

1 Turning old foes into new allies – harnessing drainage canals for biodiversity conservation in
2 desiccated novel ecosystems

3

4 Csaba Tölgyesi^{1*}, Attila Torma¹, Zoltán Bátori¹, Jelena Šeat^{1,2}, Miloš Popović³, Róbert
5 Gallé⁴, Nikolett Gallé-Szpisjak^{4,5}, László Erdős^{6,7}, Tamás Vinkó⁸, András Kelemen⁹, Péter
6 Török¹⁰

7

8 *Corresponding author, festuca7@yahoo.com

9 ¹Department of Ecology, University of Szeged, Szeged, Hungary

10 ²HabiProt, Novi Sad, Serbia

11 ³Department for Biology and Ecology, University of Niš, Niš, Serbia

12 ⁴Lendület Landscape and Conservation Ecology Research Group, Institute of Ecology and
13 Botany, Vácrátót, Hungary

14 ⁵GINOP Sustainable Ecosystems Group, Centre for Ecological Research, Tihany, Hungary

15 ⁶Centre for Ecological Research, Institute of Ecology and Botany, Vácrátót, Hungary

16 ⁷Department of Ecology, University of Debrecen, Debrecen, Hungary

17 ⁸Public Enterprise Palić-Ludaš, Palić, Serbia

18 ⁹MTA-ÖK Lendület Seed Ecology Research Group, Institute of Ecology and Botany,
19 Vácrátót, Hungary

20 ¹⁰MTA-DE Lendület Functional and Restoration Ecology Research Group, Debrecen,
21 Hungary

22 Abstract

23 1. Drainage canals are ubiquitous components of agricultural landscapes worldwide.
24 Although canals have greatly contributed to biodiversity loss by desiccating wetlands, they
25 have recently attracted conservation attention due to their potential to function as refugia for
26 native wetland-dependent species in intensively managed landscapes. However, their
27 conservation role in complex landscapes comprising a mosaic of agricultural and desiccated
28 semi-natural habitats, on which canals still pose a heavy burden, is unknown. Improved
29 understanding of drainage canals and related biodiversity in these landscapes could help
30 unlock their potential and support synergistic land management for nature conservation and
31 water management.

32 2. We applied a multitaxon approach, including plants, butterflies, true bugs, spiders and
33 birds, to (1) assess the conservation value of drainage canals in a heavily drained European
34 lowland region, (2) to test landscape-level and local canal parameters for aiding prioritization
35 among canal types, and (3) to propose a reconciliation-based management framework that
36 suits the interest of all stakeholders.

37 3. We found that drainage canals concentrate more species across most taxa than
38 adjacent semi-natural habitats, owing to the micro-environmental heterogeneity and the
39 comparatively low management intensity in the canals. The species-concentrating capacity is
40 particularly high in canals that traverse semi-natural habitats, although agricultural canals also
41 support remarkable species diversity. However, agricultural canals are important dispersal
42 corridors for invasive plants, which may negatively affect native species. Canal size has little
43 effect on biodiversity but habitat stress is an important determinant. The higher the stress (due
44 to sandiness and salinity), the higher is the added value of canals to landscape-wide
45 biodiversity.

46 *Synthesis and applications.* We provide evidence that drainage canals can harbour
47 surprisingly high levels of biodiversity and should therefore be recognized as important novel
48 ecosystems with high conservation value, even within semi-natural habitats. Canals have
49 previously been considered detrimental to nature conservation due to their association with
50 loss of wetlands. However, by reducing water loss with reversible obstructions, controlling
51 invasive species and applying specific conservation measures, they may be turned into
52 conservation allies without compromising long-term interests of water management and
53 agricultural land use.

54

55 Keywords: Drainage canal, drainage ditch, ditch bank vegetation, invasive species, linear
56 landscape element, novel ecosystem, reconciliation ecology,

57

58 Introduction

59 Drainage and subsequent land cultivation has been a major threat to global wetland
60 ecosystems for centuries (Herzon & Helenius, 2008; Blann et al., 2009; Davidson, 2016). In
61 Europe, most lowland fens have been drained (Langheinrich et al., 2004; Hill et al., 2016);
62 approximately 25% of the arable land of the United States is artificially drained (Herzon &
63 Helenius, 2008), and immense wetlands have recently been drained in tropical Southeast Asia
64 to gain land for agriculture (Aldhous, 2004). Canals, the main tools of drainage, are usually
65 retained after the draining process and are regularly managed to sustain low and stable water
66 balance in the cultivated landscape. Drainage canals are thus ubiquitous in heavily modified
67 lowland agricultural landscapes worldwide (Shaw et al., 2015; Hill et al., 2016) and can form
68 dense networks of interconnected artificial waterways. For instance, over 100,000 km of
69 canals criss-cross the farmlands of the United Kingdom (Hill et al., 2016), and the total length
70 of canals exceeds 300,000 km in the Netherlands (Blomqvist et al., 2003).

71 Despite being the main instrument of wetland loss, canals represent the only temporal
72 continuity of wetland habitat in many drained landscapes (see Manhoudt et al., 2007 for the
73 Netherlands), and are therefore refuges for organisms with high water demand (Chester &
74 Robson, 2013; Harvolk et al., 2014). This paradoxical situation has led to the recognition that
75 conservation value may be assigned to canals in agricultural landscapes, and therefore canals
76 should be considered in conservation planning and agri-environmental schemes (Blomqvist et
77 al., 2009; van Dijk et al., 2013).

78 Canals are often completely artificial with no functional or structural equivalent in the former
79 natural wetlands; their vegetation and associated fauna can thus be considered as novel
80 ecosystems (Hobbs et al., 2009). Management requirements for biodiversity in canals may be
81 substantially different from those of natural wetlands, posing new challenges for conservation
82 planners. Conventional management prescriptions of agri-environmental schemes have
83 frequently been reported as ineffective (Blomqvist et al., 2009; van Dijk et al., 2013; Shaw et
84 al., 2015). The main constraints for biodiversity in canals appear to be the high nutrient load,

85 pollution with pesticides and herbicides, and the inappropriate intensity of bed management,
86 including dredging and vegetation cutting (Herzon & Helenius, 2008; Blomqvist et al., 2009).
87 However, when land managers have the tools and incentives to optimize management for
88 biodiversity, canals can sustain populations of endangered species and high overall species
89 richness, significantly increasing landscape-level conservation value (Manhoudt et al., 2007;
90 Dorotovicova 2013; Tichanek & Tropek, 2015). Thus, canals have the potential to act as allies
91 for biodiversity conservation in heavily transformed agricultural landscapes, despite that they
92 were originally constructed to transform natural ecosystems.

93 The situation, however, is not so straightforward in moderately transformed landscapes where
94 draining was not followed by intensive agriculture but wetlands turned into drier but still
95 semi-natural habitats. In these landscapes, habitats surrounding the canals do not represent a
96 hostile matrix but can also harbour significant biodiversity. The conservation role of these
97 canals cannot be assessed in isolation, but only in conjunction with the surrounding habitats.

98 Studies on the biodiversity of canals that traverse habitats other than intensive arable fields
99 are surprisingly scarce; papers dealing with such landscape configurations have mostly
100 focussed on the hydrological, physical and chemical consequences of draining (e.g. Gasca-
101 Tucker & Acreman, 2000; Gavin, 2003; Tiemeyer & Kahle, 2014). It is thus unknown
102 whether these canals have an overall positive contribution to landscape level conservation
103 value (i.e. local biodiversity maintenance in their bed vs. desiccating effects nearby), how to
104 manage them in favour of biodiversity, or whether they should be maintained at all, if the
105 opportunity to reverse-engineer them is an option.

