      pentoxide + 12.00% potassium oxide + 2.00% magnesium oxide + 0.02% B + 0.05% Cu +

133      0.45% Fe + 0.09% cheated by EDTA + 0.06% Mn + 0.02% Mo + 0.015% Zn; Everris

134      International B.V., Geldermalsen, The Netherlands). We then homogenized pot content with

135      50 mL of activated carbon (Analytical purity of activated carbon powder, pH 5.0-7.0;

136      Sinopharm Chemical Reagent Co., Ltd, China), for a half of the pots (n=80).

137           In Experiment 1, we transplanted an individual of each of the four native herbaceous

138    species in 80 pots. A half of the pots contained activated carbon, while the other half did not.

139    The individual seedling were transplanted at equal distances from each other in a circular

140    formation. Then we introduced an individual *B. fruticosa* into the middle of the pot, for a half

141    of the pots with and without activated carbon. In experiment 2, we transplanted *B. fruticosa*

142    individuals in the center of the pot. In a half of pots with and with activated carbon treatment,

143    we transplanted an individual seedling of each of the four herbaceous species at equal

144    distances from each other in a circular formation around *B. fruticosa*. Each of the two

145    experiments had two levels of competition: (Community grown without *B. fruticosa* vs.

146    community grown with *B. fruticosa* for Experiment 1 and *B. fruticosa* grown with

147    community vs. *B. fruticosa* grown without community for Experiment 2) × 2 levels of

148    activated carbon (with vs. without activated carbon) × 20 replicates (**Figure S1**). Immediately

149    after transplant, we randomly assigned the 160 pots to positions on one greenhouse bench

150    (temperature: 22-28 °C; relative humidity 60%; natural lighting) and watered them regularly.

151    The two experiments lasted 123 days and were performed concurrently at the Northeast

152    Institute of Geography and Agroecology of the Chinese Academy of Sciences (43°59'49"N,

153    125°24'3"E).

154        On 2 July 2021, we harvested above-ground biomass of native herbaceous community in

155    Experiment 1 and above-ground biomass of *B. fruticosa* in Experiment 2. Three *B. fruticosa*

156    individuals (one grown alone) died during the experiment, thus we harvested above-ground

157    biomass of 77 *B. fruticosa* and 80 herbaceous community. All the plant materials were dried

158    at 65 °C for 72 hours and then weighed to an accuracy of 0.0001 g.

159

160    **Statistical analyses**

161    To test the mutual allelopathy between *B. fruticosa* and the native herbaceous community, we

162    fitted two separate Bayesian multilevel models in R 4.0.2 (R Core Team 2020) using the *brm*

163  function in the *brms* package (Bürkner 2017). As the above-ground biomass of *B. fruticosa*

164  and the native herbaceous community had Gaussian error distributions, we applied cube root

165  transformation of the data prior to the analysis to improve normality and homogeneity of the

166  residuals. The fixed part of each model included competition treatment (two levels each for

167  experiments 1 and 2), activated carbon treatment (with vs. without activated carbon), and

168  two-way interaction between the two factors. Each model was run with four independent

169  Markov chains of 4, 000 iterations, discarding the first 2, 000 iterations per chain as warm-up

170  and resulting in 8, 000 posterior samples overall. To directly test hypotheses about the main

171  and interactive effects based on each coefficient's posterior distribution, we used the sum

172  coding, which effectively 'centers' the effects to the grand mean (i.e., the mean value across

173  all data observations; Schad et al. 2020). To implement this in *brms*, we used the functions

174  *contrasts* and *contr.sum* of the *stats* package in R. We considered the two fixed factors

175  (competition and activated carbon), and interaction between them as significant when their 95%

176  credible interval of the posterior distribution did not overlap zero, and as marginally

177  significant when their 90% credible intervals did not overlap zero.

