

1 **The original published PDF available in this website:**

2 <https://link.springer.com/content/pdf/10.1007%2Fs10530-018-1811-3.pdf>

3

4 **TITLE PAGE**

5

6 **Authors:**

7 György Kröel-Dulay, Anikó Csecserits, Katalin Szitár, Edit Molnár, Rebeka Szabó, Gábor

8 Ónodi, Zoltán Botta-Dukát

9

10 **Title**

11 The potential of common ragweed for further spread: invasibility of different habitats and the

12 role of disturbances and propagule pressure

13

14 **Affiliation and address of the authors:**

15 MTA Centre for Ecological research, 2-4 Alkotmány u., Vácrátót, 2163-Hungary

16

17 **Corresponding author:**

18 György Kröel-Dulay

19 E-mail: kroel-dulay.gyorgy@okologia.mta.hu

20 Telephone: +36 202208614

21 ORCID: [0000-0002-0695-1232](https://orcid.org/0000-0002-0695-1232)

22

23 **Acknowledgements**

24 We thank Bernadett Kolonics, Richárdné Ribai and Sándorné Vadkerti for their help in lab

25 work. This study was funded by the Ministry of Agriculture and Rural Development (Z. B-

26 D.), by the MTA Postdoctoral Research Programme (PD-009/2017; A. C.), and by the MTA

27 János Bolyai Research Scholarship (BO/00276/15/8; G. K-D.).

28

29 **Abstract**

30 The infilling of existing suitable habitats within a landscape after establishment is of critical
31 importance for the final outcome of a plant invasion, yet it is an often overlooked process.
32 Common ragweed, *Ambrosia artemisiifolia*, is an invasive annual species in Europe causing
33 serious problems due to its highly allergenic pollen and as an agricultural weed. Recent
34 studies have modelled the broad-scale distribution of the species and assessed future invasion
35 risk, but for predicting the expected outcome of ragweed invasion we also need a mechanistic
36 understanding of its local invasion success. We conducted a field experiment to investigate
37 the invasibility of eight common non-arable habitat types and the role of soil disturbance in
38 central Hungary, in the hot spot of ragweed invasion in Europe. Seed addition alone resulted
39 in negligible amount of ragweed biomass, except for sites where disturbance was part of the
40 present management. Soil disturbance alone resulted in ragweed at those few sites where
41 ragweed seeds were present in the seed bank, related to farming in recent decades. When
42 disturbance and seed addition were combined, ragweed emerged in all habitat types and
43 reached high biomass in all habitat types except for closed forests. As our experiment showed
44 that most habitat types have high invasibility when disturbed, we conclude that ragweed has a
45 high potential for further spread, even in this heavily infested region. Management should
46 focus on preventing seed dispersal and eradicating establishing populations where ragweed is
47 still absent, while reducing soil disturbance may be needed to avoid ragweed emergence in
48 infested sites. This latter may require a reconsideration of land-use practices in infested
49 regions.

50

51 **Keywords:** *Ambrosia artemisiifolia*; Grassland; Old-field; Seed addition; Seed bank, Tree
52 plantation.

53 **Nomenclature:** Király (2009)

54 **Running head:** Ragweed, disturbance and habitat invasibility

55

56 INTRODUCTION

57 The spread of invasive species is often described by changes in broad-scale
58 distribution maps (e.g.: Mack 1981; Chauvel et al. 2006). However, the local spread within a
59 landscape that follows a successful establishment can be similarly important in predicting the
60 final outcome of an invasion (Richardson et al. 2000; Blackburn et al. 2011). This infilling of
61 existing suitable habitats can often be a complex and slowly unfolding process (With 2002),
62 which is mediated by dispersal and the invasibility of various ecosystems in the landscape.
63 Invasibility is an emergent property of ecosystems to allow or resist the establishment of
64 newly arriving species (Burke and Grime 1996; Lonsdale 1999). While invasibility of various
65 ecosystems is often estimated simply based on the presence and abundance of non-native
66 species, a reliable invasibility assessment can only be reached with experiments that control
67 for potential confounding factors, such as propagule pressure and disturbance level (Vila et al
68 2008, Von Holle and Simberloff 2005, McGlone et al. 2011).

69 Disturbances are an inherent part of ecosystem dynamics (Pickett and White 1985),
70 but disturbances are also generally considered to promote invasion (Hobbs and Huenekke
71 1992, Burke and Grime 1996). Biomass removal has been shown to favour the invasion of
72 cheatgrass in California grassland (Beckstead and Augspurger 2004), and forest canopy
73 disturbance promotes invasion in forest understory (Eschtruth and Battles 2009). By contrast,
74 disturbance has been found to negatively affect plant invasion in ephemeral wetlands
75 (Tanentzap et al. 2014) and also shrub invasion in a prairie by disturbing the cryptogam layer
76 that facilitated shrub seedling recruitment (Parker 2001). Either way, studying only intact,
77 undisturbed ecosystems may provide a biased picture on ecosystem invasibility.

78 Propagule pressure has been found to have an overwhelming influence on the success
79 of invasion (Simberloff 2009). Based on a meta-analysis, Colautti et al (2006) concluded that
80 in most studies where propagule pressure was considered, it proved to be a strong predictor of

81 invasibility. Propagule pressure has been found to override ecosystem resistance in a
82 herbaceous invasion of forest understory (Von Holle and Simberloff 2005) and also in a shrub
83 invasion of wetlands (Berg et al. 2016). In addition, the lack of invasion in some habitats does
84 not necessarily mean low invasibility, but may simply be due to the lack of propagules
85 entering into the community (Vila et al. 2008). These considerations underline the importance
86 of studying invasibility with controlled propagule pressure (Colautti et al. 2006), especially
87 when comparing the invasibility of multiple ecosystems.

88 Common ragweed (*Ambrosia artemisiifolia* L.), an annual species from the *Asteraceae*
89 family, is native to North America but is invasive in many parts of the world. In some parts of
90 Europe, it is the most important weed of arable lands (Novák et al. 2009; Galzina et al., 2010),
91 and reported yield losses associated with common ragweed may be as high as 60-80%
92 (Kazinczy et al. 2007; Bullock et al., 2012). Common ragweed is already the most important
93 allergenic plant in some parts of Europe (Burbach et al. 2009). The total costs associated with
94 ragweed invasion including agricultural, work productivity, and medical costs has been
95 estimated to be 4.5 billion Euro (Bullock et al. 2012). A better understanding of the spread
96 and success of common ragweed is needed to mitigate these broad-scale present and even
97 bigger predicted future effects (Richter et al. 2013; Hamaoui-Laguel et al. 2015).

98 Several factors have been used to explain the past and present spread, as well as to
99 predict future spreading potential of common ragweed (Essl et al. 2015). By having a
100 combination of traits that makes the species successful in some cropping systems, common
101 ragweed is primarily an agricultural weed (Pinke et al. 2011; Essl et al. 2015). It prefers full
102 sunlight (Bazzaz 1973), while no clear preference to soil type has been found (Fumanal et al.
103 2008b). The species was introduced to Europe as a crop contaminant multiple times in the
104 19th and early 20th centuries (Chauvel et al. 2006), and its subsequent spread in Europe can
105 be attributed to contaminated crops and bird feed, movement of agricultural machineries and

106 transport of soil (Essl et al. 2009; Vitalos and Karrer 2009). The species is repeatedly
107 introduced to climatic zones that are not yet suitable for its long-term persistence (Dahl et al.
108 1999; Csontos et al. 2015), but studies suggest that changing climate may facilitate its further
109 expansion (Hamaoui-Laguel et al. 2015). Future ragweed pollen load in Europe may be 2 to
110 12 times higher than it is today as a consequence of further spread of the species and changing
111 climate and land-use (Hamaoui-Laguel et al. 2015).