106 Effective land management becomes more challenging in mosaic landscapes that are
107 composed of both intensive agricultural fields and semi-natural habitats, interconnected with a
108 network of drainage canals. This type of mosaic landscape may become more common in the
109 future, due to increasing land abandonment and grassland restoration in formerly intensive
110 agricultural landscapes of developed countries (Cramer et al., 2008; Valkó et al., 2016).
111 Responsible land stewardship in these landscapes requires a complex understanding of the
112 role of drainage canals harbouring novel ecosystems, and comprehensive guidelines must be
113 developed for their management, in order to reconcile conservation purposes and immediate
114 economic needs. At present, the scientific literature offers limited guidance for this endeavour
115 but the emerging concepts of novel ecosystem management (Hobbs et al., 2009; Deák et al.,
116 2020) and reconciliation ecology (Rosenzweig, 2003; Chapman et al., 2018) offer promising

117 avenues. Considering these new fields of ecology, we aimed to understand the ecological role
118 of the drainage canal network of a large, heavily drained European lowland region composed
119 of a mosaic of intensive arable fields and semi-natural grasslands. Specifically, we aimed (1)
120 to identify the extent to which drainage canals contribute to biodiversity conservation in
121 regions rich in semi-natural habitats, (2) to test the effects of surrounding landscape matrix,
122 channel size, soil substrate type, and reed and woody species abundance on the capacity of
123 canals to sustain biodiversity, and (3) to propose reconciliation-based management guidelines
124 which address the interests of different stakeholders (i.e. nature conservation and water
125 management).

126

127 Material and methods

128 *Study area*

129 The study was carried out in the Danube-Tisza Interfluve, Central Hungary (Fig. 1). The
130 climate is continental with a mean annual precipitation of 550-600 mm and temperature of 10-
131 11°C (Tölgyesi et al., 2016). The soil substrate is diverse with mostly coarse sand in the
132 central zone, saline loam along the bordering rivers and peaty loam (fen habitats) in between.
133 Small isolated pockets of saline and fen areas also occur in the sandy central zone. This ca.
134 1 Mha lowland region used to be a mosaic of wetlands and drier habitats, but due to heavy
135 draining in the middle of the 20th century, most wetlands vanished and were transformed into
136 croplands, or gradually turned into grasslands (Biró et al., 2007; Ladányi et al., 2010). The
137 promise of higher productivity land after draining proved to be mostly false, as natural
138 ecosystems ceased to provide vital ecosystem services and productivity decreased in some
139 high-lying arable fields due to severe groundwater decline. This landscape history is well
140 reflected in the colloquial name of the main arterial drainage canal of the region: the “Cursed
141 Channel” (Újházy & Biró, 2018).

142 In the second half of the 20th century, regional aridification was further increased by climate
143 change, specifically warming, prolonged droughts and an unfavourable redistribution of
144 annual precipitation (Pongrácz et al., 2011), as well as increased groundwater extraction for
145 irrigation and excessive afforestation (Biró et al., 2007; Tölgyesi et al. 2020). As a result, the
146 water table greatly decreased (by up to 7 m in some localities; Ladányi et al., 2010) and the
147 Food and Agriculture Organization of the United Nations classified some parts of the region

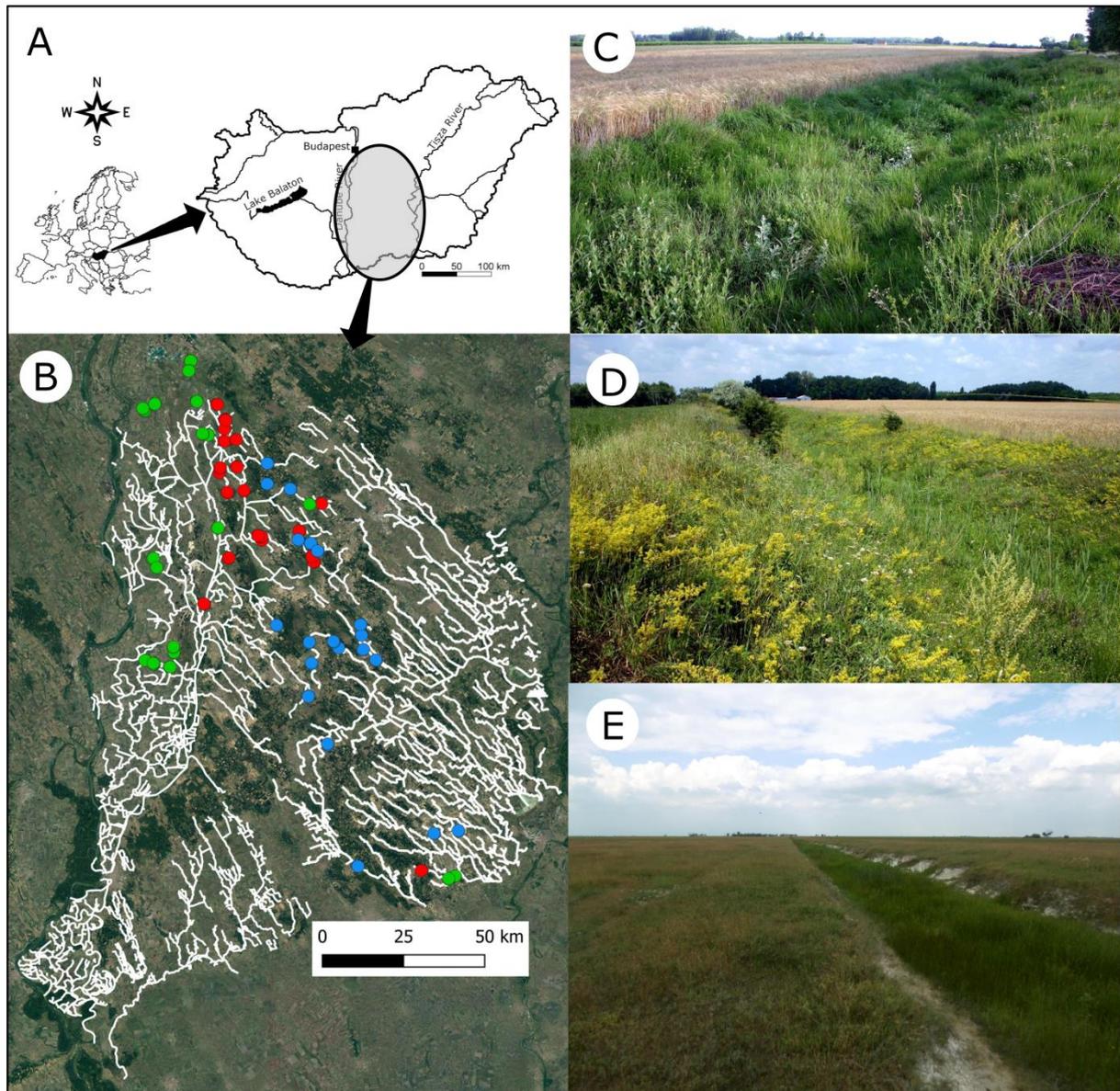
148 as semi-desert (Tölgyesi et al., 2012). To date, counteractions have been limited to the filling
149 up of some canals inside strict nature reserves and keeping sluices closed for longer periods
150 than earlier, while the majority of canals are still functional and the other causes of
151 aridification have not been addressed. The resulting environmental and biotic changes of
152 water loss may have pushed the region over a tipping point into the realm of novel ecosystems
153 (cf. Hobbs et al., 2006), in which the appropriate management of drainage canals may have a
154 central role.

155 The total length of registered canals in the region is 4723 km (Fig. 1). Canals are infrequently
156 managed by dredging (usually less than once a decade), reed cutting and shrub clearing.
157 Mowing once a year and/or extensive grazing are the main management types of adjacent
158 grasslands, but neither mowing nor grazing extends into the canals on a regular basis.
159 Permanent water in the canals is nowadays rare; most contain water only in spring and after
160 heavy rainy periods.

