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**Applied Vegetation Science****Native parasitic plants: biological control for plant invasions?**

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1 **Native parasitic plants: biological control for plant invasions?**

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12

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19

20 **Abstract**

21 Plant invasions cause biodiversity loss and degradation in ecosystems worldwide. The invasive  
22 species involved may be introduced, or native invaders, and controlling them is a major global  
23 challenge.

24 Here, we highlight an emerging role for native parasitic plants in suppressing invasive species,  
25 thus aiding in restoration of affected habitats. Compelling empirical evidence is provided by  
26 three study systems located in Central Europe, southern Australia and eastern China. Further  
27 cases of parasitism of invasive plants have been recorded across five continents.

28 We propose including the interactions between parasitic and invasive plants into the theoretical  
29 framework of the biotic resistance hypothesis concerning generalist interactions between  
30 invaders and native biota. Among parasitic plants, numerous root hemiparasites, mistletoes and  
31 parasitic vines show low host specificity and exert substantial negative effects on their hosts.  
32 These parasitic plants may interfere with key traits of invaders such as symbiotic nitrogen  
33 fixation or clonal propagation which provide them with competitive advantage over native  
34 species.

35 We contend that some parasitic plants may present a cost-effective environmentally sustainable  
36 component of invasion management schemes. Therefore, we encourage exploration of this  
37 potential and the development of methods for practical applications in ecological restoration  
38 and nature conservation.

39

40 **Keywords:** biological control, biological invasion, biotic resistance hypothesis, *Cassytha*,  
41 *Cuscuta*, mistletoe, parasitic plant, *Rhinanthus*, weed

## 42 **1. Introduction**

43 Plant invasions are one of the biggest threats to global biodiversity, ecosystem function and  
44 food security (Vilà *et al.*, 2011; Zimdahl, 2018). In addition to alien invasive species, expansions  
45 of native species (called “native invaders” or “expansive species”; Pyšek *et al.*, 2004) have been  
46 shown to have comparable consequences for the affected biota (Nackley *et al.*, 2017).

47 Regardless of origin, invasive plants compete with native species, decrease diversity, facilitate  
48 further invasions, compromise human health, impact quality and quantity of water bodies, crop  
49 yields and livestock, and decrease land aesthetics and value (Vilà *et al.*, 2011; Zimdahl, 2018).

50 Removing or reducing invasive species and preventing further invasion represent a major  
51 challenge globally.

52  
53 In this paper, we discuss the potential use of native parasitic plants as biological control agents  
54 of plant invasions. Parasitic plants comprise approximately 4500 species accounting for ca 1% of  
55 species diversity within the angiosperms (Těšitel, 2016). From a human perspective, they have  
56 traditionally been viewed as pests, and many are indeed weeds that damage agricultural crops  
57 or timber trees. In ecology, parasitic plants are frequently viewed as just a curiosity despite  
58 empirical evidence demonstrating that they are a significant component of natural vegetation  
59 worldwide affecting biodiversity and ecosystem processes and services (Westbury *et al.*, 2006;  
60 Quested, 2008; Hartley *et al.*, 2015; Watson, 2016; Fibich *et al.*, 2017). Based on the evidence

61 reviewed here, we propose that at least some parasitic plant species could be used to suppress  
62 plant invasions and help restore biodiversity.

63

## 64 **2. Parasitic plants attacking invasive species: the empirical evidence**

65 Through an extensive literature search, which included tracing references in papers identified in  
66 the primary search, we have summarized the empirical evidence for interactions between  
67 parasitic and invasive plants. While there are many reports of the attachment of a parasitic  
68 plant to an invasive species, these often lack additional information on the effect of the  
69 infection on the host. However, there is a growing body of evidence based on experimental  
70 approaches, some of which include field studies and effects on community composition, in  
71 relation to the negative impact of some parasitic plants on invasive species (Appendix S1; Figure  
72 1).

73

74 The most compelling evidence comes from three study systems, where suppression of target  
75 invasive species by native parasitic plants was demonstrated experimentally under natural  
76 conditions together with much less negative or even positive effects on co-occurring native  
77 plants. The first system comprises root-hemiparasitic *Rhinanthus* species (Orobanchaceae)  
78 which were demonstrated to suppress *Calamagrostis epigejos*, a native invader (expansive  
79 species) of Central and Eastern European grasslands (Těšitel *et al.*, 2017, 2018). The grasslands  
80 threatened by *C. epigejos* represent a global biodiversity hotspot (Dengler *et al.*, 2014), which  
81 makes the expansion a significant concern from the perspective of general biodiversity decline.