112 Arable lands harbour the largest amount of common ragweed (Essl et al. 2015), but
113 other habitats may also support varying amount of the species and may therefore facilitate its
114 spread in the landscape. Ragweed often dominates abandoned arable lands (old-fields) right
115 after abandonment, but is soon outcompeted by other species (Bazzaz 1968). Roadsides
116 (Lavoie et al. 2007; Essl et al. 2009), vacant lots (Katz et al. 2014), riverbanks (Lavoie et al.
117 2007), and tree plantations (Csecserits et al. 2016) have all been reported as ragweed habitats.
118 In addition, several shifts in habitat preferences during ragweed invasion have been reported,
119 such as from along railway lines to roadsides (Essl et al. 2009) in Austria, and from roadsides
120 to agricultural lands (Lavoie et al. 2007) in Canada. Predictions on future spread of common
121 ragweed has been primarily based on climatic factors (Richter et al. 2013, Storkey et al. 2014,
122 Leiblein-Wild et al. 2016), but landscape factors also affect spread at a finer scale Essl et al.
123 2009, Pinke et al. 2011, Skalova et al. 2017), that can be important in the infilling of suitable
124 habitats. To assess the full potential of common ragweed invasion in a heterogeneous
125 landscape we need to investigate invasibility in multiple habitat types

126 The objective of this study was to experimentally test the invasibility of eight common
127 non-arable habitat types in the hot spot of ragweed invasion in Europe, central Hungary, in
128 order to assess the potential of common ragweed for further spread. Specific objectives were
129 (a) to test the effect of seed addition on ragweed emergence and biomass, (b) to investigate

130 the role of soil disturbance in facilitating this, (c) to assess the effects of additional factors
131 such as soil texture, light conditions, and land use history on ragweed performance.

132

133

134 **MATERIALS AND METHODS**

135 **Study species**

136 Common ragweed (*Ambrosia artemisiifolia* L.) is an annual wind-pollinated herb
137 species with high plasticity in biomass, pollen and seed production in response to different
138 environmental conditions (Essl et al. 2015). Ragweed most often colonizes open, disturbed
139 habitat types (such as arable lands, ruderal habitats and old-fields), but it is rapidly replaced
140 by perennial species during succession (Bazzaz 1968; Gentili et al 2017).

141 Ragweed forms persistent seed bank as seeds can survive in the soil up to 40 years
142 (Essl et al. 2015), and disturbance has been shown to positively affect seedling recruitment
143 from the soil seed bank (Fumanal et al 2008a). After ripening in autumn, seeds are in primary
144 dormancy, which can be broken by low temperatures in winter.

145

146 **Study area**

147 The study was conducted in the Kiskunság inland sand dune system in central
148 Hungary, which is the most heavily infested region by common ragweed in Europe (Skjøth et
149 al. 2010; Hamaoui-Laguel et al. 2015). The climate of the region is moderately continental
150 with a sub-Mediterranean influence. Mean annual temperature is 10.5 °C and mean annual
151 precipitation is 500-550 mm (Kovács-Láng et al. 2000). The landscape consists of the
152 remnants of the forest steppe vegetation and cultivated land with heterogeneous and changing
153 land-use. Major habitat types include arable land (25-30%), secondary grasslands or old-fields

154 (15-20%), tree plantations (25-30%), natural grasslands (5-10%) and woodlands (2-3%)
155 (Rédei et al. 2014, Rédei et al. 2011).

156

157 **Study sites**

158 We worked in a total of 64 study sites spread over a ca. 35 km² area in the central part
159 of the Kiskunság, in the vicinity of the villages Fülöpháza and Orgovány (coordinates of NW
160 corner: N46.894, E19.386; SE corner: N46.789, E19.468). We chose eight sites in each of
161 eight widespread non-arable habitat types typical to the study area (Table 1): open secondary
162 grasslands (old-fields), closed secondary grasslands (old-fields), open natural (primary)
163 grasslands, closed natural (primary) grasslands, alien black locust (*Robinia pseudoacacia*)
164 plantations, alien pine (*Pinus sylvestris* and *P. nigra*) plantations, native poplar (*Populus alba*
165 and *P. x canescens*) woodlands, and forest-renewal stands (pine). Open grasslands occupy
166 dune tops and dune sides and are characterized by 30-60% plant cover, while closed
167 grasslands occupy lower elevation sites and are characterised by 70-100% plant cover.
168 Secondary grasslands had been arable lands or vineyards, but were abandoned at least six
169 years before the start of the experiment, with spontaneous grassland recovery taking place on
170 them. Tree plantations and woodlands were chosen to have a minimum tree age of 20 years.
171 Forest renewal stands were clear-felled pine plantations that were deep-ploughed and
172 replanted with pine (*P. nigra* or *P. sylvestris*) 1-3 years before the start of the experiment, and
173 are characterised by yearly ploughing between the rows of the tree saplings for weed control.
174 Although some of these habitats are currently not considered important ragweed habitats, a
175 large-scale survey in the study region indicated that ragweed is already present even in closed
176 grasslands and tree plantations (Csecserits et al. 2009).

177 The past land use of each study site was determined based on aerial photographs and

178 past land-use maps of the area (Rédei et al. 2014). Based on the timing of last ploughing, sites
179 were assigned to the following categories: (1) sites that were unploughed in and after 1950,
180 (2) sites that were ploughed in 1950 but not in 1986, (3) sites still ploughed in 1986.

181

182

183 Table 1 Characteristics of the habitat types studied (numbers are mean values of eight replicates)

Variable	Open secondary grassland	Closed secondary grassland	Open natural grassland	Closed natural grassland	Alien black locust plantation	Alien pine plantation	Native poplar woodland	Forest renewal stands (pine)
Sand content (%)	96.8	96.6	97.9	96.3	96.9	97.7	95.3	98.4
Soil humus content (%)	0.9	1.3	0.7	1.9	1.6	0.9	3.6	0.2
Soil pH (KCl)	7.29	7.41	7.53	7.35	7.45	7.35	7.38	7.62
Cover of herb layer (%)	60	91	40	81	72	1	12	8
Leaf area index (LAI) of tree layer	–	–	–	–	2.3	3.9	3.2	–
Current land-use	none or occasional grazing	none or occasional grazing	none	none	forestry: occasional thinning (stand age >20 years)	forestry: occasional thinning (stand age >20 years)	none or forestry: occasional thinning (stand age >20 years)	forestry: yearly tilling between rows (stand age <5 years)

184

185

186

187 **Experimental design, sampling and measurements**

188 In each study site, we established four 1 m x 1 m plots arranged in the corners of a 4 m
189 x 4 m block in November 2008. For each plot, we randomly assigned one of four treatment
190 types: (1) ragweed seed addition (0.8 g, that is 215.8 \pm 15.5 seeds collected locally in
191 September 2008) onto the soil surface without any further treatment, (2) soil disturbance
192 (digging the soil ca. 20 cm deep with a hand spade), (3) soil disturbance with subsequent seed
193 addition, and (4) control. The amount of seeds added was decided based on previous reports
194 that germination rate of ragweed is relatively low and variable, ranging from 2% to 36%
195 (Fumanal 2008a).