161

162 *Data collection*

163 We selected sixty 200 m long drainage canal sections in the Danube-Tisza Interfluve,
164 covering both agricultural and grassland canals (30 each), the three main substrate types,
165 namely fens, saline areas and sandy areas (20 each) and both small and large canals (30 each),
166 leading to five repetitions for each of the 12 category combinations (Fig. 1). Agricultural
167 canals were fringed by at least 200 m wide croplands on both sides, while grassland canals
168 were embedded in extensive grasslands that used to be wetter before draining. We identified
169 two canal size classes: small ones with a depth of 0.7 ± 0.2 m (mean \pm standard deviation) and a
170 width of 3.6 ± 1.4 m, and large ones with depth of 1.7 ± 0.5 m and a width of 6.8 ± 2.0 m. We
171 also assessed the abundance of reed and woody vegetation by measuring their cumulative
172 length along the canals and used them as additional variables to predict biodiversity. Canals
173 dredged within the past ten years were not considered in the study.



174

175 **Figure 1** A: Location of the Danube-Tisza Interfluvium in Hungary; B: registered drainage canal
176 system of the region (white lines) and the position of the 60 studied canal sections; red: fen
177 canals, green: saline canals, blue: sandy canals; C: small agricultural canal on fen substrate
178 near Tázlár; D: large agricultural canal on sandy substrate near Kerekegyháza; E: small
179 grassland canal on saline substrate near Dunapataj.

180

181 To assess the biodiversity of canals, we applied a multi-taxon approach covering various
182 functional groups, including primary producers (vascular plants), pollinating and herbivorous
183 primary consumers (butterflies and true bugs, respectively), predators (spiders) and birds as
184 representatives of large-bodied vertebrates. Vegetation was sampled in three ways during the

185 summer of 2018. First, we compiled the total species pool of vascular plants in the 200-m
186 sections (henceforth ‘gamma diversity’) and second, recorded species in eight evenly spaced
187 1-m² plots to capture plot-scale species density (henceforth ‘alpha diversity’), making a total
188 of 480 plots. Four plots were placed on the dry slopes of the bank and four plots into the
189 bottom of the bed or adjacent to the bottom if water cover was too high. Third, we assessed
190 the abundance of invasive plants. The measure was the cumulative length of invaded canal
191 bank with a resolution of 1 m. Each bank was measured separately, leading to a maximum
192 invasive plant abundance of 400 m.

193 Arthropod surveys were repeated three times in 2018: in spring (May), summer (July) and
194 autumn (September) and were performed between 9 a.m. and 6 p.m. in dry, sunny weather
195 without strong wind. We surveyed butterflies in transects along both canal banks. Each
196 transect measured 200 m long and 2 m wide. The observer walked at a slow pace along the
197 transect and counted all butterfly individuals seen 5 m in front of them (Nowicki et al., 2008).
198 We sampled true bugs and spiders with sweep-netting. Each sample contained specimens
199 from 25 sweeps prepared in a 25 m long transect, and we made four samples in every 200-m
200 canal section. Samples per section were not pooled. We surveyed birds between 5 and 9 a.m.
201 twice during the breeding season of 2019 (May and June). We scanned the area for ten
202 minutes from an observation point adjacent to the canals, without disturbing the birds, then
203 slowly walked by the canals to search for hiding individuals. We recorded every bird that
204 landed on the vegetation or the surface of the canals; fly-bys were ignored.

205 We also selected three reference transects (two 2.5 m × 400 m transects for butterflies and a
206 single 5 m × 200 m one for true bugs and spiders) parallel to every grassland canal,
207 approximately 50 m from them. We performed all vegetation and arthropod surveys in the
208 transects using the same protocol as in the canals. We did not attempt to prepare reference
209 datasets for birds, as their density in the transects was low.

210

211 *Data analysis*

212 For analysing the alpha and gamma diversity of the vegetation, we first discarded species of
213 highly degraded and segetal communities (including invasive species) and retained only
214 species of (semi-)natural grasslands and wetlands following the Flora Database of Hungary
215 (Horváth et al., 1995). In line with the species pool hypothesis of (Zobel et al., 1998), we can

216 expect different species pool sizes in different substrate types, making comparisons across
217 substrates difficult. Therefore we standardized the species richness scores of canals to
218 substrate specific average reference species richness scores, which yielded species excesses
219 (or deficits, if negative), which we expressed as percentages. The use of species excesses was
220 also beneficial because we were interested in the added conservation value of canals within a
221 broader landscape. We used the following equation for the calculations:

$$222 \quad E_i = \frac{(C_i - (\sum_{j=1}^n R_j)/n) \times 100}{(\sum_{j=1}^n R_j)/n},$$

223 where E_i is the substrate specific species excess of the i th sampling unit of a canal (one of
224 eight plots for alpha diversity or the total species count for gamma diversity), C_i is the species
225 richness of this sampling unit, R_j is the species richness of the j th sampling unit of any of the
226 reference transects belonging to the same substrate type as the canal, and n is the number of
227 such reference sampling units.

228 Invasive plant species were either absent or very scarce in reference transects; therefore, we
229 did not standardize their abundance in the canals but used the raw scores in subsequent
230 analysis. For butterflies, true bugs and spiders, we applied the above method of
231 standardization but the reference averages we used were specific to both substrate and season.
232 In birds, we used the raw species richness scores for the analysis. Invasive or noxious pest
233 species were not encountered among animal taxa; therefore, all species were retained for the
234 analysis.

235 We applied a linear modelling approach to evaluate the biotic response variables (species
236 excesses of plant and arthropod species richness, and raw invasive plant abundance and bird
237 species richness). We had three categorical (landscape matrix, substrate and size) and two
238 continuous (abundance of shrubs and reed) explanatory variables for plants and birds, while
239 we included season as a fourth categorical explanatory variable in arthropods. We checked
240 woody species and reed both as linear and quadratic terms and chose the one that resulted in a
241 higher coefficient of determination (R^2) in the models. If the quadratic term was chosen, we
242 also identified the location of the hump or pit in the modelled response curve. We included
243 canal identity as a random factor in models where multiple samples were collected in the
244 canal sections. In birds, we used sampling occasion as a random variable. There was no
245 indication of multicollinearity among the variables (generalized variance inflation factors

246 ranged between 1.00 and 1.62); therefore all *a priori* variables were included in the final
247 models.

248 In species excess type response variables, we also checked whether the mean score of each
249 level of the categorical variables differed from the reference level (i.e. from the 0 score). For
250 this analysis, we used reduced models including only one explanatory variable at a time and
251 the random term of canal identity, if needed. In the case of arthropods, we also considered the
252 repeated measures design, except when the seasons were tested for difference from the
253 reference level.

254 Models were prepared in R environment (R Core Team, 2019) using the ‘lm’, ‘lmer’ (*lme4*
255 package) or ‘glmer’ (*lme4* package, Poisson error term) functions depending on the data
256 structures. We used the ‘MOSstest’ function (*vegan* package) to identify the location of the
257 hump or pit in models with quadratic terms, and the ‘fieller.MOSstest’ function was applied to
258 calculate 95% confidence intervals. Generalized variance inflation factors were calculated
259 with the ‘vif’ function (*car* package). The significance of the explanatory variables was tested
260 using the ‘Anova’ function (*car* package). Pairwise comparisons of the levels of substrate and
261 season were performed with the ‘emmeans’ and ‘pairs’ functions (*emmeans* package).