82 *C. epigejos* is a rhizomatous grass which spreads clonally to grasslands with low-intensity human  
83 management (mowing or grazing) otherwise favorable for biodiversity preservation (Dengler *et*  
84 *al.*, 2014). In a series of manipulative sowing experiments, native *Rhinanthus* species were  
85 demonstrated to inflict extensive damage to *C. epigejos* disrupting its clonal spread and ability  
86 to recycle and store nutrients in underground organs. The suppression of *C. epigejos* above-  
87 ground growth ranged between 50 and 90% in a 2-3 year time period in comparison with  
88 control plots. The effect of hemiparasites on *C. epigejos* was additive to that of elevated mowing  
89 intensity showing complementarity of these approaches to *C. epigejos* management. The  
90 experiments also demonstrated a temporary opening of regeneration gaps in the grassland  
91 sward, and, importantly, species-composition shifts towards the natural community  
92 composition, which was much smaller at the plots with conventional intense mowing  
93 management. Currently, *Rhinanthus alectorolophus* is being used by both state nature  
94 conservation agency and NGOs as a standard tool of ecological restoration of *C. epigejos*-  
95 infested grasslands in the Czech Republic. Another native herbaceous root-hemiparasite,  
96 *Thesium linophyllon* (Thesiaceae; Santalales), has been demonstrated to parasitize *C. epigejos*  
97 and reduce its dominance in patches with high *T. linophyllon* density, in a long-term permanent-  
98 plot monitoring survey (Somodi *et al.*, 2018).

99

100 The second example comes from southern Australia where the native hemiparasitic vine  
101 *Cassytha pubescens* (Lauraceae), has been shown to have a greater impact on invasive relative  
102 to native hosts (e.g. Prider *et al.*, 2009; Shen *et al.*, 2010). The invasive hosts, *Ulex europaeus*  
103 and *Cytisus scoparius*, are so problematic in Australia that they have been designated as Weeds

104 of National Significance and *U. europaeus* is also on the world's 100 worst invasive species list  
105 (Lowe *et al.*, 2000). In a series of glasshouse experiments, *C. pubescens* biomass per unit host  
106 biomass was roughly an order of magnitude greater on the invasive host *U. europaeus* than on  
107 the native shrubs *Leptospermum myrsinoides* and *Acacia paradoxa*, regardless of light or  
108 nitrogen conditions (Cirocco *et al.*, 2016a, 2017). In these same experiments, total biomass of *U.*  
109 *europaeus* was 40-60% lower when infected, but *C. pubescens* had no effect on total biomass of  
110 the native hosts *L. myrsinoides* and *A. paradoxa* (Cirocco *et al.*, 2016a, 2017). In further  
111 experiments, biomass of *C. pubescens* (per unit *U. europaeus* biomass) was nearly three-times  
112 higher and parasite impact on total biomass of *U. europaeus* 26% stronger under high relative to  
113 low water availability (Cirocco *et al.*, 2016b). There is some evidence that *C. pubescens* impacts  
114 growth of invasive hosts by nitrogen removal and increasing host susceptibility to chronic  
115 photoinhibition. Chronic photoinhibition has been reported in both glasshouse and field studies  
116 across a range of environmental conditions (Cirocco *et al.*, 2016b, 2018). Similar evidence of  
117 chronic photoinhibition has been reported for another invader, *Cytisus scoparius*, when infected  
118 with *C. pubescens* (Shen *et al.*, 2010). Control of *U. europaeus* and *C. scoparius* by *C. pubescens*  
119 could complement biological control using phytophagous insects (Prider *et al.*, 2011).  
120 Application of such insects, however, has had mixed results, with reports of insufficient damage  
121 to the invasive plant or reduction of the phytophage population by predators (Hill *et al.*, 2009).

122  
123 The third case is represented by parasitic vines of the genus *Cuscuta* (Convolvulaceae), which  
124 were tested as potential biological control for a series of invasive plants in eastern China  
125 including: *Mikania micrantha*, *Ipomoea cairica* and *Wedelia trilobata* (Yu *et al.*, 2011). The fast-



