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Native parasitic plants: biological control for plant invasions?

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Abstract

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

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

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

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

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

1. Introduction

Plant invasions are one of the biggest threats to global biodiversity, ecosystem function and food security (Vilà *et al.*, 2011; Zimdahl, 2018). In addition to alien invasive species, expansions of native species (called “native invaders” or “expansive species”; Pyšek *et al.*, 2004) have been shown to have comparable consequences for the affected biota (Nackley *et al.*, 2017). Regardless of origin, invasive plants compete with native species, decrease diversity, facilitate further invasions, compromise human health, impact quality and quantity of water bodies, crop yields and livestock, and decrease land aesthetics and value (Vilà *et al.*, 2011; Zimdahl, 2018). Removing or reducing invasive species and preventing further invasion represent a major challenge globally.

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

2. Parasitic plants attacking invasive species: the empirical evidence

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

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

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

The second example comes from southern Australia where the native hemiparasitic vine *Cassytha pubescens* (Lauraceae)*,* has been shown to have a greater impact on invasive relative to native hosts (e.g. Prider *et al.*, 2009; Shen *et al.*, 2010). The invasive hosts, *Ulex europaeus* and *Cytisus scoparius*, are so problematic in Australia that they have been designated as Weeds of National Significance and *U. europaeus* is also on the world's 100 worst invasive species list (Lowe *et al.*, 2000). In a series of glasshouse experiments, *C. pubescens* biomass per unit host biomass was roughly an order of magnitude greater on the invasive host *U. europaeus* than on the native shrubs *Leptospermum myrsinoides* and *Acacia paradoxa*, regardless of light or nitrogen conditions (Cirocco *et al.*, 2016a, 2017). In these same experiments, total biomass of *U. europaeus* was 40-60% lower when infected, but *C. pubescens* had no effect on total biomass of the native hosts *L. myrsinoides* and *A. paradoxa* (Cirocco *et al.*, 2016a, 2017). In further experiments, biomass of *C. pubescens* (per unit *U. europaeus* biomass) was nearly three-times higher and parasite impact on total biomass of *U. europaeus* 26% stronger under high relative to low water availability (Cirocco *et al.*, 2016b). There is some evidence that *C. pubescens* impacts growth of invasive hosts by nitrogen removal and increasing host susceptibility to chronic photoinhibition. Chronic photoinhibition has been reported in both glasshouse and field studies across a range of environmental conditions (Cirocco *et al.*, 2016b, 2018). Similar evidence of chronic photoinhibition has been reported for another invader, *Cytisus scoparius,* when infected with *C. pubescens* (Shen *et al.*, 2010). Control of *U. europaeus* and *C. scoparius* by *C. pubescens* could complement biological control using phytophagous insects (Prider *et al.*, 2011). Application of such insects, however, has had mixed results, with reports of insufficient damage to the invasive plant or reduction of the phytophage population by predators (Hill *et al.*, 2009).

The third case is represented by parasitic vines of the genus *Cuscuta* (Convolvulaceae), which were tested as potential biological control for a series of invasive plants in eastern China including: *Mikania micrantha*, *Ipomoea cairica* and *Wedelia trilobata* (Yu *et al.*, 2011). The fast-growing clonal vine *M. micrantha,* originating from Central and South America, is also on the world's 100 worst invasive species list (Lowe *et al.*, 2000). All three invasive species are susceptible to infection with *C. australis,* which is native to China. Relative to uninfected controls, plants infected with *C. australis* had significantly lower nutrient content (up to 20%), biomass and cover (by 50-66% compared with control plots). The original species composition also recovered in plots containing *C. australis* (Yu *et al.*, 2011). *C. australis* also significantly suppressed growth of the invasive forb *Bidens pilosa*, but the effect was greater for young hosts, which may decrease success of biocontrol with older individuals (Li *et al.*, 2015). Also native to China, *C. chinensis*, has been found to grow more vigorously on and damage invasive hosts much more than their native congeneric species (Li *et al.*, 2012). Additional research demonstated efficiency of yet another *Cuscuta* species, *C. campestris,* in suppressing *M. micrantha* in China (e.g. Yu *et al.*, 2008) but the parasite is not native to the country. Despite this, the non-native *C. campestris* was suggested as a component of an integrated pest management stategy of *M. micrantha* (Yu *et al.*, 2011; Clements *et al.*, 2019). *Cuscuta* parasites are not currently used as the main tool of biological control of *M. micrantha* because there is an option to use an introduced host-specific fungal pathogen (Clements et al. 2019). Nevertheless, native *Cuscutas* are showing potential and deserve further study.