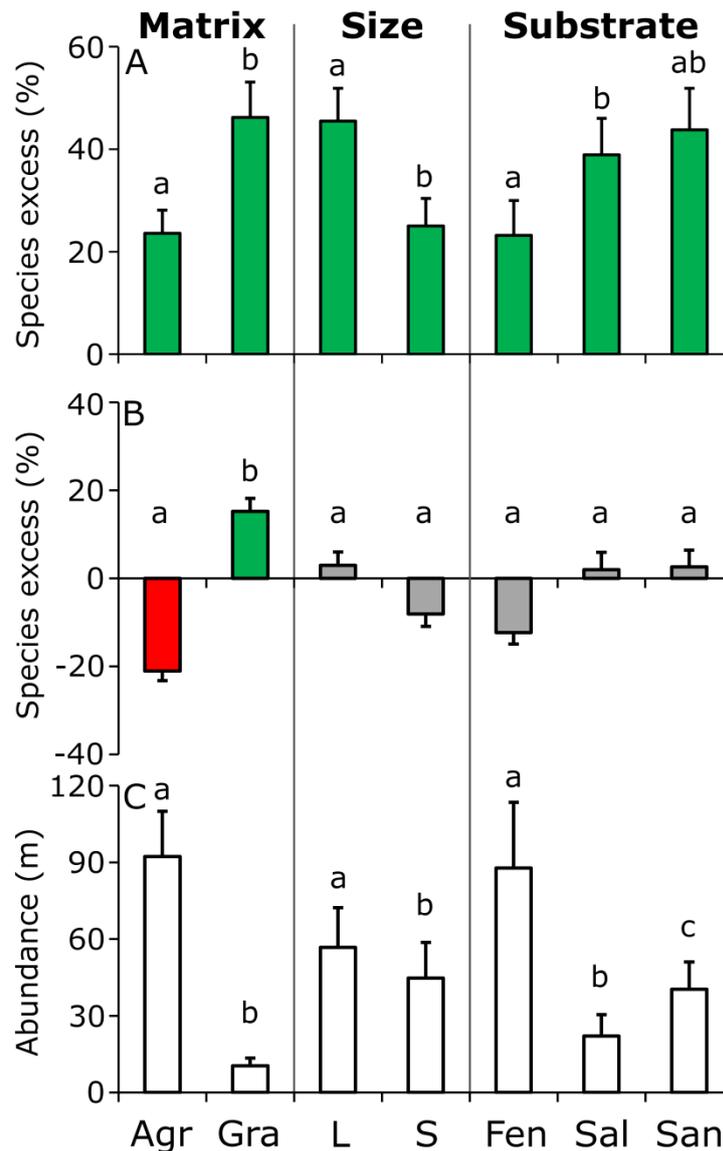
262

263 Results

264 *Plants*

265 We recorded a total of 512 plant species in the study, but only 405 of these were of
266 conservation interest (i.e. being wetland or grassland species); the remaining 107 species were
267 weeds of highly degraded or segetal communities. Of the 405 species we included in the
268 analysis, 380 occurred in the canals and 99 of these were not encountered in the reference
269 grasslands. Species excess on the gamma level was significantly higher in grassland canals
270 than in agricultural ones; large canals had higher species excesses than small ones and saline
271 canals had higher values than fen canals. Compared to the habitat specific average reference
272 levels, all levels of all categorical variables had significantly positive species excesses.
273 Woody vegetation affected gamma diversity in a hump-shaped manner; the hump was located
274 at 141.7 m but the upper limit of its confidence interval was beyond the upper limit of
275 available woody abundance, rendering the prediction unreliable. The abundance of reed had
276 no effect on the variation of the data (Fig. 2A, Table S1-3, Fig. S1A-B)

277 We had more moderate results for species excesses on the alpha level, as it was not affected
278 by canal size, substrate or the abundance of woody species and reed. However, agricultural
279 canals had lower species excesses than grassland canals, and the former remained below the
280 reference level (i.e. showed species deficit), while the latter slightly exceeded it. Mean values
281 of small and large canals and canals of different substrate types did not differ from the
282 reference levels (Fig. 2B, Table S1-3 and Fig. S1C-D).



283

284 **Figure 2** The effects of landscape matrix, canal size and substrate type on the species
285 excesses of plants on the gamma (A) and the alpha (B) levels (i.e. considering total species
286 counts of 200 m long canal sections and 1-m² plots, respectively), and on the abundance of
287 invasive species (C). Different lowercase letters within each canal parameter identify

288 significantly different groups. Shading is used to denote differences from the reference level
289 (i.e. the 0 score). Green and red indicate significantly positive and negative differences,
290 respectively, while grey shading is used when no significant difference was detected from the
291 reference level. Species excess is the proportional difference from the habitat specific
292 reference averages expressed in per cents. No reference was generated for the abundance of
293 invasives; therefore, no shading is used in subplot C. Agr: agricultural canals, Gra: grassland
294 canals, L: large canals, S: small canals, Fen: fen substrate, Sal: saline substrate, San: sandy
295 substrate. Whiskers show standard errors of the means.

296

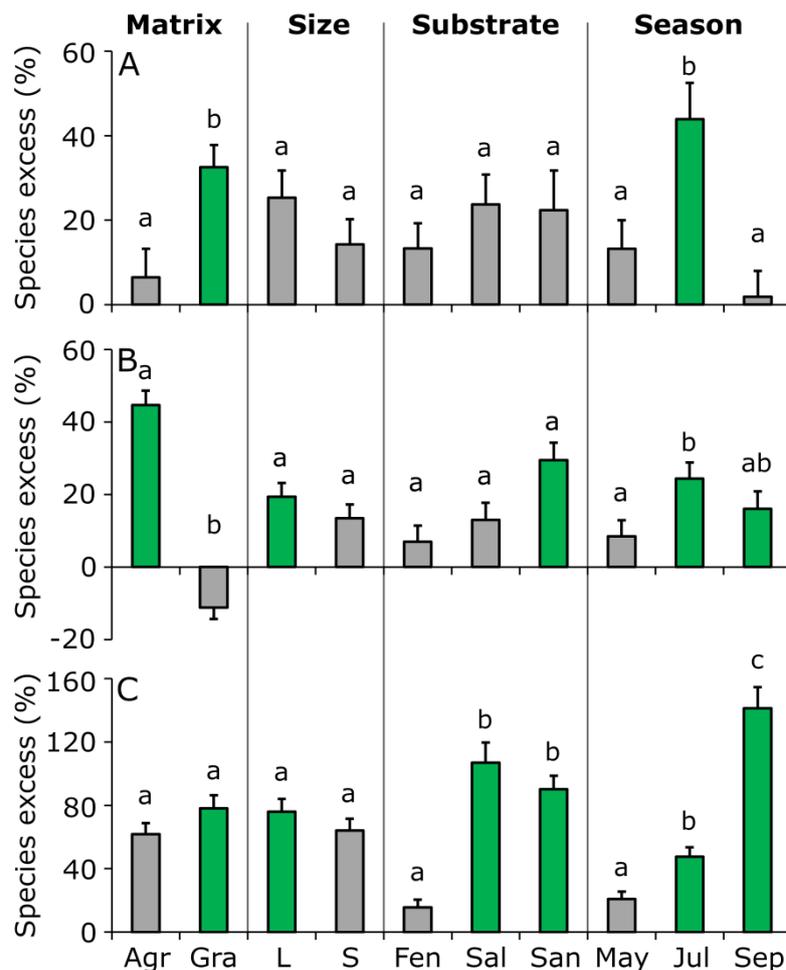
297 We encountered several invasive plant species along the canal sections. Their cumulative
298 abundance ranged between 0 m (absent) and 400 m (every metre of both banks invaded). The
299 most abundant invasive species were *Asclepias syriaca*, *Solidago gigantea*, *S. canadensis* and
300 *Aster lanceolatus* agg. Agricultural canals demonstrated a higher level of invasion than
301 grassland canals, and large canals had more invasive species than small ones. Saline canals
302 were the most intact, while fen and sandy canals had similar levels of invasion. The use of a
303 quadratic term yielded better model fit for reed abundance and woody species abundance. The
304 former had a significant effect on invasive species abundance with a pit at 69.4 m; however,
305 the 95% confidence limits were beyond the available range, i.e. 0-200 m. The latter showed a
306 hump at 70.3 m (95% confidence interval: 55.4 m – 97.8 m; Fig. 2C, Table S1-3 and Fig.
307 S1E-F).

308

309 *Arthropods*

310 We recorded 58 butterfly species (5962 adult individuals) in the study and 55 occurred in the
311 canals, of which 19 were encountered only in the canals and not in the reference transects.
312 Higher species excesses were found in grassland canals than in agricultural ones and the
313 linear variant of woody abundance had a positive effect on butterfly species excess. Species
314 excesses were higher in summer than in spring and autumn. Neither reed abundance, nor
315 canal size, nor substrate had a significant effect on species excess. Compared to the substrate
316 and season specific reference levels, only grassland canals and canals in summer had
317 significantly positive species excesses (Fig. 3A, Table S1-3 and Fig. S2A-B).