126 growing clonal vine *M. micrantha*, originating from Central and South America, is also on the  
127 world's 100 worst invasive species list (Lowe *et al.*, 2000). All three invasive species are  
128 susceptible to infection with *C. australis*, which is native to China. Relative to uninfected  
129 controls, plants infected with *C. australis* had significantly lower nutrient content (up to 20%),  
130 biomass and cover (by 50-66% compared with control plots). The original species composition  
131 also recovered in plots containing *C. australis* (Yu *et al.*, 2011). *C. australis* also significantly  
132 suppressed growth of the invasive forb *Bidens pilosa*, but the effect was greater for young hosts,  
133 which may decrease success of biocontrol with older individuals (Li *et al.*, 2015). Also native to  
134 China, *C. chinensis*, has been found to grow more vigorously on and damage invasive hosts  
135 much more than their native congeneric species (Li *et al.*, 2012). Additional research  
136 demonstrated efficiency of yet another *Cuscuta* species, *C. campestris*, in suppressing *M.*  
137 *micrantha* in China (e.g. Yu *et al.*, 2008) but the parasite is not native to the country. Despite  
138 this, the non-native *C. campestris* was suggested as a component of an integrated pest  
139 management strategy of *M. micrantha* (Yu *et al.*, 2011; Clements *et al.*, 2019). *Cuscuta* parasites  
140 are not currently used as the main tool of biological control of *M. micrantha* because there is an  
141 option to use an introduced host-specific fungal pathogen (Clements *et al.* 2019). Nevertheless,  
142 native *Cuscutas* are showing potential and deserve further study.

143  
144 As mentioned previously, there are numerous reports of other instances of interactions  
145 between invasive hosts and parasitic plants in the literature. The herbaceous root-hemiparasite  
146 *Pedicularis palustris* (Orobanchaceae) native to fen wetlands was observed to suppress tall  
147 sedge *Carex acuta* (90% decrease in biomass production in six years) and common reed

148 (*Phragmites australis*) and restore highly valuable species-rich fen wetlands (Decleer *et al.*,  
149 2013; Ekrťová *et al.*, 2018). Although these hosts are both native species, *P. australis* can be  
150 considered a native invader transforming species-rich communities into monodominant stands.  
151 This species is also recognized as a harmful invader outside its native range (Pyšek *et al.* 2019).  
152 Another species of *Pedicularis* – *P. canadensis* was tested as a potential biocontrol of an invasive  
153 herb *Lespedeza cuneata* in North American prairies. The experiment, however, found that *L.*  
154 *cuneata* seedlings exploited gaps created by the hemiparasite in the prairie. As a result, the  
155 hemiparasite actually facilitated the spread of the invasive plant.

156  
157 Numerous observations of interactions between mistletoes and non-native trees can also be  
158 found in the literature. A monograph was published in 1974 listing associations between native  
159 mistletoes and alien tree species (Hawksworth, 1974). More recent studies come mainly from  
160 large-scale surveys of urban habitats where the hosts were not, or were not considered to be,  
161 invasive. Despite observations of heavy mistletoe infections of some problematic invasive plants  
162 (e.g. *Melia azedarach*, *Casuarina equisetifolia*, *Populus x euamericana*; Dean, Midgley & Stock,  
163 1994; Zachwatowicz *et al.*, 2008; Qasem, 2009; Gairola *et al.*, 2013; see also Appendix 2) and  
164 numerous studies of mistletoes in a range of ecosystems (Watson, 2016), no detailed accounts  
165 or experimental evidence on the negative effects of mistletoes on invasive species are currently  
166 available. This is probably caused by rather long-term nature of the effect of mistletoes on the  
167 hosts, which is difficult to study.

168

169       **3. Suppression of plant invasions by parasitic plants as a case of the biotic resistance**  
170       **hypothesis**

171 We suggest that interactions between parasitic and invasive plants are examples of the biotic  
172 resistance hypothesis (BRH; Maron and Vilà 2001). This hypothesis postulates that invasion  
173 success of an alien species may be restricted by generalist enemies native to the invaded area.  
174 Other empirical demonstrations of the biotic resistance hypothesis include native herbivores  
175 and competitors suppressing invasive plant abundance, through impacts on establishment and  
176 performance (Levine et al. 2004; Parker and Hay 2005). One critical advantage of the use of  
177 native biocontrol agents is that it avoids introducing non-native enemies of invaders, which  
178 may themselves become problematic introductions. Furthermore, native enemies may provide  
179 effective control of both alien and native invaders, the latter of which may spread e.g. due to  
180 land-use or climate change. By contrast, previous approaches to biological control have been  
181 based on the the enemy release hypothesis (ERH; Keane and Crawley 2002), which assumes that  
182 the success of invasive species in their introduced range is caused by lack of their natural  
183 enemies. Thus the ERH-based biocontrol includes an intentional introduction of a specialized  
184 enemy from the invader's native range and by definition is only applicable on alien invasions.