196 In each site, soil samples were taken from three points to a depth of 20 cm with a soil
197 sampler of 5 cm in diameter in November 2008. The three soil samples were fully mixed
198 before analyses. Soil samples were analysed for texture (percent sand, silt, and clay content),
199 humus content (%), and pH(KCl). The leaf area index (LAI) of the woody canopy of each
200 forested habitat was measured above the herbaceous layer (1 m) in May 2009 using a LAI
201 2000 Plant Canopy Analyser instrument (LI-COR, Inc. 1992). We use LAI as a proxy for
202 light conditions in forests, where higher Leaf Area Index values represent lower light
203 availability.

204 In order to test ragweed seed availability in the soil seed bank, we collected soil
205 samples for seed bank analysis from all sites of five habitat types (open and closed primary
206 grasslands, open and closed secondary grasslands, black locust plantations), where ragweed
207 was expected to occur based on previous field experience (results provided further support
208 that habitats not sampled for ragweed seeds were free from ragweed seeds; see the Results).

209 In each sampled site, six samples were taken to a depth of 0-10 cm with a soil sampler of 5
210 cm in diameter. This resulted in approx. 1178cm³ soil per stand, which was mixed thoroughly
211 and sieved. Intact ragweed seeds were counted in the soil samples by visual screening using a
212 stereo microscope.

213 In mid July, when ragweed germination ceased, we counted the number of ragweed
214 plants in each study plot in the field. In early September, before seed ripening, we harvested
215 the total aboveground biomass of ragweed in each plot and measured the dry weight after
216 three days of drying at 80 °C.

217

218 **Data analysis**

219 We used Friedman-ANOVA to test if there are significant differences in the number of
220 ragweed seedlings and in ragweed aboveground biomass among the four treatment
221 combinations within each habitat type, and post-hoc test using the "symmetry_test" function
222 (Hothorn et al. 2008) to test pairwise differences between treatments if the global test
223 indicated significant difference. We also conducted these tests including all sites (irrespective
224 of habitats) to test for overall treatment effect. We used non-parametric statistics, because data
225 had skewed distribution and very many zero values (where no ragweed was found). Although
226 the original experimental design included two factors, seed addition and soil disturbance, each
227 of them with two treatment levels (yes/no), we used unifactorial test because no non-
228 parametric test is available for a multifactorial design where replicates are arranged in blocks
229 (site).

230 To test the effect of disturbance on growth we used Wilcoxon signed-rank test to
231 compare the mean size an average ragweed seedling could reach (overall aboveground
232 ragweed biomass in September divided by the number of seedlings in July) between seeded-

233 only and disturbed-and-seeded plots. We used these two plot types, because only few
234 disturbed-only and control plots had any ragweed (see the Results). Only sites that had
235 ragweed in both the seeded-only and disturbed-and-seeded plots were used for this analysis.

236 Kruskal-Wallis test was used to compare ragweed biomass in disturbed-and-seeded
237 plots of different habitat types, and Dunn-test was used as a posthoc test to check pairwise
238 differences (Hollander and Wolfe 1999). Similarly, Kruskal-Wallis test was used to compare
239 ragweed biomass in disturbed-only plots among sites abandoned at different times in the past.

240 Spearman rank correlation was used to test relationship between ragweed biomass and
241 soil texture (sand content) or soil humus content in herbaceous and forested habitats
242 separately. Spearman rank correlation was also used to test the relationship between ragweed
243 biomass and LAI of the woody canopy in forested habitats.

244 In order to test whether soil disturbance effectively triggers ragweed emergence in the
245 disturbed-only plots, we conducted Pearson's Chi-squared test with Yates' continuity
246 correction to compare ragweed emergence (yes/no) and documented ragweed occurrence in
247 the seed bank (yes/no). As we found ragweed seeds in nine sites, with only four sites having
248 more than three seeds (Online Resource 1), we did not analyse further the size of the seed
249 bank.

250 All statistical tests were performed in R statistical environment (R Core Team 2016),
251 using the coin (Hothorn et al. 2008) and multcomp (Hothorn et al. 2008) packages.

252

253

254 **RESULTS**

255 **The effect of seed addition and disturbance on ragweed emergence and biomass in** 256 **different habitat types**

257 Of the 64 sites, in July 2008 we found ragweed in five control plots (live ragweed in
258 five plots in September), in 30 seeded-only plots (in 19 plots in September), in 11 disturbed-
259 only (in 11 plots in September), and in 61 disturbed-and-seeded plots (in 56 plots in
260 September). There were significant treatment effects on ragweed biomass in all of the eight
261 habitat types in September (Fig. 1). Disturbed-and-seeded plots had higher ragweed biomass
262 than control plots in all habitat types (Fig. 1). By contrast, neither disturbed-only plots nor
263 seeded-only plots differed from control plots in any of the habitat types (Fig. 1). Accordingly,
264 an overall analysis across all the 64 sites showed that disturbed-and-seeded plots had high
265 biomass, while the other three types had low biomass similar to each other (Online Resource
266 2). The only habitat type where seed addition alone induced a substantial amount of ragweed
267 biomass was forest renewal stands (Fig. 1h). The only habitat types where disturbance alone
268 triggered a considerable ragweed biomass were open and closed secondary grasslands (Fig 1a
269 and 1b). Seedling numbers in July showed generally similar patterns to that of ragweed
270 biomass in September (Online Resource 3), with the only notable difference that seedling
271 numbers in seeded-only plots did not differ from those in disturbed-and-seeded plots also in
272 pine plantations and black locust plantations (Online Resource 3).

273 The size that an average ragweed plant could reach by September (September biomass
274 divided by July seedling number) was much larger in disturbed-and-seeded plots than in
275 seeded-only plots (Wilcoxon signed rank test, $n=28$, $V=346$, $p=1.577*10^{-5}$). Average size
276 reached by a ragweed plant was 9.24 g (median: 1.45 g) and 1.77 g (median: 0.017 g) in
277 disturbed-and-seeded and seeded-only plots, respectively.

278

279 **Ragweed biomass in the disturbed-and-seeded plots: the effect of habitat type, soil**
280 **attributes, and light availability**

281 Although disturbed-and-seeded plots had the highest ragweed biomass in all habitat
282 types studied (Fig. 1), the absolute numbers varied largely among habitat types (Fig. 2;
283 Kruskal-Wallis test, $\text{Chi}^2 = 28.6$, $\text{df} = 7$, $p = 0.0002$). Ragweed biomass was very low in
284 native poplar woodlands and alien pine plantations, while it was highest in open secondary
285 grasslands and closed natural grasslands. The other four habitat types were intermediate, with
286 huge within-type variation.

287 Ragweed biomass in the disturbed-and-seeded grassland plots (open and closed natural
288 and secondary grasslands; $n=32$) was negatively correlated with the sand fraction of the soil
289 (Spearman's $\rho=-0.54$, $p=0.0017$), and marginally positively correlated with soil humus
290 content (Spearman's $\rho=0.35$, $p=0.056$). Ragweed biomass in the disturbed-and-seeded plots
291 of woody habitats (black locust plantations, pine plantations, poplar woodlands; $n=24$) was
292 correlated neither with the sand fraction of the soil (Spearman $\rho=-0.021$, $p=0.92$), nor with
293 the soil humus content (Spearman $\rho=0.091$, $p=0.67$), but it was negatively correlated with
294 leaf area index (LAI) of the forest canopy (Spearman $\rho=-0.44$, $p=0.031$).