318 We collected a total of 246 true bug species (30,012 adult individuals) in the study, and 219
 319 occurred in the canals, of which 82 were collected exclusively there. Species excesses were
 320 affected only by matrix and season, with higher scores in agricultural canals than in grassland
 321 ones, and higher scores in summer than in spring. Compared to the reference levels, the
 322 statistics confirmed significant species excess in agricultural canals but not in grassland ones,
 323 in large canals but not in small ones, and on sandy substrate but not on fen or saline
 324 substrates. Species excess was highly positive in summer but significant difference was also
 325 confirmed for autumn data (Fig. 3B, Table S1-3 and Fig. S2C-D).



326

327 **Figure 3** The effects of landscape matrix, canal size, substrate type and season on the species
 328 excesses of butterflies (A), true bugs (Heteroptera) (B) and spiders (C). Different lowercase
 329 letters within each canal parameter identify significantly different groups. Green shading
 330 indicates significantly positive difference from the reference level (i.e. the 0 score), while
 331 grey shading is used when no significant difference was detected from the reference level.
 332 Species excess is the proportional difference from the habitat and season specific reference

333 averages. Agr: agricultural canals, Gra: grassland canals, L: large canals, S: small canals, Fen:
334 fen substrate, Sal: saline substrate, San: sandy substrate. Whiskers show standard errors of the
335 means.

336

337 We recorded 134 spider species (6718 adult individuals) in the study; 114 occurred in the
338 canals, of which 38 were found only there. Substrate and season had significant effects on
339 species excesses, while matrix and size did not. Saline and sandy canals had higher species
340 excesses than fen canals, and the excesses increased as the seasons progressed from spring
341 through summer to autumn. Species excess was negatively affected by the linear variant of
342 reed abundance, but woody cover had no detectable effect. Compared to the substrate and
343 season specific reference levels, grassland canals had positive excesses but agricultural ones
344 did not. Both large and small canals tended to have significantly positive scores, and among
345 different substrate types, we could confirm positive species excesses for saline and sandy
346 canals. Species excesses were significantly positive in summer and autumn but not in spring
347 (Fig. 3C, Table S1-3 and Fig. S2E-F).

348

349 *Birds*

350 We observed 38 bird species (892 individuals) during the study. We found that birds similarly
351 frequented agricultural and natural canals and there was no difference among size classes and
352 substrate types. However, the abundance of woody species and reed had significant effects
353 and the models with quadratic terms fitted better than linear variants. Species excess had a
354 hump along woody abundance at 113.6 m, although the upper confidence limit fell beyond the
355 available range. In the case of reed, the hump itself was projected beyond the maximum of
356 reed abundance (Fig. S2G-H, Fig. S3 and Table S1-3).

357

358 Discussion

359 *Biodiversity of drainage canals*

360 Drainage canals are ubiquitous components of managed lowland landscapes worldwide (Shaw
361 et al., 2015; Hill et al., 2016). Although drainage is among the primary causes of the loss of
362 the original biodiversity, there is growing evidence that canals can act as refuges for a variety
363 of native species in desiccated and transformed landscapes (Chester & Robson, 2013;
364 Golubovic et al., 2017; Torma et al., 2018), reinforcing the importance of moist
365 microenvironments in the face of local and global environmental changes (Keppel et al.,
366 2011; Mclaughlin et al., 2017). Our findings go one step further, as we show that canals not
367 only function as secondary habitat for a certain subset of the native biodiversity, but they
368 concentrate more species than adjacent semi-natural grasslands across a wide range of taxa.
369 One reason for this diversity may be the micro-environmental heterogeneity offered by the
370 canals (Stein et al., 2014). A wide moisture gradient is traversed from the dry top zone of the
371 canal banks down to the bottom, enabling plant species with contrasting moisture demand to
372 co-exist in close proximity, whereas the flat surrounding areas are characterized by more
373 homogeneous environmental conditions. As a result, both grassland and agricultural canals
374 could harbour more plant species of conservation interest (i.e. non-ruderal species) at the
375 gamma level than semi-natural grasslands. Grassland canals had higher species richness even
376 on the alpha level, despite the lack of annual management, which usually enhances the fine-
377 scale co-existence of species (Klimek et al., 2007; Vadász et al., 2016).

378 The high diversity of plants, in turn, seems to cascade up to the level of primary consumers
379 (butterflies and true bugs) and predatory arthropods (spiders). Nevertheless, some structural
380 and functional features of the canals may have also contributed to the high arthropod richness
381 we detected. Canals, which are local depressions in flat landscapes, can provide wind shelter
382 for flying insects, including butterflies (Dover, 1996). Furthermore, canals provide
383 overwintering opportunities for arthropods in the soil, litter and standing vegetation such as
384 hollow stems, whereas soil disturbance in arable land impedes successful overwintering
385 (Herzon & Helenius, 2008). Semi-natural grasslands and grassland canals may be similar in
386 suitability for overwintering in the soil, but the management (i.e. mowing or grazing) of
387 grasslands leaves little standing vegetation and litter into the winter for species that
388 overwinter in these substrates. A variety of other non-cropped linear landscape elements, such
389 as road verges, flower rich field margins or hedgerows have also been shown to be important

390 for overwintering (Ramsden et al., 2015; Gallé et al. 2018), and canals are also likely to fulfil
391 this function.

392 Arthropods greatly benefited from canals also in summer, as the highest species excesses
393 were found in this period. Summers in the region are dry; thus canals can be important
394 sources of water and fresh vegetation for true bugs and floral resources for butterflies.
395 Furthermore, several studies emphasize that agricultural areas usually have “hunger periods”
396 for arthropods in summer when there is a mismatch between resource demand and supply due
397 to the synchronized phenology of cropped plants (Timberlake et al., 2019; Wintermantel et
398 al., 2019). At the same time, canals are rich in resources throughout the vegetation period,
399 including times when agricultural areas experience supply gaps. Although less commonly
400 studied, this may also apply to managed grasslands. Grassland vegetation after being mown
401 with powerful machinery provides little resource for either pollinators or other herbivory
402 insects. Grassland canals are usually avoided during mowing, and thus represent continuity in
403 food supply, similar to intentionally uncut vegetation strips in hay meadows (Buri et al., 2013;
404 Kühne et al., 2015). Thus, canals are not just locally species-rich strips but are potentially
405 important functional cornerstones of landscape-wide arthropod diversity.

406 Besides the local and landscape-level effects of canals on biodiversity, they may have
407 consequences on even larger spatial scales. Canals often form continuous networks,
408 overarching large regions and connecting isolated habitat fragments, similar to other linear
409 landscape elements such as road verges and hedgerows (Vanniste et al., 2020). Canals, if
410 longitudinally permeable for native species, can act as green corridors of dispersal, increasing
411 regional connectivity and alleviating deficiencies of meta-population dynamics (van Geert et
412 al., 2010; van Dijk et al., 2013), or can even act as conduits of climate change mediated range
413 shifts, which would otherwise be hindered by extensive hostile areas, such as arable lands or
414 exotic tree plantations (Saura et al., 2014; Robillard et al., 2015). Our findings, however,
415 highlight that invasive species also use canals as dispersal corridors, especially in agricultural
416 areas (see also Maheu-Giroux & de Blois 2007). As a result, canals can facilitate the invasion
417 of otherwise intact and isolated habitats, and highly invaded canal sections may represent
418 points of high resistance for native dispersal. Thus, controlling invasive species, particularly
419 in agricultural canals, is a pressing issue that should be included in regional conservation
420 strategies.