178

179  **Results**

180  Above-ground biomass of *B. fruticosa* was significantly influenced by main and interactive

181  effects of competition and activated carbon treatments (**Table 2; Fig. 1**). In the absence of

182  activated carbon, competition from the community reduced above-ground biomass of *B.*

183  *fruticosa* by 68.43% (**Fig. 1a**). However, in the presence of activated carbon, *B. fruticosa*

184  produced similar above-ground biomass in the presence (1.16 g) vs. absence (1.32 g) of

185  competition from the herbaceous community (**Fig. 1a**). By contrast, above-ground biomass of

186  the resident herbaceous community was significantly influenced by the main effect of

187  competition from *B. fruticosa* and marginally by an interaction between activated carbon and

188 competition (**Table 2; Fig. 1).** Specifically, averaged across the activated carbon treatments,

189 competition from *B. fruticosa* reduced mean above-ground biomass of the herbaceous

190 community by 19.4% (**Fig. 1b**). Nevertheless, presence of activated carbon marginally

191 aggravated the suppressive effect of *B. fruticosa* on the community above-ground biomass

192 (**Fig. 1c**). Specifically, competition from *B. fruticosa* reduced the community above-ground

193 biomass by 30.33% in the presence of activated carbon and by 5.7% in the absence of

194 activated carbon (**Fig. 1c**).

195

196 **Discussion**

197 We tested allelopathic interactions between a range-expanding native shrub *B. fruticosa* and a

198 native herbaceous community, and results suggest that presence of activated carbon

199 ameliorated suppressive effects of the resident herbaceous community on above-ground

200 biomass of *B. fruticosa* (**Fig. 1a**). By contrast, presence of activated carbon tended to

201 aggravate suppressive effects of the range-expander shrub on the resident herbaceous

202 community (**Fig. 1c**). Overall, these results suggest that the resident herbaceous community

203 had a strong allelopathic effect on *B. fruticosa*, and that these effects were neutralized or

204 reduced by activated carbon. On the other hand, *B. fruticosa* had little allelopathic effect on

205 the community. Taken together, the results provide a strong support for the homeland security

206 hypothesis (Cummings et al. 2012), but little support for the novel weapons hypothesis

207 (Callaway and Ridenour 2004).

208     The present results complement those of the few other studies that tested whether the

209 novel-weapons hypothesis and homeland-security hypothesis can both explain competitive

210 interactions between alien and native plant species within the same community, with mixed

211 findings. While the novel weapons hypothesis predicts strong allelopathic effects of alien

212 plant species on native plant species (Callaway and Ridenour 2004), the homeland security

213  hypothesis posits that the reverse should also be true (Cummings et al. 2012). A recent study

214  of interactions between five alien and five native herbaceous species in China found that alien

215  species had negative allelopathic and resource-based competitive effects on native plants,

216  while the reverse was also true (Yuan et al. 2021). The native plant *Sesbania virgata* had

217  strong allelopathic effects on the alien plant *Leucaena leucocepahala* in Brazil, while the

218  alien did not affect the native through allelopathy (Mignoni et al. 2018). Other studies have

219  demonstrated allelopathic effects of native plant species on alien species but did not

220  simultaneously test allelopathic effects of aliens on natives (e.g., Cummings et al. 2012; Hou

221  et al. 2011; Weidenhamer and Romeo 2005). More studies are needed to enhance

222  understanding of the generality of both novel weapons hypothesis and homeland security

223  hypothesis operating in the same invaded communities.

224      Our result showed that suppressive effects of *B. fruticosa* on the native herbaceous

225  community tended to be stronger in the presence (rather than absence) of activated carbon

226  (**Fig. 1c**). This could partly reflect that activated carbon released the allelopathic suppression

227  among native species in the non-invaded community, and thus increased their biomass

228  production. On the other hand, activated carbon tended to facilitate greater growth of *B.*

229  *fruticosa* in the invaded community, and hence it's stronger suppressive effects on the

230  community. Activated carbon has been successfully used in several studies on allelopathy

231  (e.g., Inderjit and Callaway 2003; Lankau 2010; Mahall and Callaway 1992; Mangla,

232  Callaway 2008; Yuan et al. 2021). However, activated carbon can alter soil nutrient

233  availability and plant growth even in the absence of the focal allelopathic agent (e.g.,

234  Kabouw et al. 2010; Lau et al. 2008; Weißhuhn and Prati 2009). For example, activated

235  carbon caused an increase in the specific root length and root branching in a study of 10 plant

236  species (Yuan et al. 2021). In the present case, it is likely that activated carbon caused a

237  reduction in soil nutrient availability to plants by adsorbing the nutrients leading to stronger

238    competitive effects of *B. fruticosa* on the resident herbaceous community.