295

296 **Ragweed in the disturbed-only plots: the effect of the time of abandonment**

297 The occurrence of ragweed in some of the control and seeded-only plots (open
298 secondary grasslands, closed secondary grasslands, black locust plantations) means that
299 ragweed was present in the seed bank at these sites. Indeed, seed bank analysis confirmed that
300 ragweed was present at these sites, but not in others. There was a strong correlation between
301 the presence of ragweed seeds in the seed bank and ragweed emergence in the disturbed-only
302 plots (Pearson's Chi-squared test with Yate's continuity correction, $\text{Chi}^2 = 29.05$, $\text{df} = 1$, $p =$
303 $7.06 \cdot 10^{-8}$), with ragweed seeds found in 9 out of 10 sites where ragweed emerged (one site
304 with ragweed emergence was not tested for ragweed seeds), but in none of the other 29 sites
305 checked for ragweed seed bank.

306 Analysis of historical maps revealed that 34 out of the 64 study sites were ploughed
307 and used as arable land or vineyard in the 1950s (the time of first map with high enough
308 resolution), and 13 sites were still farmed after 1986. Of the 11 sites where ragweed occurred
309 in the disturbed-only plots, all were ploughed after 1950, and ten even after 1986. Therefore,
310 ragweed biomass in disturbed-only plots was strongly related to the time of abandonment
311 (Kruskal-Wallis test, $\text{Chi}^2 = 39.37$, $\text{df} = 2$, $p = 2.8 \times 10^{-9}$; Fig. 3), with recently abandoned sites
312 having high ragweed biomass when disturbed.

313

314 **DISCUSSION**

315 Our study was designed to test the effects of seed addition (controlled propagule
316 pressure) and soil disturbance on the biomass of common ragweed in eight major non-arable
317 habitat types in a heavily infested landscape. We found that disturbance alone triggered high
318 ragweed biomass only where ragweed seeds were already present due to land-use legacy
319 (recent farming). Seed addition alone induced high ragweed biomass only where disturbance
320 was part of the present management (forest renewal). In full agreement with these unifactorial
321 results, when seed addition and disturbance were combined experimentally, ragweed
322 established in all habitat types and could reach high biomass in all habitat types, except for
323 closed-canopy forests. These results suggest that common ragweed has huge potential to
324 expand even in already infested landscapes, if soil disturbance occurs and seeds are either
325 present in the seed bank or dispersed in the landscape.

326 Our results confirm previous findings that propagule pressure is a key factor in
327 determining true invasibility of target ecosystems (Colautti et al. 2006, Simberloff 2009). In
328 particular, our results highlight that low propagule pressure can limit the infilling of suitable
329 habitats even in a heavily infested landscape. Our finding that high propagule pressure and
330 disturbance are both needed for a successful invasion is similar to results found during the

331 invasion of *Anthriscus caucalis*: low invasibility of grasslands in the absence of disturbance
332 (grazing) irrespective of propagule pressure, but high invasibility in the presence of
333 disturbance (Wallace and Prather 2016). Eschtruth and Battles (2009) also found that high
334 level of canopy disturbance and high propagule pressure are needed for a successful invasion
335 of forest understory species, but response differed among species. By contrast, McGlone et al.
336 (2011) found that perennial grassland under ponderosa pine are resistant to invasion by
337 cheatgrass even at high propagule pressure and even in the presence of disturbance.

338

339 **Ragweed in control and disturbed-only plots, and the importance of land-use history**

340 Our study area is among the regions most heavily infested by common ragweed in
341 Europe (Skjøth et al. 2010; Hamaoui-Laguel et al. 2015), where highest ragweed pollen load
342 ever recorded in Europe was detected (Skjøth et al. 2010). Yet, we found that ragweed was
343 present only in five control plots and 11 disturbed-only plots of the 64 study sites. Since we
344 found that most habitat types are highly suitable for ragweed, the low frequency of ragweed is
345 most likely related to dispersal limitation. Because long-distance ragweed dispersal is mostly
346 linked to human activity (Essl et al 2015), measures that prevent, or slow down anthropogenic
347 seed dispersal are crucially important to avoid a further increase in ragweed abundance and
348 thus in pollen load. Future seed dispersal was also highlighted as a major source of
349 uncertainty regarding the rate of increase in the European-scale ragweed pollen load
350 (Hamaoui-Laguel et al. 2015).

351 Where seeds were present in the seed bank, such as in several of the open and closed
352 secondary grasslands, disturbance alone led to high ragweed biomass. This triggering effect of
353 disturbance on dormant seeds has already been shown for common ragweed in set-aside lands
354 (Fumanal et al. 2008a), and it is typical of annual species (Hobbs and Mooney 1985). The
355 strong correlation between ragweed presence in the seed bank and ragweed presence in

356 disturbed-only plots suggests that the disturbance applied could efficiently induce germination
357 of dormant ragweed seeds. Because ragweed is quickly suppressed in the absence of
358 disturbance, such as after abandonment (Bazzaz 1968, Gentili et al. 2017) but its seeds remain
359 viable for several decades (Essl et al. 2015), such standardised small-scale disturbances or
360 seed bank surveys may be used to show a true infestation map, as opposed to that based on
361 ragweed occurrence in the vegetation. Ragweed distribution maps often form the basis for
362 broad scale predictive modelling (Richter et al. 2013; Hamaoui-Laguel et al. 2015), thus
363 improving the accuracy of these maps by including this hidden infestation (dormant seeds)
364 may be important.

365 The presence of ragweed at the study sites was closely related to previous land-use,
366 which indicates a strong land-use legacy (Foster et al. 2003). All 11 sites where ragweed was
367 present in disturbed-only plots were ploughed after 1950, and 10 of the 11 sites were still
368 under cultivation in the 1980s. This result in line with previous findings that the distribution
369 patterns of invasive species that are agricultural weeds may be related to historical pattern of
370 croplands (González-Moreno et al. 2017). According to the national (Hungarian) weed
371 surveys (Novák et al. 2009), common ragweed became a widespread weed in these decades: it
372 was only the twenty-first most dominant arable weed in 1950, but already the fourth in 1988.
373 In addition, a reconstruction of ragweed spread shows that it was not yet abundant in our
374 study region in the 1970s (Béres and Hunyadi 1991). These findings suggest that if farming in
375 a given field ceased only after ragweed had spread and become abundant in a region, such as
376 the 1980s in our study region, abandoned agricultural lands are most likely infested with the
377 species, even if it is not present in the herb layer.

378

379 **The effect of seed addition across habitat types**

380 The very low ragweed biomass we found in most seeded-only plots is due to a
381 combination of low germination rate and limited growth, as we found that seedlings in non-
382 disturbed plots grow very small. Ragweed germination in these plots may be limited by low
383 light levels in intact vegetation (Bazzaz 1968), and growth is strongly suppressed by other
384 plants, because ragweed is a weak competitor (Gentili et al. 2017). The low frequency of
385 occurrence, as well as the low biomass of ragweed in seeded-only plots indicates that seed
386 addition alone is not enough for inducing high ragweed biomass. This implies that although
387 seed dispersal is a key factor of uncertainty when predicting future ragweed abundance
388 (Hamaoui-Laguel et al. 2015), seed presence alone does not necessarily lead to higher
389 ragweed biomass and pollen production. The only habitat type where some seeded-only plots
390 had high ragweed biomass was forest renewal sites, where yearly soil disturbance is part of
391 the management in the early years after tree planting.