421

422 *Effects of canal parameters*

423 We compared the biodiversity concentrating capacity of different canal types to aid
424 prioritization among them, in order to channel conservation efforts where they are most
425 needed. Although grassland canals proved to be more species rich for most taxa than
426 agricultural ones, both types deserve our attention, as grassland ones exceed adjacent semi-
427 natural grassland richness and agricultural canals represent the only conservation value in
428 hostile agricultural landscapes. Large canals may be expected to have higher conservation
429 value than small ones (Hill et al., 2016), but we found little evidence for this, as butterfly, true
430 bug, spider and bird richness were not affected by canal size. Although plant species richness
431 on the gamma level was higher in large canals, the abundance of invasive species was also
432 higher in them, meaning that they are stronger conduits of plant invasion than small canals.

433 Conversely, substrate type provides more guidance for prioritization (see also Manhoudt et
434 al., 2007). Fen canals proved to be the least valuable as (i) the rate of invasion was the highest
435 in them, (ii) they had lower plant species excess than saline canals on the gamma level, and
436 (iii) had lower spider species excess than the two other substrates. The reason for this may be
437 twofold. Fen habitats provide the most benign conditions for plants as water availability is
438 relatively high and stable, and no other stressors constrain plant life. These factors favour
439 competitors, native and invasive ones alike, which can limit the number of co-existing species
440 in canals (Blomqvist et al., 2003; Houlihan & Findlay, 2004) as compared to canals on other
441 substrates. At the same time, adjacent fen grasslands are regularly managed to suppress
442 competitors and sustain high species richness (Vadász et al., 2016), making habitat-specific
443 reference species richness rather high.

444 The overall lower water supply and the more pronounced moisture gradient of canals on sand
445 substrate (cf. Tölgyesi et al., 2016) may be the reason for the higher species excesses
446 compared to fen canals. In saline canals, competitors may be further suppressed by the salt
447 stress, and the gradients of salt and moisture can create diverse sets of micro-site conditions
448 and associated species, similar to natural saline habitats with diverse micro-topography
449 (Kelemen et al., 2013).

450 Regarding priority order, we conclude that landscape matrix and size are not decisive but
451 substrate type should direct conservation efforts, as the higher the habitat stress (salinity in
452 our model system), the higher the potential added conservation value. If this value cannot
453 manifest on its own due to local conditions, these conditions should be identified and

454 alleviated to ensure the full potential of canals in biodiversity concentration. In contrast, we
455 cannot expect the same levels of added conservation value from canals under no-stress
456 regimes; therefore, large scale conservation strategies should not target bringing the
457 biodiversity level of these canals up to the same level as canals on other substrate types. This
458 would be an unrealistic and/or an economically unfeasible aim.

459 Besides *a priori* canal parameters, we also tested the effects of parameters that can be
460 modified by management (i.e. the abundance of woody species and reed). Moderate woody
461 abundance had positive effects on biodiversity, while the effect tended to rebound at high
462 abundances, leading to a hump for plants and birds and a pit for invasive species. Therefore
463 some woody cover seems to have a positive effect on overall biodiversity. This finding was
464 expectable, as sparse woody cover has been shown to introduce heterogeneity into micro-
465 environmental conditions and vegetation structure (López-Pintor et al., 2006), both of which
466 are known to boost biodiversity (Herzon & Helenius, 2008; Teleki et al., 2020).

467 The effect of reed abundance is more difficult to evaluate because it was contrasting among
468 taxa (positive for birds but also positive for invasive plants, while negative for spiders). In
469 fact, this was the only parameter that showed clear taxon specificity, suggesting that
470 conservationists may need to choose which taxon to favour. Some authors have come to the
471 conclusion that reed should regularly be cut along ditches for the benefit of biodiversity (e.g.
472 Tichanek & Tropek, 2015) but these were mostly single-taxon studies, none of which
473 considered birds. Since birds are declining rapidly in human-modified landscapes (Donald et
474 al., 2001), the complete suppression of reed should be avoided to ensure that canals function
475 as good quality refuge sites for them.

476

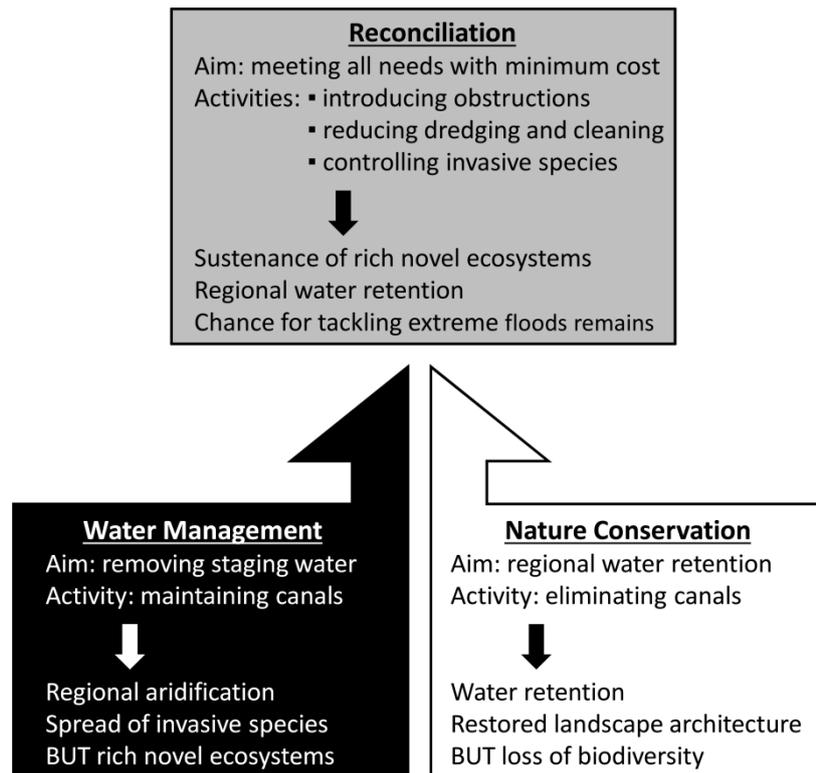
477 *Reconciliation between conservation and water management*

478 Our findings highlight the high conservation value of drainage canals, but we need to
479 emphasize that canals in their present form are not yet true allies in nature conservation. They
480 still remove significant amounts of water from the surrounding landscape, contributing to
481 water shortage both in semi-natural habitats (Ladányi et al., 2010; Pongrácz et al., 2011) and
482 in agricultural production systems (Szinell et al., 1998). To make canals net positive
483 contributors to conservation, the draining effect should be minimized while maintaining the
484 canal profile with all the diverse microhabitats, flora and fauna. This can be achieved by

485 introducing more sluices and semi-permanent obstructions, such as earthen plugs (see also
486 Tichanek & Tropek, 2015). Canals that are permanently dry require no modification of the
487 bed.

488 To date, conservationists have aimed to reverse-engineer entire canal sections in Hungary to
489 fight against their draining effect (Valkó et al., 2017). This is extremely cost-intensive and,
490 according to our results, the conservation benefit is questionable. Our recommendation is a
491 more budget-friendly solution with no loss of biodiversity. If financial resources can be
492 spared, they should be reallocated to identifying weak points of the canal network where the
493 potential substrate-specific biodiversity concentrating effect is hindered by local factors, such
494 as disturbance, pollution, and invasive infestation, and to designing customized local
495 interventions to mitigate them.

496 We suppose that the introduction of more sluices and earthen obstructions would be more
497 acceptable for water management authorities than removing the canals, since canals would
498 thus remain available for reopening in case extreme water levels require. However, we
499 discourage the application of regular dredging. In intensive agricultural areas of Western
500 Europe, where canals experience high nutrient and pollutant loads, dredging is often
501 recommended to suppress weedy species (Hill et al., 2016), but the canals in our study did not
502 seem to require this intervention, which would probably promote invasive species.
503 Furthermore, we encourage the retention of moderate amounts of woody plants and reed as
504 they can increase the quality of canals as refuge sites for biodiversity. Implementation of
505 these proposed guidelines would constitute a cost-effective, viable alternative to presently
506 applied practices (Fig. 4), which can successfully reconcile nature conservation aims and
507 water management in agricultural landscapes.