239        The present results suggesting significant negative allelopathic effects of a native plant

240    community on the range-expander *B. fruticosa*, complement those of a few other studies that

241    tested for allelopathic effects of native plant communities on alien plant species, with mixed

242    results. For instance, native plant communities had negative allelopathic effects on the

243    invader *Solidago canadensis* in China (Adomako et al. 2019). Ning et al. (2016) also found

244    evidence for allelopathic effects of native plant communities on alien species in Germany.

245    These findings provide support for the homeland-security hypothesis. In contrast,

246    allelochemicals of diverse native plant communities did not provide resistance but instead

247    facilitated the germination of six alien invasive plant species (Yuan et al. 2022). However, as

248    the few studies that have tested allelopathic effects of native plants on invasive plants have

249    focused on herbaceous invasive species only, it remains unclear whether allelopathic effects

250    of native plant communities may differ between woody and non-woody invasive species.

251        In conclusion, our results suggest an asymmetric allelopathic interaction between the

252    native herbaceous community and *B. fruticosa* as the native herbaceous community likely

253    had strong negative effect on *B. fruticosa* through alleloptahy, but the reverse was not true. In

254    line with the homeland security hypothesis, strong biotic resistance of the resident herbaceous

255    community may limit invasion success of the range-expander *B. fruticosa*.

256

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262

263 **Conflict of interest**

264 The authors have declared that no competing interests exist.

265

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269

270 **Author contributions**

271 YL conceived the idea and designed the experiment. LW performed the experiment. LW and

272 YL analyzed the data. LW wrote the draft of the manuscript, with further inputs from YL and

273 AMOO.

274

275 **Data accessibility**

276 Should the manuscript be accepted, the data supporting the results will be archived in Dryad

277 and the data DOI will be included at the end of the article.

## References

Abhilasha D, Quintana N, Vivanco J et al (2008) Do allelopathic compounds in invasive *Solidago canadensis* s.l. restrain the native European flora? J Ecol 96:993-1001. https://doi.org/10.1111/j.1365-2745.2008.01413.x

Adomako MO, Ning L, Tang M et al (2019) Diversity- and density-mediated allelopathic effects of resident plant communities on invasion by an exotic plant. Plant Soil 440:581-592. 10.1007/s11104-019-04123-9

Baker HG (1974) The evolution of weeds. Annu Rev Ecol Syst 5:1-24. https://www.jstor.org/stable/2096877

Becerra PI, Catford JA, Inderjit et al (2018) Inhibitory effects of Eucalyptus globulus on understorey plant growth and species richness are greater in non-native regions. Global Ecol Biogeogr 27:68-76. https://doi.org/10.1111/geb.12676

Bürkner PC (2017) Advanced Bayesian multilevel modeling with the R package brms. arXiv preprint arXiv:1705.11123. http://arxiv.org/abs/1705.11123

Callaway RM, Aschehoug ET (2000) Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. Science 290:521-523. https://doi.org/10.1126/science.290.5491.521

Callaway RM, Ridenour WM (2004) Novel weapons: invasive success and the evolution of increased competitive ability. Front Ecol Environ 2:436-443. https://doi.org/10.1890/1540-9295

Christina M, Rouifed S, Puijalon S et al (2015) Allelopathic effect of a native species on a major plant invader in Europe. Sci Nat-Heidelberg 102:12. https://doi.org/10.1007/s00114-015-1263-x

Cummings JA, Parker IM, Gilbert GS (2012) Allelopathy: a tool for weed management in forest restoration. Plant Eco 213:1975-1989. https://doi.org/10.1007/s11258-012-0154-x