392

393 **The combined effects of seed addition and disturbance, and the role of soil attributes**
394 **and light availability**

395 We found that when seed addition was combined with soil disturbance, ragweed
396 reached higher biomass than in other treatments in every habitat types, although absolute
397 numbers differed greatly. This result reinforces the findings from the single treatments that
398 seed addition and disturbance are both needed for high ragweed cover. This high biomass in
399 disturbed-and-seeded plots resulted from a high seedling emergence in these plots combined
400 with a bigger size that emerged seedlings reached in disturbed plots compared to undisturbed
401 plots. Early and rapid seed germination may have a crucial role in inducing high ragweed
402 cover, as it has been generally found for invasive species (Gioria and Pyšek 2017), especially
403 because common ragweed is a weak competitor (Bazzaz 1968).

404 The substantial biomass in most disturbed-and-seeded plots means substantial pollen
405 production, as ragweed plant biomass has been shown to be highly correlated to pollen
406 production (Fumanal et al. 2007). In addition, biomass has also been shown to be highly
407 correlated to seed production (Fumanal et al. 2007), which is of high importance with regards
408 to persistence in and further spread from a given site. The low biomass values in some forest
409 types may be due to the fact that ragweed grows best in full sunlight (Bazzaz 1973), and these
410 forest types have closed canopy (Table 1). The negative correlation between the soil sand
411 content and ragweed biomass and the positive correlation between soil humus content and
412 ragweed biomass across sites may be related to water holding capacity associated with these
413 soil attributes. This is in agreement with previous reports, that ragweed favours habitats of
414 relatively good water supply (Essl et al. 2015), even if our study covered a rather narrow and
415 extreme range of potential soils (sand soil with low humus content; Table 1).

416 Our results show high invasibility for most ecosystems occurring in this heterogeneous
417 cultural landscape when disturbance is present. This suggests that although common ragweed
418 has most often been reported from arable lands and roadsides (Lavoie et al. 2007, Pinke et al.
419 2011; Essl et al. 2009), it has the potential to invade additional habitats such as grasslands and
420 open forests, if they are disturbed. Such disturbances in our study area may include small-
421 scale animal disturbances and grazing, but more importantly, large-scale conversion of
422 croplands and previous croplands (oldfields) to tree plantations (Csecserits et al. 2013).

423 Several shifts in habitat preferences have been observed for common ragweed in the
424 past (Lavoie et al. 2007; Essl et al. 2009), and our results on habitat invasibility hint that such
425 changes may occur also in the future. Our results also highlight that assessing invasibility
426 without disturbance may easily underestimate invasibility, because invasion is often
427 facilitated by disturbances (Hobbs and Huenekke 1992; Burke and Grime, 1996). Intact
428 ecosystems may resist invasion, but when disturbed, they can be more susceptible to changes,

429 as it has also been observed in the context of climate change (Kröel-Dulay et al. 2015).
430 Because disturbances are an inherent part of ecosystem dynamics (Pickett and White 1985),
431 and all ecosystems are sooner or later disturbed, it is critically important to assess ecosystem
432 sensitivity (including invasibility) in combination with disturbance.

433 Our conclusion from this experiment is that common ragweed has huge potential for
434 further spread even within already infested landscapes. Indeed, in a broad-scale survey in the
435 same study region we found that many habitat types that have not been traditionally
436 considered as ragweed habitats, such as tree plantations or natural grasslands, are also infested
437 by ragweed (Cseceserits et al. 2009). The findings in our field experiment provides field-based
438 support for results from recent broad-scale modelling studies that also forecast ragweed
439 spread, including range expansion (Storkey et al. 2014; Leiblein-Wild et al. 2016), increased
440 productivity (Leiblein-Wild et al. 2016), and increased pollen load (Hamaoui-Laguel et al.
441 2015) and associated allergy costs (Richter et al. 2013). In particular, Hamaoui-Laguel et al.
442 (2015) predicts a two-fold increase in pollen load for our study region, the Pannonian plain,
443 based on a combination of a regional climate model, a chemistry-transport model and a
444 simplified spread model. Our study confirms that this is a realistic scenario because not all
445 suitable habitats have yet been colonised by ragweed. Empirical data from such field-based
446 studies may also improve broad-scale modelling (Storkey et al. 2014) through, for instance,
447 providing better habitat suitability maps. Such field-based data may also help to eliminate
448 some of the limitations identified in recent modelling frameworks, such as assuming no
449 competition for ragweed (Leiblein-Wild et al. 2016), or neglecting population growth within
450 large (35 km²) grid cells (Richter et al. 2013).

451 Finally, based on our results obtained in non-arable habitats combined with results
452 from previous works that also included arable habitats (Bullock et al. 2012; Smith et al. 2013;

453 Essl et al. 2015), we provide a list of recommendations for land managers and land use
454 planners regarding ragweed management at the landscape scale.

455 1. Because infestation by ragweed is not always visible in the vegetation due to
456 suppression and seed dormancy, a survey of the true pattern and level of infestation would be
457 necessary to get baseline data as a basis for land use planning.

458 2. When a landscape is completely free of ragweed, emphasis should be placed on
459 avoiding ragweed seed dispersal and eradicating establishing populations in the early phase.
460 Because long-distance dispersal is mostly human-mediated, controlling seed dispersal means
461 avoiding seed contamination, as well as the movement of agricultural or construction vehicles
462 and soil among landscapes or regions (Vitalos and Karrer 2009; Lavoie et al., 2007).

463 3. Since our results show that even in a highly infested region many habitat patches
464 may still be free of ragweed (including the seed bank), preventing seed dispersal must remain
465 a priority even within infested landscapes to avoid or slow down the further infilling of
466 suitable habitats.

467 4. Reducing soil disturbance in all landscapes irrespective of infestation level is of
468 particular importance. This may reduce the chance of ragweed establishment when ragweed is
469 not present but dispersal events happen, and may prevent or greatly reduce ragweed
470 emergence from the seed bank when it is there. Our results highlight that combining
471 knowledge on the historical timing of ragweed arrival in a region with that on the last soil
472 disturbance (farming or tree planting) may help to identify infested patch types.

473 Certainly, soil disturbance is an inherent feature of many human land uses (farming,
474 forest renewal, construction, etc.), thus fully avoiding soil disturbance is not a realistic option.
475 However, a reconsideration of the intensity, extent, frequency and timing of all current soil

476 disturbing practices in relation to ragweed biology may be needed to reach a substantial
477 reduction in ragweed abundance and associated pollen load in already infested regions.

478

479 **Acknowledgements**

480 We thank Bernadett Kolonics, Richárdné Ribai and Sándorné Vadkerti for their help in lab
481 work. This study was funded by the Ministry of Agriculture and Rural Development (Z. B-
482 D.), by the MTA Postdoctoral Research Programme (PD-009/2017; A. C.), and by the MTA
483 János Bolyai Research Scholarship (BO/00276/15/8; G. K-D.).

484

485 **Authors' Contributions**

486 G. K-D, A. C. and Z. B-D. conceived the research. All authors were involved in data
487 collection in the field. Z. B-D. analysed the data. G. K-D. led the writing of the manuscript,
488 with major input from A. C., Z. B-D., and K S. All authors contributed substantially to the
489 draft, and gave final approval for publication.

490

491 **References**

492 Bazzaz FA (1968) Succession on abandoned fields in the Shawnee Hills, Southern Illinois.

493 *Ecology* 49:924–936

494 Bazzaz FA (1973) Photosynthesis of *Ambrosia artemisiifolia* L. plants grown in greenhouse

495 and in the field *American Midland Naturalist* 90:186-190.