185

186 The BRH assumes generalist biological interactions; thus the parasitic plants involved need to  
187 display a wide range of potential hosts. For efficient biological control of plant invasions, it is  
188 necessary that the net effect of parasitism on invasive plants is more negative than that on the  
189 co-occurring native species, resulting in a shift in competitive balance in favour of the latter.

190 Based on the BRH, three main parasitic plant functional types seem promising in this regard:  
191 root hemiparasites, parasitic vines, and mistletoes (Figure 1a-c). Each of these three functional  
192 types contains species that are generalists and capable of inflicting substantial harm to the host,  
193 either through extensive resource removal (Glatzel and Geils, 2009; Kaiser *et al.*, 2015; Těšitel *et*  
194 *al.*, 2015), and/or disruption to host physiology (Cirocco *et al.*, 2016a, 2018). Remarkably, the  
195 parasitism seems to particularly affect invasive species displaying traits usually associated with  
196 fast growth or high competitive ability, such as symbiotic nitrogen fixation, tree growth form or  
197 clonal spreading by rhizomes or other vegetative means (Yu *et al.*, 2011; Cirocco *et al.*, 2017;  
198 Těšitel *et al.*, 2017). Many invasive species with these traits belong among harmful transformer  
199 invaders, which attain dominance in invaded communities and strongly impact ecosystem  
200 functioning (Pyšek *et al.*, 2004). Root hemiparasites, mistletoes and parasitic vines generally  
201 need light at least for seedling germination and development before attaching to the host  
202 vascular bundles (Těšitel, 2016). Therefore, there seems to be an adaptive value associated with  
203 harm inflicted to the host, which opens sward/canopy and increases light availability, in addition  
204 to the benefits of resource uptake from hosts (Lepš and Těšitel, 2015). Simultaneous  
205 attachment to multiple hosts by some root hemiparasites and parasitic vines reduces their need  
206 to preserve a particular living host as a fundamental source of resources. Amongst root  
207 hemiparasites, parasitic vines, and mistletoes, there are species that are host generalists, and  
208 thus more likely to be able to establish functional haustorial connections with a range of  
209 potential hosts. Lack of host specificity crucial for BRH-based biocontrol enables greater  
210 opportunities to control invasive species and also the potential to control multiple invasive  
211 plants which often co-occur (an advantage over ERH-based biocontrol). In mistletoes, root-

212 hemiparasites and vines of the genus *Cassytha*, the predominant low host specificity is  
213 associated with their attachment to host xylem only, which does not require as specific  
214 histochemical compatibility with the host species as phloem connection (Těšitel, 2016). *Cuscuta*  
215 vines acquire resources from host phloem, yet seem to display lower host specificity than most  
216 other phloem-feeding parasitic plants (Kaiser *et al.*, 2015).

217

218 **4. Additional parasitic plants may be identified as prospective biocontrols and embedded into**  
219 **invasion management schemes**

220 Taking into account the examples above and that most parasitic plant species have yet to be  
221 investigated, we reason that the potential of parasitic plants to control plant invasions is  
222 broader than the empirical evidence currently available. Therefore, we encourage further  
223 research aiming at identification of novel invasive host-parasitic plant combinations, testing the  
224 efficiency of biocontrol and embedding the application of parasitic plants into current invasion  
225 management schemes. In the first step, candidate invasive-parasitic species combinations may  
226 be identified based on potentially compatible traits using extensive trait databases (e.g. Kattge  
227 *et al.* 2011). Common geographical ranges or even co-occurrence of such species may be  
228 detected in large vegetation-plot databases (e.g. European Vegetation Archive; Chytrý *et al.*  
229 2016). Field research focusing on observations under natural conditions and consequent  
230 experimental testing follows as the crucial next step. These should include field assessments of  
231 any off-target impacts and glasshouse experiments testing whether candidates are more  
232 effective under certain environmental conditions, providing stakeholders a strategic advantage