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

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

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

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

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

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

Based on the BRH, three main parasitic plant functional types seem promising in this regard: root hemiparasites, parasitic vines, and mistletoes (Figure 1a-c). Each of these three functional types contains species that are generalists and capable of inflicting substantial harm to the host, either through extensive resource removal (Glatzel and Geils, 2009; Kaiser *et al.*, 2015; Těšitel *et al.*, 2015), and/or disruption to host physiology (Cirocco *et al.*, 2016a, 2018). Remarkably, the parasitism seems to particularly affect invasive species displaying traits usually associated with fast growth or high competitive ability, such as symbiotic nitrogen fixation, tree growth form or clonal spreading by rhizomes or other vegetative means (Yu *et al.*, 2011; Cirocco *et al.*, 2017; Těšitel *et al.*, 2017). Many invasive species with these traits belong among harmuful transformer invaders, which attain dominance in invaded communities and strongly impact ecosystem functioning (Pyšek *et al.*, 2004). Root hemiparasites, mistletoes and parasitic vines generally need light at least for seedling germination and development before attaching to the host vascular bundles (Těšitel, 2016). Therefore, there seems to be an adaptive value associated with harm inflicted to the host, which opens sward/canopy and increases light availability, in addition to the benefits of resource uptake from hosts (Lepš and Těšitel, 2015). Simultaneous attachment to multiple hosts by some root hemiparasites and parasitic vines reduces their need to preserve a particular living host as a fundamental source of resources. Amongst root hemiparasites, parasitic vines, and mistletoes, there are species that are host generalists, and thus more likely to be able to establish functional haustorial connections with a range of potential hosts. Lack of host specificity crucial for BRH-based biocontrol enables greater opportunities to control invasive species and also the potential to control multiple invasive plants which often co-occur (an advantage over ERH-based biocontrol). In mistletoes, root-hemiparasites and vines of the genus *Cassytha*, the predominant low host specificity is associated with their attachment to host xylem only, which does not require as specific histochemical compatibility with the host species as phloem connection (Těšitel, 2016). *Cuscuta* vines acquire resources from host phloem, yet seem to display lower host specificity than most other phloem-feeding parasitic plants (Kaiser *et al.*, 2015).