496 Beckstead J, Augspurger C (2004) An experimental test of resistance to cheatgrass invasion:

497 limiting resources at different life stages. *Biological Invasions* 6:417–432.

498 Béres I, Hunyadi K (1991) Az *Ambrosia elatior* elterjedése Magyarországon. *Növényvédelem*

499 27:405–410

500 Berg JA, Meyer, GA, Young EB (2016) Propagule pressure and environmental conditions
501 interact to determine establishment success of an invasive plant species, glossy
502 buckthorn (*Frangula alnus*), across five different wetland habitat type. *Biological*
503 *Invasions* 18:1363-1373

504 Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JR, Richardson
505 DM (2011). A proposed unified framework for biological invasions. *Trends in*
506 *Ecology and Evolution* 26:333-339

507 Bullock J, Chapman D, Schaffer S, Roy D, Girardello M, Haynes T, Beal S, Wheeler B,
508 Dickie, I. et al. (2012) Assessing and controlling the spread and the effects of common
509 ragweed in Europe (ENV.B2/ETU/2010/0037). European Commission, Final Report

510 Burbach GJ, Heinzerling LM, Röhnelt C, Bergmann KC, Behrendt H, Zuberbier T (2009)
511 Ragweed sensitization in Europe—GA2LEN study suggests increasing prevalence.
512 *Allergy* 64:664-665.

513 Burke MJW. Grime JP (1996) An experimental study of plant community invasibility.
514 *Ecology* 77:776-790

515 Chauvel B, Dessaint F, Legrand C, Bretagnolle F (2006) The historical spread of *Ambrosia*
516 *artemisiifolia* L. in France from herbarium records. *Journal of Biogeography* 33:665-
517 673

518 Colautti RI, Grigorovich IA, MacIsaac HJ (2006) Propagule pressure: a null model for
519 biological invasions. *Biological Invasions* 8:1023-1037.

520 Csecserits A, Botta-Dukát Z, Kröel-Dulay G, Lhotsky B, Ónodi G, Rédei T, Szitár K. Halassy
521 M (2016) Tree plantations are hot-spots of plant invasion in a landscape with
522 heterogeneous land-use. *Agriculture, Ecosystems and Environment* 226:88-98

- 523 Csecserits A, Kröel-Dulay G, Molnár E, Rédei T, Szabó R, Szitár K, Botta-Dukát Z (2009) A
524 parlagfű (*Ambrosia artemisiifolia* L.) előfordulása és tömegessége változatos
525 tájhasználatú mozaikos tájban. *Gyomnövények, gyomirtás* 10:44-51.
- 526 Csontos P, Angyal Z, Chmura D, Nagy J, Halbritter A, Tamás J (2015) New Stand of Invasive
527 Neophyte *Ambrosia artemisiifolia* L. and Its Potential Reproduction. *Polish Journal of*
528 *Ecology* 63:453-459
- 529 Dahl A, Strandhede SO, Wihl, JA (1999) Ragweed – An allergy risk in Sweden?
530 *Aerobiologia* 15:293–297
- 531 Eschtruth AK, Battles JJ (2009) Assessing the relative importance of disturbance, herbivory,
532 diversity, and propagule pressure in exotic plant invasion. *Ecological Monographs*
533 79:265-280
- 534 Essl F, Biró K, Brandes D, Broennimann O, Bullock JM, Chapman DS, Chauvel B, Dullinger,
535 S, Fumanal B et al. (2015) Biological flora of the British Isles: *Ambrosia*
536 *artemisiifolia*. *Journal of Ecology* 103:1069-1098
- 537 Essl F, Dullinger S, Kleinbauer I (2009) Changes in the spatio-temporal patterns and habitat
538 preferences of *Ambrosia artemisiifolia* during its invasion of Austria *Preslia* 81:119–
539 133
- 540 Foster DR, Swanson F, Aber J, Burke I, Brokaw B, Tilman D, Knapp A (2003) The
541 importance of land-use legacies to ecology and conservation. *Bioscience* 53:77–88
- 542 Fumanal B, Chauvel B, Bretagnolle F (2007) Estimation of pollen and seed production of
543 common ragweed in France. *Annals of Agricultural and Environmental Medicine*
544 14:233–236
- 545 Fumanal B, Gaudot I, Bretagnolle F (2008a) Seed-bank dynamics in the invasive plant,
546 *Ambrosia artemisiifolia* L. *Seed Science Research* 18:101–114

- 547 Fumanal B, Girod C, Fried G, Bretagnolle F, Chauvel B (2008b) Can the large ecological
548 amplitude of *Ambrosia artemisiifolia* explain its invasive success in France? *Weed*
549 *Research* 48:349–359
- 550 Galzina N, Barić K, Šćepanović M, Goršić M, Ostojić Z (2010) Distribution of invasive weed
551 *Ambrosia artemisiifolia* L. in Croatia. *Agriculturae Conspectus Scientificus*, 75: 75-81
- 552 Gentili R, Montagnani R, Gilardelli F, Guarino MF, Citterio S (2017) Let native species take
553 their course: *Ambrosia artemisiifolia* replacement during natural and artificial
554 succession. *Acta Oecologica* 82:32-40.
- 555 Gioria M, Pyšek P (2017) Early bird catches the worm: germination as a critical step in plant
556 invasion. *Biological Invasions* 19:1055–1080
- 557 González-Moreno P, Pino J, Cózar A, García-de-Lomas, Vilà M (2017) The effects of
558 landscape history and time-lags on plant invasion in Mediterranean coastal habitats.
559 *Biological Invasions* 19:549–561
- 560 Hamaoui-Laguél L, Vautard R, Liu L, Solmon F, Viovy N, Khvorostyanov D, Essl F, Chuine
561 I, Colette A, et al. (2015) Effects of climate change and seed dispersal on airborne
562 ragweed pollen loads in Europe. *Nature Climate Change* 5:766–771
- 563 Hobbs RJ, Huenneke LF (1992) Disturbance, diversity, and invasion: implications for
564 conservations. *Conservation Biology* 6:324-337
- 565 Hobbs RJ, Mooney HA (1985) Community and population dynamics of serpentine grassland
566 annuals in relation to gopher disturbance. *Oecologia* 67:342-351
- 567 Hollander M, Wolfe DA (1999) *Nonparametric Statistical Methods*, 2nd Edition. New York:
568 John Wiley & Sons, p244

- 569 Hothorn T, Hornik K, van de Wiel MA, Zeileis A (2008) Implementing a Class of
570 Permutation Tests: The coin Package. *Journal of Statistical Software* 28:1-23. URL
571 <http://www.jstatsoft.org/v28/i08/>
- 572 Hothorn T, Bretz F, Westfall P (2008) Simultaneous Inference in General Parametric Models.
573 *Biometrical Journal* 50:346-363
- 574 Katz DS, Barrie BTC, Carey TS (2014) Urban ragweed populations in vacant lots: An
575 ecological perspective on management. *Urban Forestry and Urban Greening* 13:756-
576 760
- 577 Kazinczi G, Béres I, Varga P, Kovács I, Torma M (2007) A parlagfű (*Ambrosia artemisiifolia*
578 L.) és a kultúrnövények közötti versengés szabadföldi additív kísérletekben. *Magyar*
579 *Gyomkutatás és Technológia* 8:41–47
- 580 Király G (ed.) (2009) Új Magyar Fűvészkönyv, Magyarország hajtásos növényei. Aggteleki
581 Nemzeti Park Igazgatóság, Jósvalfő, Hungary
- 582 Kovács-Láng E, Kröel-Dulay G, Kertész M, Fekete G, Mika J, Dobi-Wantuch I, Rédei T,
583 Rajkai K, Hahn I, Bartha S (2000) Changes in the composition of sand grasslands
584 along a climatic gradient in Hungary and implications for climate change.
585 *Phytocoenologia* 30:385–408
- 586 Kröel-Dulay G, Ransijn J, Schmidt IK, Beier C, De Angelis P, de Dato G, Dukes JS, Emmett
587 B, Estiarte M et al. (2015) Increased sensitivity to climate change in disturbed
588 ecosystems. *Nature Communications* 6:6682
- 589 Lavoie C, Jodoin Y, Goursaud de Merlis A (2007) How did common ragweed (*Ambrosia*
590 *artemisiifolia* L.) spread in Quebec? A historical analysis using herbarium records.
591 *Journal of Biogeography* 34:1751–1761