233 on where best to first deploy the biocontrol, saving money, time and effort. In some cases, even  
234 compatible interactions may not be observed in nature due to blocks on dispersal or  
235 establishment of native parasites (e.g. cessation of mowing suppresses hemiparasitic  
236 *Rhinanthus* spp. irrespective of host suitability; Mudrak *et al.*, 2014). Therefore, it may be  
237 worthwhile also exploring associations not observed in nature. While experiments conducted  
238 under controlled conditions (e.g. glasshouse) may allow numerous host-parasite combinations  
239 to be tested rapidly, they should only be considered as a first approximate step. Some parasites  
240 may be difficult to grow under such conditions, which may cause false negative results; some  
241 others may be supported by particular conditions in the glasshouse and thus overcome  
242 limitations which may cause failure in the field. Field trials therefore represent crucial evidence  
243 to demonstrate the biocontrol potential of parasitic plants. For example, trials are already  
244 underway for *Cassytha pubescens* as a biocontrol of *U. europaeus*, *Cytisus scoparius* along with  
245 *Rubus fruticosus* agg., one of Australia's most problematic invasive plants. These field studies  
246 should not only demonstrate the successful parasitism and suppression of target invasive hosts  
247 but also community and long-term effects to exclude or minimize the possibility of some  
248 invasive species benefiting from indirect parasite effects as observed by Walder *et al.* (2018).  
249 Comparison of efficiency and assessment of compatibility with standard practices of invasion  
250 control is another important aspect. To justify the use of a native parasitic plant, it should be  
251 efficient, relatively easy to deploy and less costly than alternative means of control. Parasitic  
252 plants may also complement the other control practices in an integrated invasion management  
253 scheme, as was demonstrated for the root-hemiparasitic *Rhiananthus* spp. in a combination  
254 with regular meadow mowing (Teřitel *et al.*, 2017, 2018). Similarly, the use of *Cassytha*

255 *pubescens* against *Ulex europaeus* and *Cytisus scoparius* may be complementary to the standard  
256 biocontrol using insects, most of which are seed predators (Hill *et al.*, 2010; Prider *et al.*, 2011).  
257 More studies on potential synergies among weed management practices including native  
258 parasitic plants with classical biocontrols are needed.

259 Future research should also take into account genetic variability of both native parasites and the  
260 target invasive host(s). The interaction between parasitic plants and their hosts may be strongly  
261 affected by genotypic variability of either the host or the parasite (Rowntree *et al.*, 2011).  
262 Therefore, results based on testing plant material from just a single source (e.g. a particular wild  
263 population) may not be representative. Testing of different genotypes may produce more  
264 effective control measures for certain populations of invasive species. Beyond the natural  
265 variability found in wild populations, novel strains or cultivars of parasitic plants may be  
266 developed using plant breeding techniques, which may further increase the application  
267 potential on additional target invasive species.

268

## 269 **5. Risk assessment**

270 We believe there is valid current and future potential for parasitic plants as biocontrol for  
271 invasive plants. However, we are also aware of concerns with the introduction of even  
272 geographically native species to habitats from which they were previously absent or had low  
273 natural abundance. Major risks include genetic erosion of natural populations of the introduced  
274 parasites and undesirable non-target effects on the community (e.g. parasitic infection and  
275 consequent decline of non-target species or release of another invasive species from

276 competition). Development of new genotypes overcoming major evolutionary constraints e.g.  
277 on host specificity or dispersal may in the long term result in uncontrolled spread of a given  
278 parasitic species, which may then itself become a weed inflicting environmental and/or  
279 economic impacts. Risk levels, however, could be reduced if only geographically native non-  
280 weedy parasites are used and transfer is conducted among similar habitats. In any case,  
281 biological control using parasitic plants should be used with caution and only after extensive  
282 research of potential wider impacts on non-target species. Moreover, implementation should  
283 first target areas where native distribution of the parasite overlaps with invaded habitat.  
284 Experimental investigation of haustorial formation (i.e. connectivity) on various native and  
285 invasive species would be valuable in helping predict potential for parasite spread, differential  
286 impact and off target risks to native biota. Local seed sources should be used where possible. An  
287 ideal case includes seed transfers within a single site, which complies with the strictest  
288 requirements of nature conservation to preserve genetic resources and thus can be used even  
289 in nature reserves (Těšitel *et al.*, 2018) though this may be in conflict with the maximal  
290 efficiency of the biocontrol. Development of approaches to control potential unwanted spread  
291 of the parasitic plants, such as early mowing regime exterminating populations of annual  
292 *Rhinanthus* spp. (Blažek and Lepš, 2015), may further restrict the risk level.

293

## 294 **6. Conclusion**

295 We estimate great potential in native parasitic plants as a valuable tool in management of plant  
296 invasions and thus biodiversity restoration and conservation. Particularly harmful transformer



297 invasive plants with high competitive ability may be especially susceptible to suppression by  
298 native parasitic plants, and could be effectively controlled using this approach in combination  
299 with other control measures. The use of parasitic plants in invasion management schemes  
300 seems complementary and compatible with many standard measures of invasive plant  
301 suppression. Nevertheless, we are still at the beginning of empirical and applied research which  
302 should aim at a deeper exploration of the parasitic plant potential and develop methodologies  
303 for their practical use, respectively.