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

Taking into account the examples above and that most parasitic plant species have yet to be investigated, we reason that the potential of parasitic plants to control plant invasions is broader than the empirical evidence currently available. Therefore, we encourage further research aiming at identification of novel invasive host-parasitic plant combinations, testing the efficiency of biocontrol and embedding the application of parasitic plants into current invasion management schemes. In the first step, candidate invasive-parasitic species combinations may be identified based on potentially compatible traits using extensive trait databases (e.g. Kattge *et al.* 2011). Common geographical ranges or even co-occurrence of such species may be detected in large vegetation-plot databases (e.g. European Vegetation Archive; Chytrý *et al.* 2016). Field research focusing on observations under natural conditions and consequent experimental testing follows as the crucial next step. These should include field assessments of any off-target impacts and glasshouse experiments testing whether candidates are more effective under certain environmental conditions, providing stakeholders a strategic advantage on where best to first deploy the biocontrol, saving money, time and effort. In some cases, even compatible interactions may not be observed in nature due to blocks on dispersal or establishment of native parasites (e.g. cessation of mowing suppresses hemiparasitic *Rhinanthus* spp. irrespective of host suitability; Mudrák *et al.*, 2014). Therefore, it may be worthwhile also exploring associations not observed in nature. While experiments conducted under controlled conditions (e.g. glasshouse) may allow numerous host-parasite combinations to be tested rapidly, they should only be considered as a first approximate step. Some parasites may be difficult to grow under such conditions, which may cause false negative results; some others may be supported by particular conditions in the glasshouse and thus overcome limitations which may cause failure in the field. Field trials therefore represent crucial evidence to demonstrate the biocontrol potential of parasitic plants. For example, trials are already underway for *Cassytha pubescens* as a biocontrol of *U. europaeus*, *Cytisus scoparius* along with *Rubus fruticosus* agg., one of Australia's most problematic invasive plants. These field studies should not only demonstrate the successful parasitism and suppression of target invasive hosts but also community and long-term effects to exclude or minimize the possibility of some invasive species benefiting from indirect parasite effects as observed by Walder *et al.* (2018). Comparison of effciency and assessment of compatibility with standard practices of invasion control is another important aspect. To justify the use of a native parasitic plant, it should be efficient, relatively easy to deploy and less costly than alternative means of control. Parasitic plants may also complement the other control practices in an integrated invasion management scheme, as was demonstrated for the root-hemiparasitic *Rhiananthus spp*. in a combination with regular meadow mowing (Těšitel *et al.*, 2017, 2018). Similarly, the use of *Cassytha* *pubescens* against *Ulex europaeus* and *Cytisus scoparius* may be complementary to the standard biocontrol using insects, most of which are seed predators (Hill *et al.*, 2010; Prider *et al.*, 2011). More studies on potential synergies among weed management practices including native parasitic plants with classical biocontrols are needed.

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

5. Risk assessment

We believe there is valid current and future potential for parasitic plants as biocontrol for invasive plants. However, we are also aware of concerns with the introduction of even geographically native species to habitats from which they were previously absent or had low natural abundance. Major risks include genetic erosion of natural populations of the introduced parasites and undesirable non-target effects on the community (e.g. parasitic infection and consequent decline of non-target species or release of another invasive species from competition). Development of new genotypes overcoming major evolutionary constraints e.g. on host specificity or dispersal may in the long term result in uncontrolled spread of a given parasitic species, which may then itself become a weed inflicting environmental and/or economic impacts. Risk levels, however, could be reduced if only geographically native non-weedy parasites are used and transfer is conducted among similar habitats. In any case, biological control using parasitic plants should be used with caution and only after extensive research of potential wider impacts on non-target species. Moreover, implementation should first target areas where native distribution of the parasite overlaps with invaded habitat. Experimental investigation of haustorial formation (i.e. connectivity) on various native and invasive species would be valuable in helping predict potential for parasite spread, differential impact and off target risks to native biota. Local seed sources should be used where possible. An ideal case includes seed transfers within a single site, which complies with the strictest requirements of nature conservation to preserve genetic resources and thus can be used even in nature reserves (Těšitel *et al.*, 2018) though this may be in conflict with the maximal efficiency of the biocontrol. Development of approaches to control potential unwanted spread of the parasitic plants, such as early mowing regime exterminating populations of annual *Rhinanthus* spp. (Blažek and Lepš, 2015), may further restrict the risk level.

6. Conclusion

We estimate great potential in native parasitic plants as a valuable tool in management of plant invasions and thus biodiversity restoration and conservation. Particularly harmful transformer invasive plants with high competitive ability may be especially susceptible to suppression by native parasitic plants, and could be effectively controlled using this approach in combination with other control measures. The use of parasitic plants in invasion management schemes seems complementary and compatible with many standard measures of invasive plant suppression. Nevertheless, we are still at the beginning of empirical and applied reseach which should aim at a deeper exploration of the parasitic plant potential and develop methodologies for their practical use, respectively.