Essl F, Dullinger S, Genovesi P et al (2019) A Conceptual framework for range-expanding species that track human-induced environmental change. BioScience 69:908-919. https://doi.org/10.1093/biosci/biz101

Gallien L, Carboni M (2017) The community ecology of invasive species: where are we and

307    what's next? Ecography 40:335-352. https://doi.org/10.1111/ecog.02446

308    Hickman DT, Rasmussen A, Ritz K, et al (2021) Review: Allelochemicals as multi-kingdom

309        plant defence compounds: towards an integrated approach. Pest Manag Sci

310        77:1121-1131. https://doi.org/10.1002/ps.6076

311    Hou YP, Peng SL, Chen BM et al (2011) Inhibition of an invasive plant (*Mikania micrantha*

312        H.B.K.) by soils of three different forests in lower subtropical China. Biol Invasions

313        13:381-391. https://doi.org/10.1007/s10530-010-9830-8

314    Inderjit, Callaway RM (2003) Experimental designs for the study of allelopathy. Plant Soil

315        256:1-11. https://doi.org/10.1023/A:1026242418333

316    Inderjit, Evans H, Crocoll C et al (2011) Volatile chemicals from leaf litter are associated

317        with invasiveness of a Neotropical weed in Asia. Ecology 92:316-324.

318        https://doi.org/10.1890/10-0400.1

319    Kabouw P, Nab M, van Dam NM (2010) Activated carbon addition affects substrate pH and

320        germination of six plant species. Soil Biol Biochem 42:1165-1167.

321        https://doi.org/10.1016/j.soilbio.2010.02.022

322    Kalisz S, Kivlin SN, Bialic-Murphy L (2021) Allelopathy is pervasive in invasive plants. Biol

323        Invasions 23:367-371. https://doi.org/10.1007/s10530-020-02383-6

324    Lankau R (2010) Soil microbial communities alter allelopathic competition between *Alliaria*

325        *petiolata* and a native species. Biol Invasions 12:2059-2068.

326        https://doi.org/10.1007/s10530-009-9608-z

327    Lau JA, Puliafico KP, Kopshever JA et al (2008) Inference of allelopathy is complicated by

328        effects of activated carbon on plant growth. New Phytol 178:412-423.

329        https://doi.org/10.1111/j.1469-8137.2007.02360.x

330    Lee A, Fujita H, Kobayashi H (2017) Effects of drainage on open-water mire pools: open

331        water shrinkage and vegetation change of pool plant communities. Wetlands 37:741-751.

332        https://doi.org/10.1007/s13157-017-0907-3

333    Lett S, Dorrepaal E (2018) Global drivers of tree seedling establishment at alpine treelines in

334        a changing climate. Funct Ecol 32:1666-1680. https://doi.org/10.1111/1365-2435.13137

335    Mahall BE, Callaway RM (1992) Root communication mechanisms and intracommunity

336        distributions of two Mojave Desert shrubs. Ecology 73:2145-2151.

337    https://doi.org/10.2307/1941462

338    Mangla S, Callaway RM (2008) Exotic invasive plant accumulates native soil pathogens

339    which inhibit native plants. J Ecol 96:58-67.

340    https://doi.org/10.1111/j.1365-2745.2007.01312.x

341    Mignoni DSB, Simões K, Braga MR (2018) Potential allelopathic effects of the tropical

342    legume *Sesbania virgata* on the alien *Leucaena leucocephala* related to seed

343    carbohydrate metabolism. Biol Invasions 20:165-180.

344    https://doi.org/10.1007/s10530-017-1524-z

345    Ning L, Yu FH, van Kleunen M (2016) Allelopathy of a native grassland community as a

346    potential mechanism of resistance against invasion by introduced plants. Biol Invasions

347    18:3481-3493. https://doi.org/10.1007/s10530-016-1239-6

348    Oduor AMO, van Kleunen M, Stift M (2020) Allelopathic effects of native and invasive

349    *Brassica nigra* do not support the novel-weapons hypothesis. Am J Bot 107:1106-1113.