304

### 305 **Acknowledgements**

306 We thank Martin Večeřa for plotting the map of case studies.

### 307 **Supplementary Information**

308 Appendix 1. Photographic documentation of mistletoe *Viscum album* infecting alien trees  
309 *Juglans nigra* and *P. × canadensis* in the surrounding of Břeclav (Czech Republic).

### 310 **Author Contribution**

311 All authors conceived the idea. JT and RMC wrote the manuscript draft which was commented  
312 and edited by JRW and JMF. JT drew the figure 1. All authors approved the final version of the  
313 manuscript.

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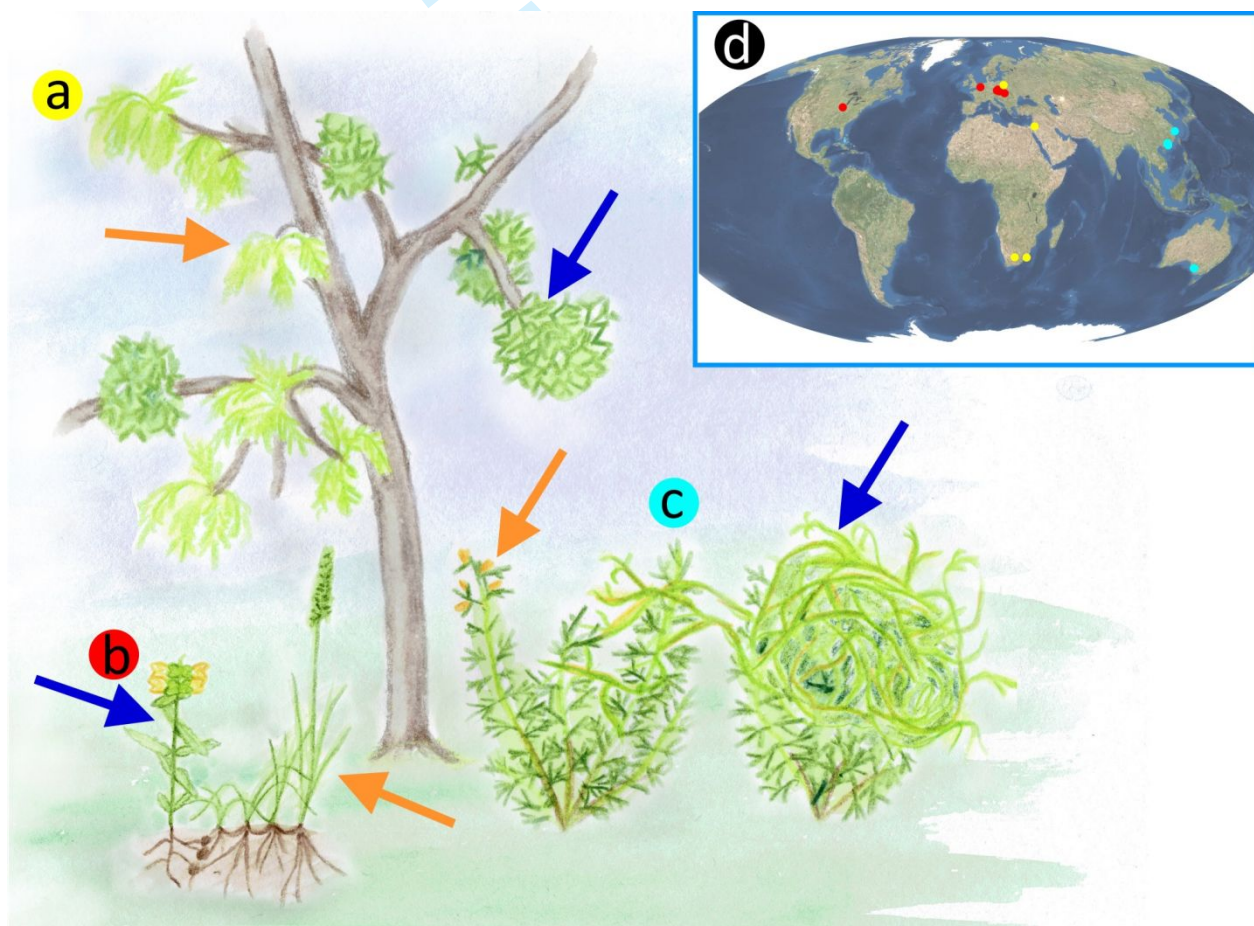
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441 **Figures**

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445 Figure 1. Examples of three parasitic functional types in which native parasites have been  
446 reported to have interactions with invasive plant species. Invasive hosts and parasitic plants are  
447 represented by orange and blue arrows, respectively. (a) A mistletoe parasitizing a tree invader  
448 (b) A root-hemiparasite attacking an invasive clonal plant and (c) Parasitic vine attacking an  
449 invasive shrub. (d) Geographical distribution of the examples presented in Table 1.