508

509 Figure 4. The main components of our management framework for drainage canals, showing
510 the differing aims of stakeholders in the landscape and the related environmental impacts of
511 their management (bottom left and right), and our proposed cost-effective management
512 alternatives (top).

513

514 Author Contributions

515 CT conceived the ideas and designed the methodologies, CT, JS, AT, RG, NG-S, MP, TV,
516 ZB and AK participated in data collection, CT analysed the data, and all authors contributed
517 to the writing of the manuscript.

518

519 Acknowledgements

520 The support of the Hungarian Scientific Research Fund is greatly acknowledged (CT: 132131,
521 ZB: K124796). The contribution of MP was funded by the Ministry of Education, Science and
522 Technological Development of the Republic of Serbia (Project No. 173025). AK was
523 supported by the Bolyai János Research Scholarship of the Hungarian Academy of Sciences,

524 and JŠ received funding from the Stipendium Hungaricum Scholarship of the Tempus Public
525 Foundation. The authors are grateful to Emmeline Topp for proofreading the manuscript.

526

527 Data Availability

528 Data will be stored on the Dryad Digital Repository.

529

530 References

531 Aldhous, P. (2004). Borneo is burning. *Nature*, 432, 144-146.

532 Biró, M., Révész, A., Molnár, Z., Horváth, F. (2007). Regional habitat pattern of the Danube-
533 Tisza Interfluvium in Hungary, I. *Acta Botanica Hungarica*, 49, 267-303.

534 Blann, K.L., Anderson, J.L., Sands, G.R., Vondracek, B. (2009). Effects of Agricultural
535 Drainage on Aquatic Ecosystems: A Review. *Critical Reviews in Environmental Science and*
536 *Technology*, 11, 909-1001.

537 Blomqvist, M.M., Vos, P., Klinkhamer, P.G.L., ter Keurs, W.J. (2003). Declining plant
538 species richness of grassland ditch banks—a problem of colonisation or extinction. *Biological*
539 *Conservation*, 109, 391-406.

540 Blomqvist, M.M., Tamis, W.L.M., de Snoo, G.R. (2009). No improvement of plant
541 biodiversity in ditch banks after a decade of agri-environment schemes. *Basic and Applied*
542 *Ecology*, 10, 368-378.

543 Buri, P., Arlettaz, R., Humbert, J.-Y. (2013). Delaying mowing and leaving uncut refuges
544 boosts orthopterans in extensively managed meadows: Evidence drawn from field-scale
545 experimentation. *Agriculture, Ecosystems and Environment*, 181, 22-30.

546 Chapman, M.G., Underwood, A.J., Browne, M.A. (2018). An assessment of the current usage
547 of ecological engineering and reconciliation ecology in managing alterations to habitats in
548 urban estuaries. *Ecological Engineering*, 120, 560-573.

549 Chester, E.T., Robson, B.J. (2013). Anthropogenic refuges for freshwater biodiversity: Their
550 ecological characteristics and management. *Biological Conservation*, 166, 64-75.

- 551 Cramer, V.A., Hobbs, R.J., Standish, R.J. (2008). What's new about old fields? Land
552 abandonment and ecosystem assembly. *Trends in Ecology and Evolution*, 23, 104-112.
- 553 Davidson, N.C. (2016). Wetland Losses and the Status of Wetland-Dependent Species. In:
554 Finlayson, C., Milton, G., Prentice, R., Davidson, N. (Eds.) *The Wetland Book* (pp. 369-381).
555 Dordrecht: Springer.
- 556 Deák, B., Valkó, O., Nagy, D.D., Török, P., Torma, A., Lőrinczi, G., ... Tóthmérész, B.
557 (2020). Habitat islands outside nature reserves—Threatened biodiversity hotspots of grassland
558 specialist plant and arthropod species. *Biological Conservation*, 108254.
- 559 Donald, P.F., Green, R.E., Heath, M.F. (2001). Agricultural intensification and the collapse of
560 Europe's farmland bird populations. *Proceedings of the Royal Society B*, 268, 25-29.
- 561 Dorotovicova, C. (2013). Man-made canals as a hotspot of aquatic macrophyte biodiversity in
562 Slovakia. *Limnologica*, 43, 277-287.
- 563 Dover, J.W. (1996). Factors affecting the distribution of Satyrid butterflies on arable
564 farmland. *Journal of Applied Ecology*, 33, 723-734.
- 565 Gallé, R., Császár, P., Makra, T., Gallé-Szpisjak, N., Ladányi, Z., Torma, A., ... Szilassi, P.
566 (2018). Small-scale agricultural landscapes promote spider and ground beetle densities by
567 offering suitable overwintering sites. *Landscape Ecology*, 33, 1435-1446.
- 568 Gasca-Tucker, D.L., Acreman, M.A. (2000). Modelling ditch water levels on the pevensey
569 levels wetland, a Lowland wet grassland wetland in East Sussex, UK. *Physics and Chemistry
570 of the Earth, Part B: Hydrology, Oceans and Atmosphere*, 25, 593-597.
- 571 Gavin, H. (2003). Impact of ditch management on the water levels of a wet grassland in
572 Southeast England. *Agriculture Ecosystems and Environment*, 99, 51-60.
- 573 Golubovic, A., Grabovac, D., Popovic, M. (2017). Actual and potential distribution of the
574 European pond turtle, *Emys orbicularis* (L., 1758) in Serbia, with conservation implications.
575 *Acta Zoologica Bulgarica*, 69, 49-56.
- 576 Harvolk, S., Symmank, L., Sundermeier, A, Otte. A, Donath, T.W. (2014). Can artificial
577 waterways provide a refuge for floodplain biodiversity? A case study from North Western
578 Germany. *Ecological Engineering*, 73, 31-44.

- 579 Herzon, I., Helenius, J. (2008). Agricultural drainage ditches, their biological importance and
580 functioning. *Biological Conservation*, 141, 1171-1183.
- 581 Hill, M.J., Chadd, R.P., Morris, N., Swaine, J.D., Wood, P.J. (2016). Aquatic
582 macroinvertebrate biodiversity associated with artificial agricultural drainage ditches.
583 *Hydrobiologia*, 776, 249-260.
- 584 Hobbs, R.J., Higgs, E., Harris, J.A. (2009). Novel ecosystems: implications for conservation
585 and restoration. *Trends in Ecology and Evolution*, 24, 599-605.
- 586 Horváth, F., Dobolyi, Z.K., Morschhauser, T., Lőkös, L., Karas, L., Szerdahelyi, T. (1995).
587 *Flora Database of Hungary 1.2. Vácrátót: MTA-ÖBKI.*
- 588 Houlanke, J.E., Findlay, C.S. (2004). Effect of Invasive Plant Species on Temperate Wetland
589 Plant Diversity. *Conservation Biology*, 18, 1132-1138.
- 590 Kelemen, A., Török, P., Valkó, O., Migléc, T., Tóthmérész, B. (2013). Mechanisms shaping
591 plant biomass and species richness: plant strategies and litter effect in alkali and loess
592 grasslands. *Journal of Vegetation Science*, 24, 1195-1203.
- 593 Keppel, G., Van Niel, K., Wardell-Johnson, G. W., Yates, C. J., Byrne, M., Mucina, L., ...
594 Franklin, S. E. (2012). Refugia: Identifying and understanding safe havens for biodiversity
595 under climate change. *Global Ecology and Biogeography*, 21, 393-404.
- 596 Klimek, S., Kemmermann, A.R., Hofmann, M., Isselstein, J. (2007). Plant species richness
597 and composition in managed grasslands: The relative importance of field management and
598 environmental factors. *Biological Conservation*, 134, 559-570.
- 599 Kühne, I., Arlettaz, R., Pellet, J., Bruppacher, L., Humbert, J.-Y. (2015). Leaving an uncut
600 grass refuge promotes butterfly abundance in extensively managed lowland hay meadows in
601 Switzerland. *Conservation Evidence*, 12, 25-27.
- 602 Ladányi, Z., Deák, J.Á., Rakonczai, J. (2010). The effect of aridification on dry and wet
603 habitats of Illancs microregion, SW Great Hungarian Plain, Hungary. *AGD Landscape and
604 Environment*, 4, 11-22.
- 605 Langheinrich, U., Tischew, S., Gersberg, R.M., Lüderitz, V. (2004). Ditches and canals in
606 management of fens: opportunity or risk? A case study in the Drömling Natural Park,
607 Germany. *Wetlands Ecology and Management*, 12, 429-445.