350    https://doi.org/10.1002/ajb2.1516

351    Rabotnov T (1982) Importance of the evolutionary approach to the study of allelopathy.

352    Ékologia 3:5-8. (translated from Russian)

353    Ridenour WM, Callaway RM (2001) The relative importance of allelopathy in interference:

354    the effects of an invasive weed on a native bunchgrass. Oecologia 126:444-450.

355    https://doi.org/10.1007/s004420000533

356    Schad DJ, Vasishth S, Hohenstein S et al (2020) How to capitalize on a priori contrasts in

357    linear (mixed) models: A tutorial. J Mem Lang 110:104038.

358    https://doi.org/10.1016/j.jml.2019.104038

359    Schaffner U, Steinbach S, Sun Y et al (2020) Biological weed control to relieve millions from

360    *Ambrosia* allergies in Europe. Nat Commun 11:1745.

361    https://doi.org/10.1038/s41467-020-15586-1

362    Seebens H, Bacher S, Blackburn TM et al (2021) Projecting the continental accumulation of

363    alien species through to 2050. Global Change Biol 27:970-982.

364    https://doi.org/10.1111/gcb.15333

365    Team RC R 2020. R: A language and environment for statistical computing. R Foundation for

366    Statistical Computing. Vienna, Austria: URL http://www. R-project. org/.

Theoharides KA, Dukes JS (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. New Phytol 176:256-273. https://doi.org/10.1111/j.1469-8137.2007.02207.x

Thorpe AS, Thelen GC, Diaconu A et al (2009) Root exudate is allelopathic in invaded community but not in native community: field evidence for the novel weapons hypothesis. J Ecol 97:641-645. https://doi.org/10.2307/20528894

Vilà M, Hulme PE (2017) Impact of biological invasions on ecosystem services. Springer, Berlin.

Vuorinen KEM, Oksanen L, Oksanen T et al (2017) Open tundra persist, but arctic features decline—Vegetation changes in the warming Fennoscandian tundra. Global Change Biol 23:3794-3807. https://doi.org/10.1111/gcb.13710

Weidenhamer JD, Romeo JT (2005) Allelopathy as a mechanism for resisting invasion: the case of *Polygonella myriophylla*. In: Inderjit (Eds.) Invasive plants: ecological and agricultural aspects. Birkhäuser Basel, Basel, pp. 167-177

Weißhuhn K, Prati D (2009) Activated carbon may have undesired side effects for testing allelopathy in invasive plants. Basic Appl Ecol 10:500-507. https://doi.org/10.1016/j.baae.2008.10.009

Yuan L, Li JM, Yu FH et al (2021) Allelopathic and competitive interactions between native and alien plants. Biol Invasions 23:3077-3090. 10.1007/s10530-021-02565-w

Yuan L, Li J, van Kleunen M (2022) Diversity of resident plant communities could weaken their allelopathic resistance against alien and native invaders. Biol Invasions 24:607-619. 10.1007/s10530-021-02667-5

Zhang X, Jiang S, Jiang W et al (2021a) Shrub encroachment balances soil organic carbon pool by increasing carbon recalcitrance in a temperate herbaceous wetland. Plant Soil 464:347-357. https://doi.org/10.1007/s11104-021-04975-0

Zhang Z, Liu Y, Yuan L et al (2021b) Effect of allelopathy on plant performance: a meta-analysis. Ecol Lett 24:348-362. https://doi.org/10.1111/ele.13627

**Tables**

**Table 1.** Information on the plant species that were used in the present study

| Species | Family | Growth form | Life cycle | Reproduction mode |
|---|---|---|---|---|
| *Betula fruticosa* | Betulaceae | Shrub | Perennial | Seed |
| *Sanguisorba officinalis* | Rosaceae | Herbaceous | Perennial | Seed |
| *Gentiana manshurica* | Gentianaceae | Herbaceous | Perennial | Seed |
| *Sium suave* | Apiaceae | Herbaceous | Perennial | Seed |
| *Deyeuxia angustifolia* | Poaceae | Herbaceous | Perennial | Seed |