592 Leiblen-Wild MC, Steinkamp J, Hickler T, Tackenberg O (2016) Modelling the potential
593 distribution, net primary production and phenology of common ragweed with a
594 physiological model. *Journal of Biogeography* 43:544-554

595 LI -COR Inc)1992) LAI-2000 plant canopy analyzer instruction manual. LI-COR Inc.,
596 Lincoln.

597 Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility.
598 *Ecology* 80:1522-1536

599 Mack RN (1981) Invasion in *Bromus tectorum* L. into western North America: an ecological
600 chronicle. *Agro-Ecosystems* 7:145-165

601 McGlone CM, Sieg CH, Kolb TE (2011) Invasion resistance and persistence: established
602 plants win, even with disturbance and high propagule pressure. *Biological Invasions*
603 13: 291-304.

604 Novák R, Dancza I, Szentey L, Karamán J (2009) Arable weeds of Hungary. The 5th national
605 weed survey (2007–2008). Ministry of Agriculture and Rural Development. Budapest,
606 Hungary

607 Parker IM (2001) Safe site and seed limitation in *Cytisus scoparius*(Scotch broom):
608 invasibility, disturbance, and the role of cryptogams in a glacial outwash prairie.
609 *Biological Invasions* 3:323-332

610 Pickett AT, White PS (1985) *The Ecology of Natural Disturbances and Patch Dynamics*
611 (Elsevier)

612 Pinke G, Karácsony P, Czúcz B, Botta-Dukát Z (2011) Environmental and land-use variables
613 determining the abundance of *Ambrosia artemisiifolia* in arable fields in Hungary.
614 *Preslia* 83:219-235

615 R Core Team (2016) R: A language and environment for statistical computing. R Foundation
616 for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>, Version
617 3.3.2

618 Rédei T, Csecserits A, Barabás S, Halassy M, Kröel-Dulay G, Lellei-Kovács E, Ónodi G,
619 Pándi I, Somay L, Szabó R, Szitár K, Török K (2011) Tájhasználat és biodiverzitás
620 kapcsolatának regionális léptékű vizsgálata a Kiskunságban: A Kiskun LTER
621 mintaterület- hálózat bemutatása. In: Verő György (ed.) *Természetvédelem és kutatás*
622 *a Duna–Tisza közti homokhátságon. Rosalia 6*. Budapest: Duna-Ipoly Nemzeti Park
623 Igazgatóság. pp. 423-445.

624 Rédei T, Szitár K, Czúcz B, Barabás S, Lellei-Kovács E, Pándi I, Somay L, Csecserits A
625 (2014) Weak evidence of long-term extinction debt in Pannonian dry sand grasslands.
626 *Agriculture, Ecosystems and Environment* 182:137-143

627 Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000)
628 Naturalization and invasion of alien plants: concepts and definitions. *Diversity and*
629 *distributions* 6:93-107

630 Richter R, Berger UE, Dullinger S, Essl F, Leitner M, Smith M, Vogl G (2013) Spread of
631 invasive ragweed: climate change, management and how to reduce allergy costs.
632 *Journal of Applied Ecology* 50:1422-1430

633 Simberloff D (2009) The Role of Propagule Pressure in Biological Invasions *Annual Review*
634 *of Ecology, Evolution and Systematics* 40:81–102

635 Skalova H, Guo W-Y, Wild J, Pyšek P (2017) *Ambrosia artemisiifolia* in the Czech Republic:
636 history of invasion, current distribution and prediction of future spread. *Preslia* 89: 1-
637 16.

638 Skjøth CA, Smith M, Šikoparija B, Stach A, Myszkowska D, Kasprzyk I, Radišić P,
639 Stjepanović B, Hrga I et al. (2010) A method for producing airborne pollen source
640 inventories: An example of Ambrosia (ragweed) on the Pannonian Plain. *Agricultural
641 and Forest Meteorology* 150:1203-1210

642 Smith M, Cecchi L, Skjøth CA, Karrer G, Šikoparija B (2013) Common ragweed: a threat to
643 environmental health in Europe. *Environment International* 61:115–126

644 Storkey J, Stratonovitch P, Chapman DS, Vidotto F, Semenov MA (2014) A process-based
645 approach to predicting the effect of climate change on the distribution of an invasive
646 allergenic plant in Europe. *PLoS One* 9:e88156

647 Tanentzap AJ, Lee WG, Monks A, Ladley K, Johnson PN, Rogers GM, Comrie JM, Clarke
648 DA, Hayman E (2014) Identifying pathways for managing multiple disturbances to
649 limit plant invasions. *Journal of Applied Ecology* 51:1015-1023

650 Von Holle B, Simberloff D (2005) Ecological resistance to biological invasion overwhelmed
651 by propagule pressure. *Ecology* 86: 3212-3218

652 Vilà M, Siamantziouras ASD, Brundu G, Camarda I, Lambdon P, Médail F, Moragues E,
653 Suehs CM, Traveset A, Troumbis AZ, Hulme PE (2008) Widespread resistance of
654 Mediterranean island ecosystems to the establishment of three alien species. *Diversity
655 and Distributions* 14:839-851

656 Vitalos M, Karrer G (2009) Dispersal of Ambrosia artemisiifolia seeds along roads: the
657 contribution of traffic and mowing machines. *Neobiota* 8:53-60

658 Wallace JM, Prather TS (2016) Invasive spread dynamics of Anthriscus caucalis at an
659 ecosystem scale: propagule pressure, grazing disturbance and plant community
660 susceptibility in canyon grasslands. *Biological Invasions* 8:145-157.

661 With K (2002) The landscape ecology of invasive spread. *Conservation Biology* 16:1192-
662 1203

663

664 **Electronic Supplementary Material:**

665 **Online Resource 1** Number of ragweed seeds found in the soil samples.