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Appendix S1. Documented interactions between parasitic plants and their invasive hosts

Parasitic species	Life form	Invasive host	Host status*	Evidence type**	Evidence level***	References
<i>Cassytha pubescens</i>	vine	<i>Cytisus scoparius</i>	A	Nat. Cond.	Exp.	Prider <i>et al.</i> , 2009; Shen <i>et al.</i> , 2010
		<i>Ulex europaeus</i>	A	Nat. Cond.	Exp.	Cirocco <i>et al.</i> , 2016a,b, 2017, 2018
<i>Cuscuta australis</i>	vine	<i>Ipomoea cairica</i> <i>Mikania micrantha</i> <i>Wedelia trilobata</i>	A	Comm.	Exp.	Yu <i>et al.</i> , 2011
		<i>Bidens pilosa</i>	A	Glass.	Exp.	Li <i>et al.</i> , 2015
<i>Cuscuta chinensis</i>	vine	<i>Bidens pilosa</i> <i>Ipomoea cairica</i> <i>Solidago canadensis</i>	A	Glass.	Exp.	Li <i>et al.</i> , 2012
<i>Erianthemum dregei</i>	mistletoe	<i>Melia azederach</i>	A	Urban cultivation	Obs.	Gairola <i>et al.</i> , 2013
<i>Pedicularis canadensis</i>	Herbaceous, root hemiparasite	<i>Lespedeza cuneata</i>	A	Comm.	Exp.	Walder <i>et al.</i> , 2018
<i>Pedicularis palustris</i>	Herbaceous, root hemiparasite	<i>Carex</i> spp.	N	Comm.	Obs.	Decleer <i>et al.</i> , 2013
		<i>Phragmites australis</i>	N	Comm.	Obs.	Ekrťová <i>et al.</i> , 2018
<i>Plicosepalus acaciae</i>	mistletoe	<i>Melia azedarach</i> , <i>Casuarina equisetifolia</i>	A	Nat. Cond.	Obs.	Qasem, 2009

<i>Rhinanthus alectorolophus</i>	Herbaceous, root hemiparasite	<i>Calamagrostis epigejos</i>	N	Comm.	Exp.	Těšitel <i>et al.</i> , 2017
<i>Rhinanthus major</i>	Herbaceous, root hemiparasite	<i>Calamagrostis epigejos</i>	N	Comm.	Exp.	Těšitel <i>et al.</i> , 2018
<i>Tapinanthus</i> spp., <i>Viscum</i> spp. and other mistletoes	mistletoe	<i>Acacia cyclops</i> , <i>Acacia saligna</i>	A	Nat. Cond.	Obs.	Dean <i>et al.</i> , 1994
<i>Thesium linophyllum</i>	Herbaceous, root hemiparasite	<i>Calamagrostis epigejos</i>	N	Comm.	Obs.	Somodi <i>et al.</i> , 2018
<i>Viscum album</i>	mistletoe	<i>Populus x euamericana</i> , <i>Robinia pseudoacacia</i>	A	Urban cultivation	Obs.	Zachwatowicz <i>et al.</i> , 2008

\* A = alien, N = native; \*\* Community = natural community context with documented effect on community composition; Glass. = glasshouse or pot experiment; Nat. Cond. = natural community context without studying effects on community composition; \*\*\* Exp. = experimental evidence, Obs. = observational evidence.

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Appendix S2. Photographic documentation of mistletoe *Viscum album* attacking alien trees *Juglans nigra* and *P. × canadensis*.