**Table 2** Output of two separate Bayesian multilevel models that were run to test the effects of competition treatment (Community grown without

*B. fruticosa* vs. community grown with *B. fruticosa* for Experiment 1 and *B. fruticosa* grown with community vs. *B. fruticosa* grown without

community for Experiment 2), activated carbon treatment (with vs. without activated carbon), and two-way interaction between the two

treatments on above-ground biomass of *B. fruticosa* and a resident herbaceous community in each pot. Shown are the model estimates and

standard errors (SE) as well as the lower (L) and upper (U) values of the 95% and 90% credible intervals (CI).

|  |  | Estimate | SE | L95%CL | U95%CL | L90%CL | U90%CL |
|---|---|---|---|---|---|---|---|
| **Above-ground biomass of *B. fruticosa*** | Intercept | 0.958* | 0.053 | 0.854 | 1.061 | 0.869 | 1.045 |
|  | Activated carbon (A) | 0.114* | 0.053 | 0.01 | 0.218 | 0.027 | 0.202 |
|  | Competition (C) | 0.130* | 0.052 | 0.027 | 0.233 | 0.044 | 0.217 |
|  | A×C | 0.128* | 0.054 | 0.021 | 0.236 | 0.04 | 0.217 |
| **Above-ground biomass of resident herbaceous community** | Intercept | 1.796* | 0.025 | 1.748 | 1.844 | 1.755 | 1.837 |
|  | Activated carbon (A) | -0.008 | 0.024 | -0.056 | 0.04 | -0.048 | 0.033 |
|  | Competition (C) | 0.071* | 0.025 | 0.022 | 0.119 | 0.029 | 0.111 |
|  | A×C | -0.048 † | 0.024 | -0.095 | 0.001 | -0.087 | -0.008 |

Model estimates whose 95% credible intervals do not overlap with zero are indicated with asterisks (*), and those whose 90% credible intervals do not

overlap with zero are indicated with daggers (†).
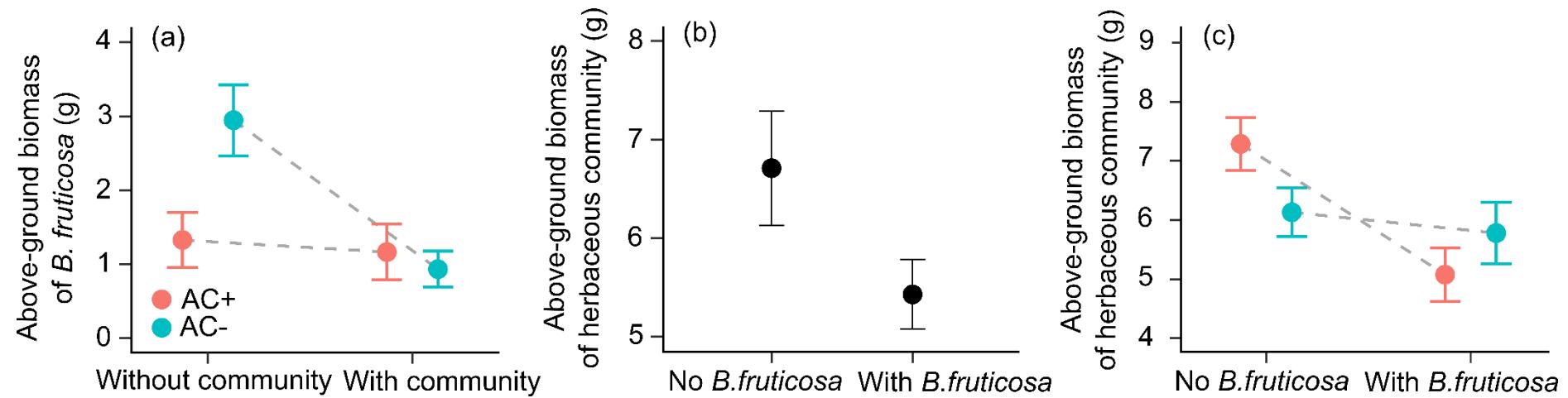
**Figures**