- 608 López-Pintor, A., Sal, A.G., Benayas, J.M.R. (2006). Shrubs as a source of spatial
609 heterogeneity—the case of *Retama sphaerocarpa* in Mediterranean pastures of central Spain.
610 *Acta Oecologica*, 29, 247-255.
- 611 Manhoudt, A.G.E., Visser, A.J., de Snoo, G.R. (2007). Management regimes and farming
612 practices enhancing plant species richness on ditch banks. *Agriculture, Ecosystems and*
613 *Environment*, 119, 353-358.
- 614 Maheu-Giroux, M., de Bois, S. (2007). Landscape ecology of *Phragmites australis* invasion in
615 networks of linear wetlands. *Landscape Ecology*, 22, 285-301.
- 616 Mclaughlin, B.C., Ackerly, D.D., Klos, P.Z., Natali, J., Dawson, T.E., Thompson, S.E.
617 (2017). Hydrologic refugia, plants, and climate change. *Global Change Biology*, 23, 2941-
618 2961.
- 619 Nowicki, P., Settele, J., Henry, P.-Y., Woyciechowski, M. (2008). Butterfly Monitoring
620 Methods: The ideal and the Real World. *Israel Journal of Ecology and Evolution*, 54, 69-88.
- 621 Pongrácz, R., Bartholy, J., Miklós, E. (2011). Analysis of projected climate change for
622 Hungary using ENSEMBLES simulations. *Applied Ecology and Environmental Research*, 9,
623 387-398.
- 624 R Core Team. (2019). R: A language and environment for statistical computing. R Foundation
625 for Statistical Computing. Vienna, Austria.
- 626 Ramsden, M.W., Menéndez, R., Leather, S.R., Wäckersa, F. (2015). Optimizing field margins
627 for biocontrol services: The relative role of aphid abundance, annual floral resources, and
628 overwinter habitat in enhancing aphid natural enemies. *Agriculture, Ecosystems and*
629 *Environment*, 199, 94-104.
- 630 Robillard, C.M., Cristine, L.E., Soares, R.N., Kerr, J.T. (2015). Facilitating climate-change-
631 induced range shifts across continental land-use barriers. *Conservation Biology*, 29, 1586-
632 1595.
- 633 Rosenzweig, M.L. (2003). *Win-win ecology: How the Earth's species can survive in the midst*
634 *of human enterprise*. New York, NY: Oxford University Press.

- 635 Saura, S., Bodin, Ö., Fortin, M.-J. (2014). Stepping stones are crucial for species' long-
636 distance dispersal and range expansion through habitat networks. *Journal of Applied Ecology*,
637 51, 171-182.
- 638 Shaw, R.F., Johnson, P.J., MacDonald, D.W., Feber, R.E. (2015). Enhancing the biodiversity
639 of ditches in intensively managed UK farmland. *PLoS ONE*, 10, e0138306.
- 640 Stein, A., Gerstner, K., Kreft, H. (2014). Environmental heterogeneity as a universal driver of
641 species richness across taxa, biomes and spatial scales. *Ecology Letters*, 17, 866-880.
- 642 Szinell, C.S., Bussay, A., Szentimrey, T. (1998). Drought tendencies in Hungary.
643 *International Journal of Climatology*, 18, 1479-1491.
- 644 Teleki, B., Sonkoly, J., Erdős, L., Tóthmérész, B., Prommer, M., Török, P. (2020). High
645 resistance of plant biodiversity to moderate native woody encroachment in loess steppe
646 grassland fragments. *Applied Vegetation Science*, 23, 175-184.
- 647 Tichanek, F., Tropek, R. (2015). Conservation value of post-mining headwaters: drainage
648 channels at a lignite spoil heap harbour threatened stream dragonflies. *Journal of Insect*
649 *Conservation*, 19, 975-985.
- 650 Tiemeyer, B., Kahle, P. (2014). Nitrogen and dissolved organic carbon (DOC) losses from an
651 artificially drained grassland on organic soils. *Biogeosciences*, 11, 4123-4137.
- 652 Timberlake, T.P., Vaughan, I.P., Memmott, J. (2019). Phenology of farmland resources
653 reveals seasonal gaps in nectar availability for bumblebees. *Journal of Applied Ecology*, 56,
654 1585-1596.
- 655 Torma, A., Bozsó, M., Gallé, R. (2018). Secondary habitats are important in biodiversity
656 conservation: a case study on orthopteras along ditch banks. *Animal Biodiversity and*
657 *Conservation*, 41, 97-108.
- 658 Tölgyesi, C., Körmöczi, L. (2012). Structural changes of a Pannonian grassland plant
659 community in relation to the decrease of water availability. *Acta Botanica Hungarica*, 54,
660 413-431.
- 661 Tölgyesi, C., Zalatnai, M., Erdős, L., Bátori, Z., Hupp, N., Körmöczi, L. (2016). Unexpected
662 ecotone dynamics of a sand dune vegetation complex following water table decline. *Journal*
663 *of Plant Ecology*, 9, 40-50.

- 664 Tölgyesi, C., Török, P., Hábenczyus, A.A., Bátori, Z., Valkó, O., Deák, B., ... Kelemen A.
665 (2020). Underground deserts below fertility islands? – Woody species desiccate lower soil
666 layers in sandy drylands. *Ecography*, in press, DOI:10.1111/ecog.04906.
- 667 Újházy, N., Biró, M. (2018). The ‘Cursed Channel’: utopian and dystopian imaginations of
668 landscape transformation in twentieth-century Hungary. *Journal of Historical Geography*, 61,
669 1-13.
- 670 Vadász, C., Máté, A., Kun, R., Vadász-Besnyői, V. (2016). Quantifying the diversifying
671 potential of conservation management systems: An evidence-based conceptual model for
672 managing species-rich grasslands. *Agriculture, Ecosystems and Environment* 234, 134-141.
- 673 Valkó, O., Deák, B., Török, P., Kelemen, A., Miglécz, T., Tóth, K., Tóthmérész, B. (2016).
674 Abandonment of croplands: problem or chance for grassland restoration? Case studies from
675 Hungary. *Ecosystem Health and Sustainability*, 2, e01208.
- 676 Valkó, O., Deák, B., Török, P., Kelemen, A., Miglécz, T., Tóthmérész, B. (2017). Filling up
677 the gaps—Passive restoration does work on linear landscape elements. *Ecological*
678 *Engineering*, 102, 501-508.
- 679 van Dijk, W.F.A., Schaffers, A.P., Leewis, L., Barendse, F. (2013). Temporal effects of agri-
680 environmental schemes on ditch bank plant species. *Basic and Applied Ecology*, 14, 289-297.
- 681 van Geert, A., van Rossum, F., Triest, L. (2010). Do linear landscape elements in farmland act
682 as biological corridors for pollen dispersal? *Journal of Ecology*, 98, 178-187.
- 683 Vanneste, T., Govaert, S., De Kesel, W., Van Den Berge, S., Vangansbeke, P., Meeussen, C.,
684 De Frenne, P. (2020). Plant diversity in hedgerows and road verges across Europe. *Journal of*
685 *Applied Ecology*, in press, DOI:10.1111/1365-2664.13620
- 686 Wintermanetel, D., Odoux, J.-P., Chadaeuf, J., Bretagnolle, V. (2019). Organic farming
687 positively affects honeybee colonies in a flower-poor period in agricultural landscapes.
688 *Journal of Applied Ecology*, 56, 1960-1969.
- 689 Zobel, M., van der Maarel, E., Dupré, C. (1998). Species pool: the concept, its determination
690 and significance for community restoration. *Applied Vegetation Science*, 1, 55-66.