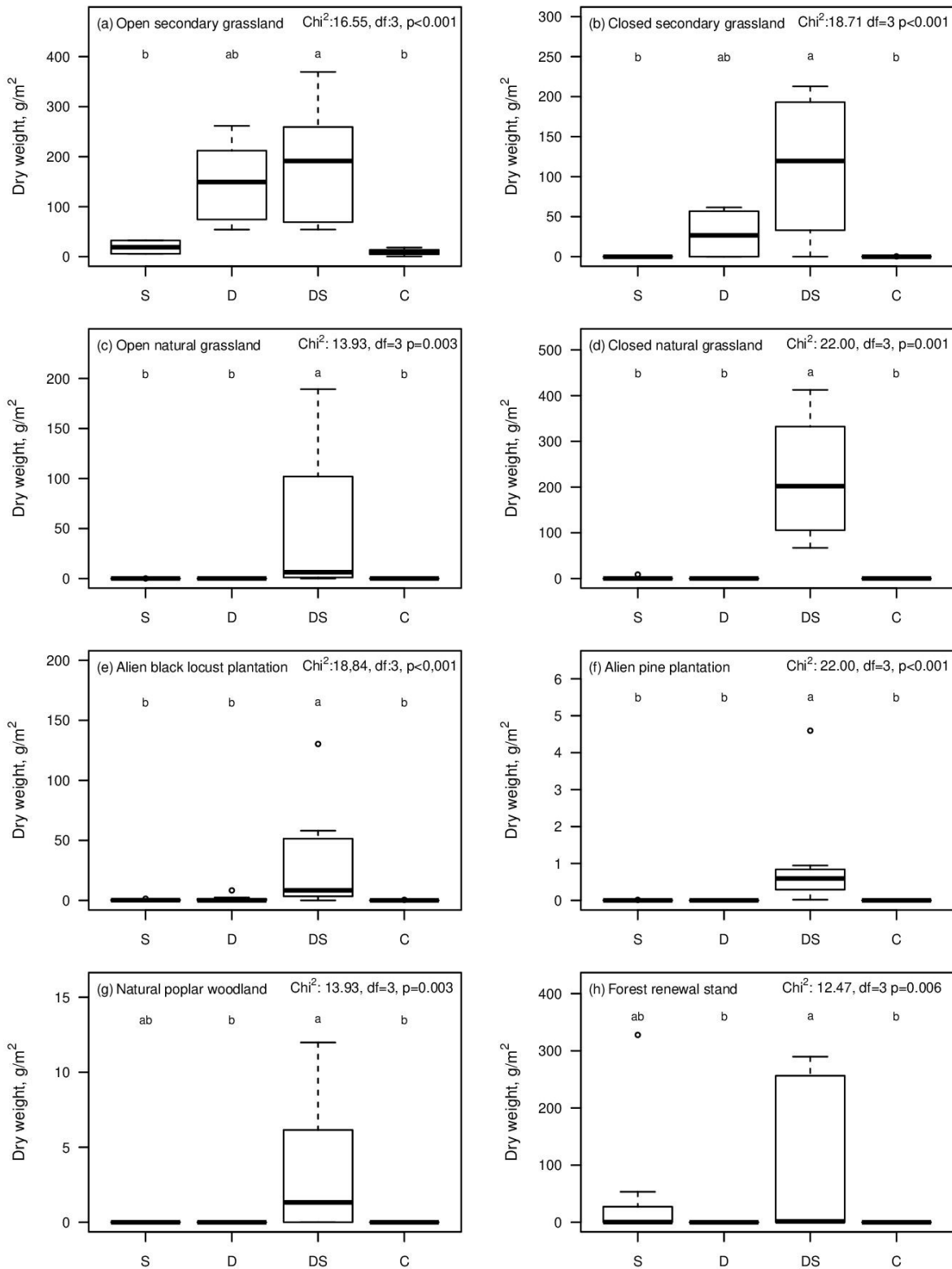
666 **Online Resource 2.** Boxplots of ragweed aboveground biomass in the four treatments across
667 all sites

668 **Online Resource 3** Boxplots of ragweed seedling numbers in July in the four treatments in
669 each of the eight habitat types.

670 **Online Resource 4** Boxplots of ragweed aboveground biomass in the four treatments in each
671 of the eight habitat types based on the non-zero data points only.

672

673

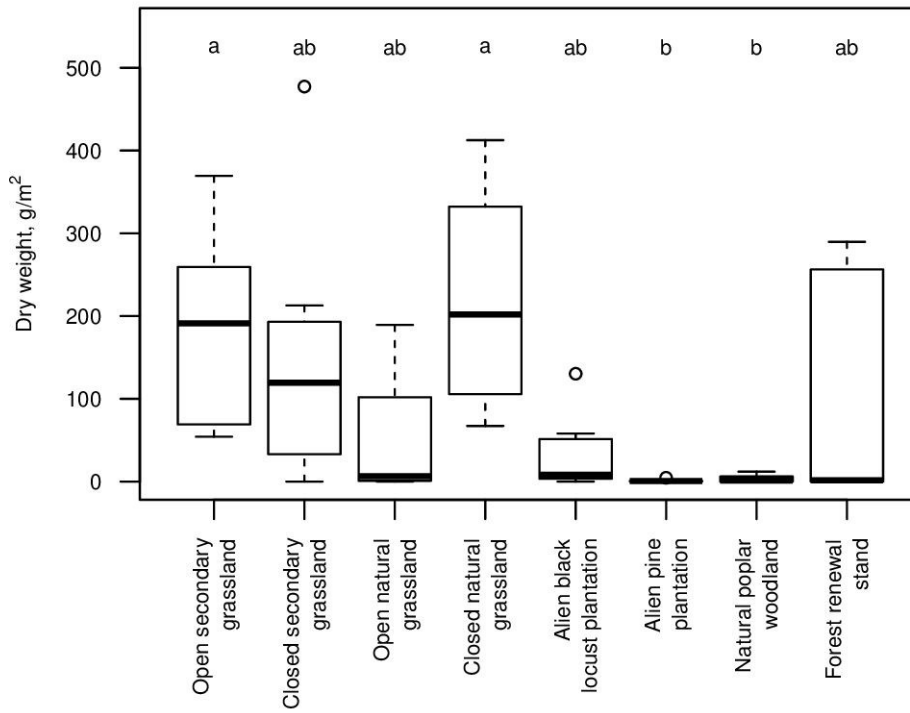


675

676 **Fig. 1** Boxplots of ragweed aboveground biomass in the four treatments in each of the eight

677 habitat types (S: seeded-only plots; D: disturbed-only plots; DS: disturbed-and-seeded plots;

678 C: control plots). χ^2 and p values refer to results from Friedman-ANOVA (n=8, df=3).
679 Different letters indicate significant differences among treatments within a habitat type. Note
680 that scaling of y-axis varies among subplots for a better visibility of within-habitat
681 differences. (For a version of this Figure that is based on the non-zero data points only, see
682 Online Resource 4).
683

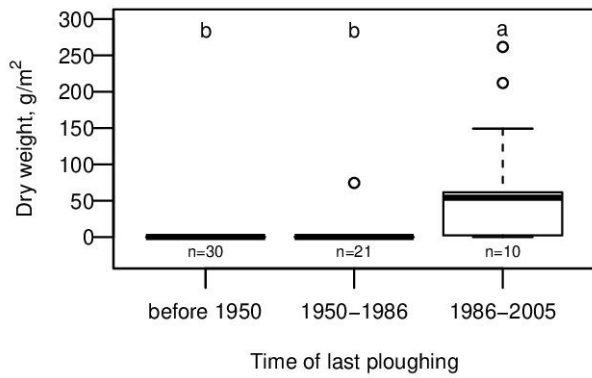


685

686 **Fig. 2** Boxplots of ragweed biomass in the disturbed-and-seeded plots in the eight habitat
 687 types. Different letters indicate significant differences between habitat types (Dunn-test for
 688 pairwise comparisons).

689

690



691

692 **Fig. 3** Boxplots of ragweed biomass in the disturbed-only plots, grouped according to the date
693 of last ploughing. Different letters indicate significant differences between age groups (Dunn-
694 test for pairwise comparisons).

695

696