Figure 1 Mean values (± SE) of above-ground biomass of *B. fruticosa* (**a**), herbaceous community (**b & c**). Shown are main and interactive effects of    presence (with community) vs. absence (without community) of competition from a resident herbaceous community, presence (AC+) vs. absence (AC-) of activated carbon, and presence (with *B. fruticosa*) vs. absence (No *B. fruticosa*) of competition from *B. fruticosa* (*cf.* **Table 2**).

**Supporting information**
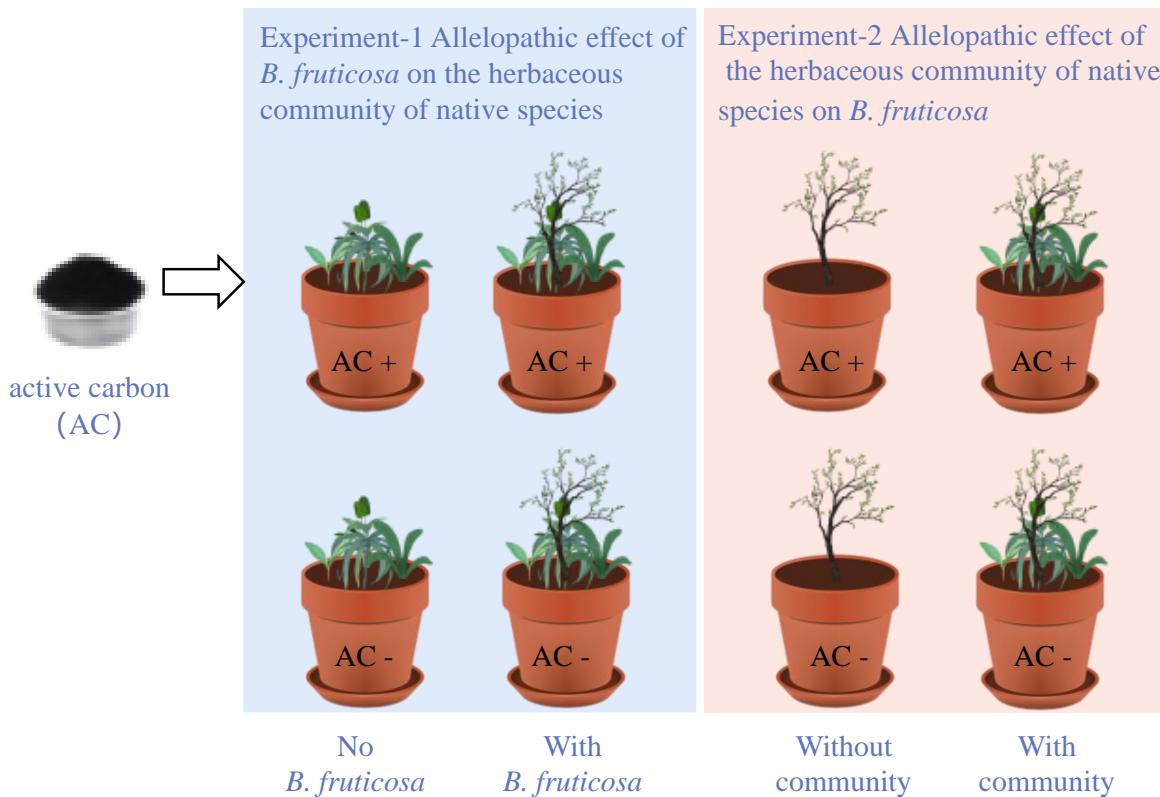


**Figure S1.** A schematic of an experimental set-up to test allelopathic interactions between a range-expanding species *Betulla fruticosa* and a native plant community of four species *Sanguisorba officinalis, Gentiana manshurica, Sium suave*, and *Deyeuxia angustifolia*. Activated carbon was used to neutralize allelochemicals.