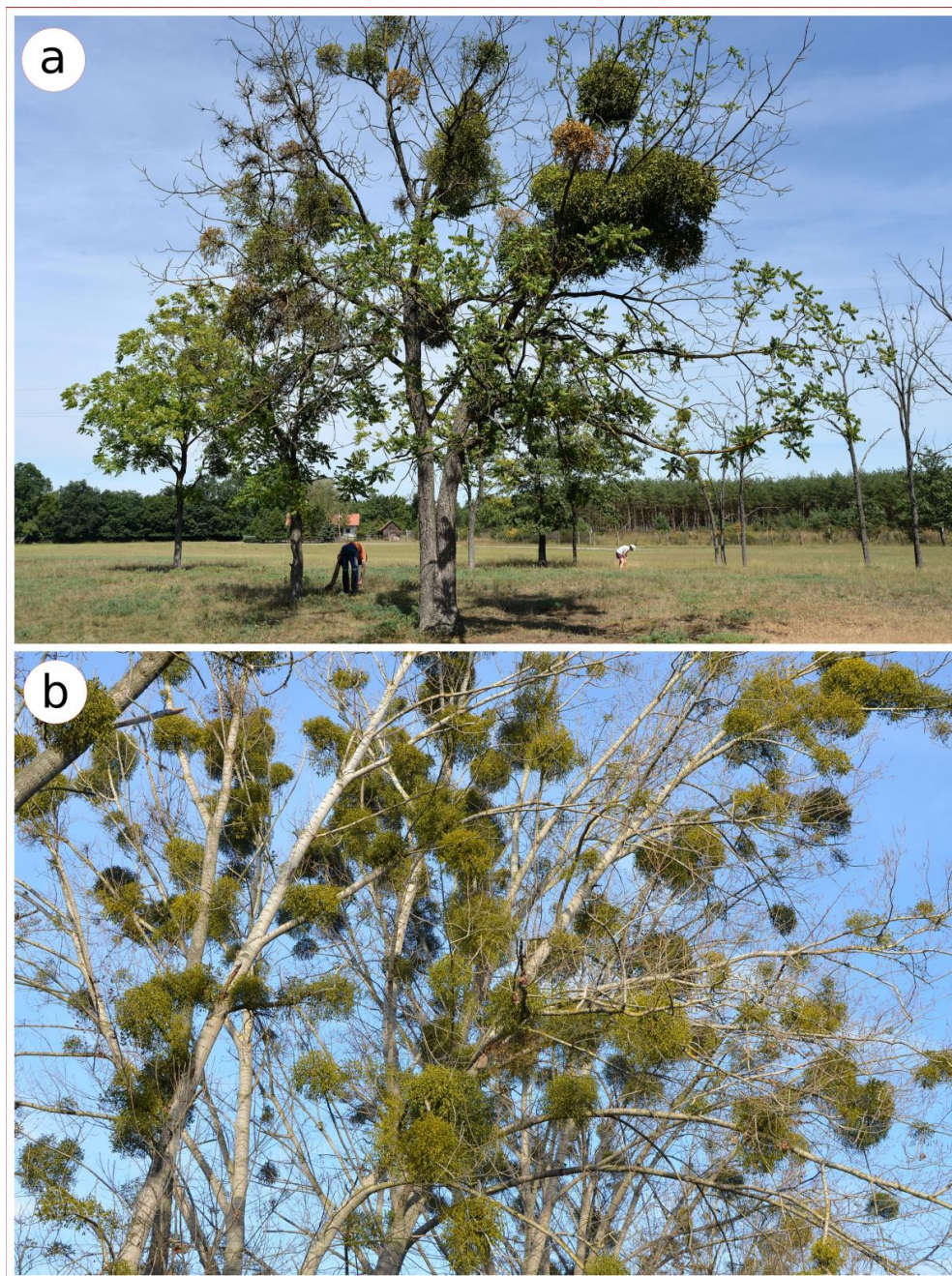


Figure S2. Mistletoe *Viscum album* attacking alien trees in the surrounding of Břeclav (Czech Republic). (a) Extensive damage (eventually resulting in mortality) inflicted by the mistletoe to alien *Juglans nigra* growing on a valuable sandy steppe meadow. *J. nigra* was introduced into the region in 19<sup>th</sup> century for timber production. This species could spread further but is heavily infected and damaged by *Viscum*

*album* which prevented both the spontaneous spread and cultivation by the foresters. (b) Heavy infection of *Viscum album* attacking alien invasive *Populus × canadensis*. *P. × canadensis* is a frequently cultivated tree in the whole Central European region. It spreads spontaneously and represents a threat to native *P. nigra* due to competitive exclusion and genetic erosion. In comparison to *P. nigra*, *P. × canadensis* seems to be more heavily infected and damaged by *Viscum album*, which may at least partially restrain its invasive potential. Note that this photograph was taken in winter with leaves of the host shed for physiological reasons.

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