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Supplementary Information

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

Author Contribution

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

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Figures

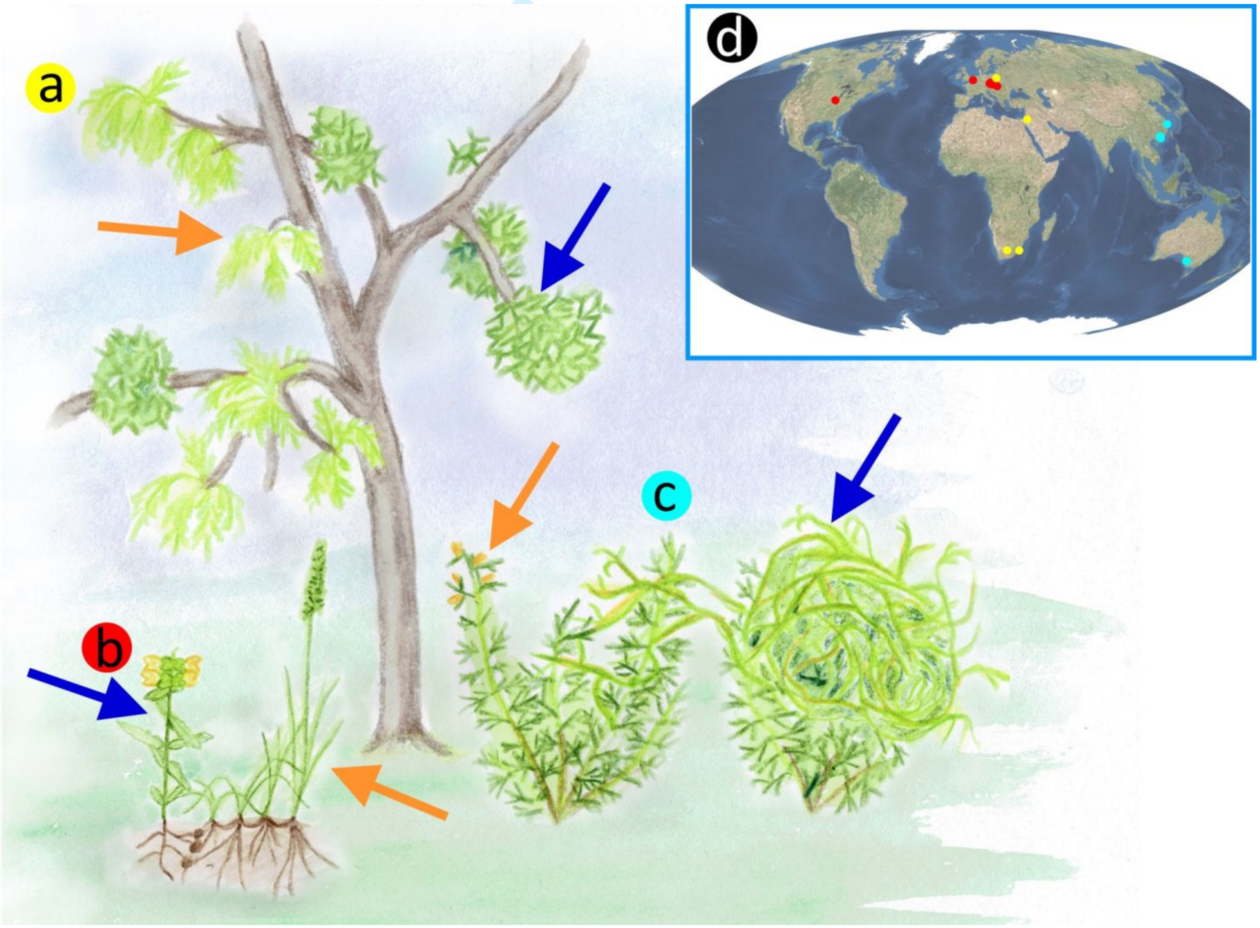

Figure 1. Examples of three parasitic functional types in which native parasites have been reported to have interactions with invasive plant species. Invasive hosts and parasitic plants are represented by orange and blue arrows, respectively. (a) A mistletoe parasitizing a tree invader (b) A root-hemiparasite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

Supporting Information to the paper Těšitel et al. Native parasitic plants: biological control for plant invasions? *Applied Vegetation Science*.

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

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

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

Supporting Information to the paper Těšitel et al. Native parasitic plants: biological control for plant invasions? *Applied Vegetation Science*.

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

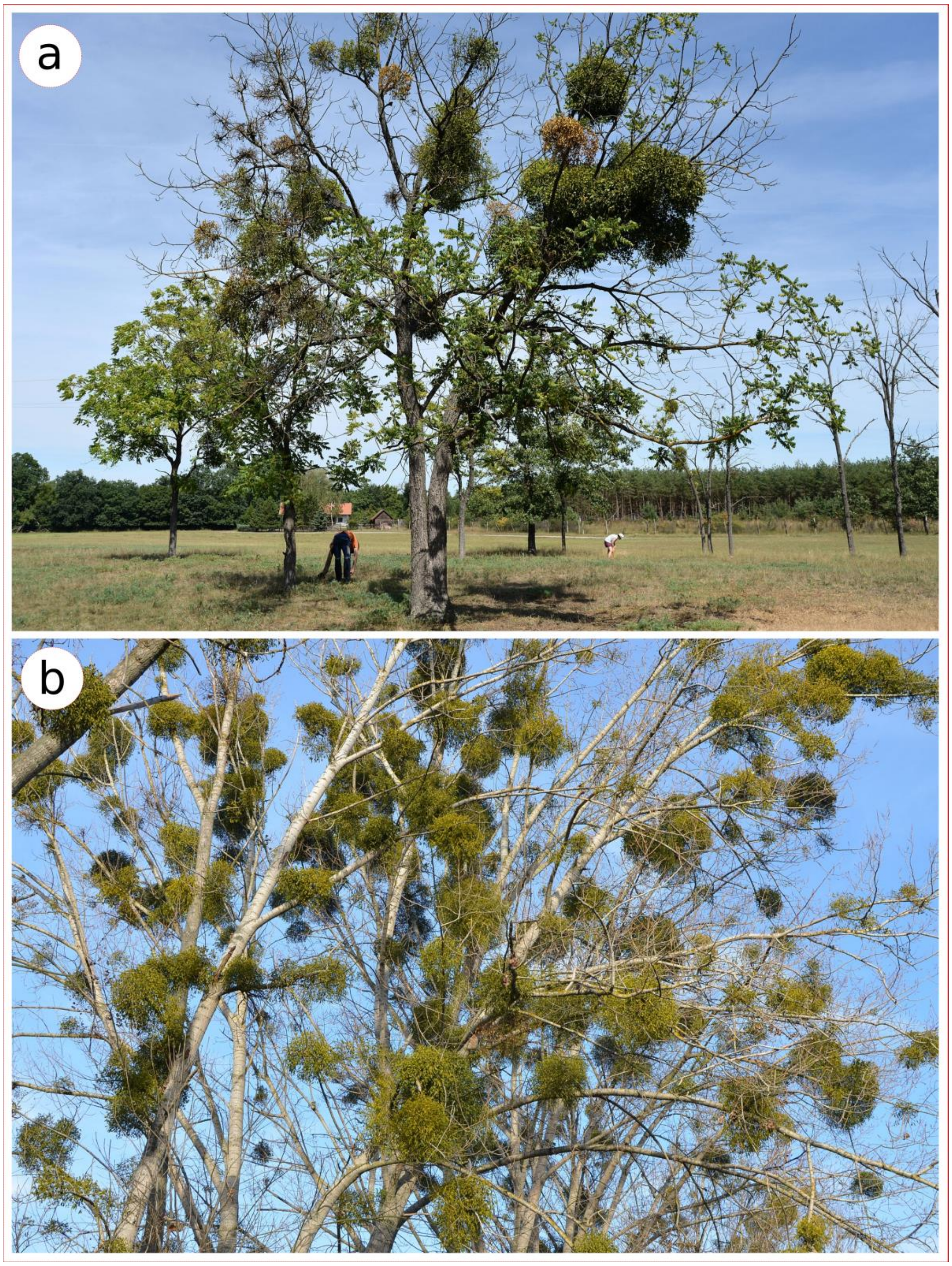

Figure S2. Mistletoe *Viscum album* attacking alien trees in the surrounding of Břeclav (Czech Republic). (a) Extensive damage (eventually resulting in mortality) inflicted by the mistletoe to alien *Juglans nigra* growing on a valuable sandy steppe meadow. *J. nigra* was introduced into the region in 19th 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.