1   Turning old foes into new allies – harnessing drainage canals for biodiversity conservation in

2   desiccated novel ecosystems

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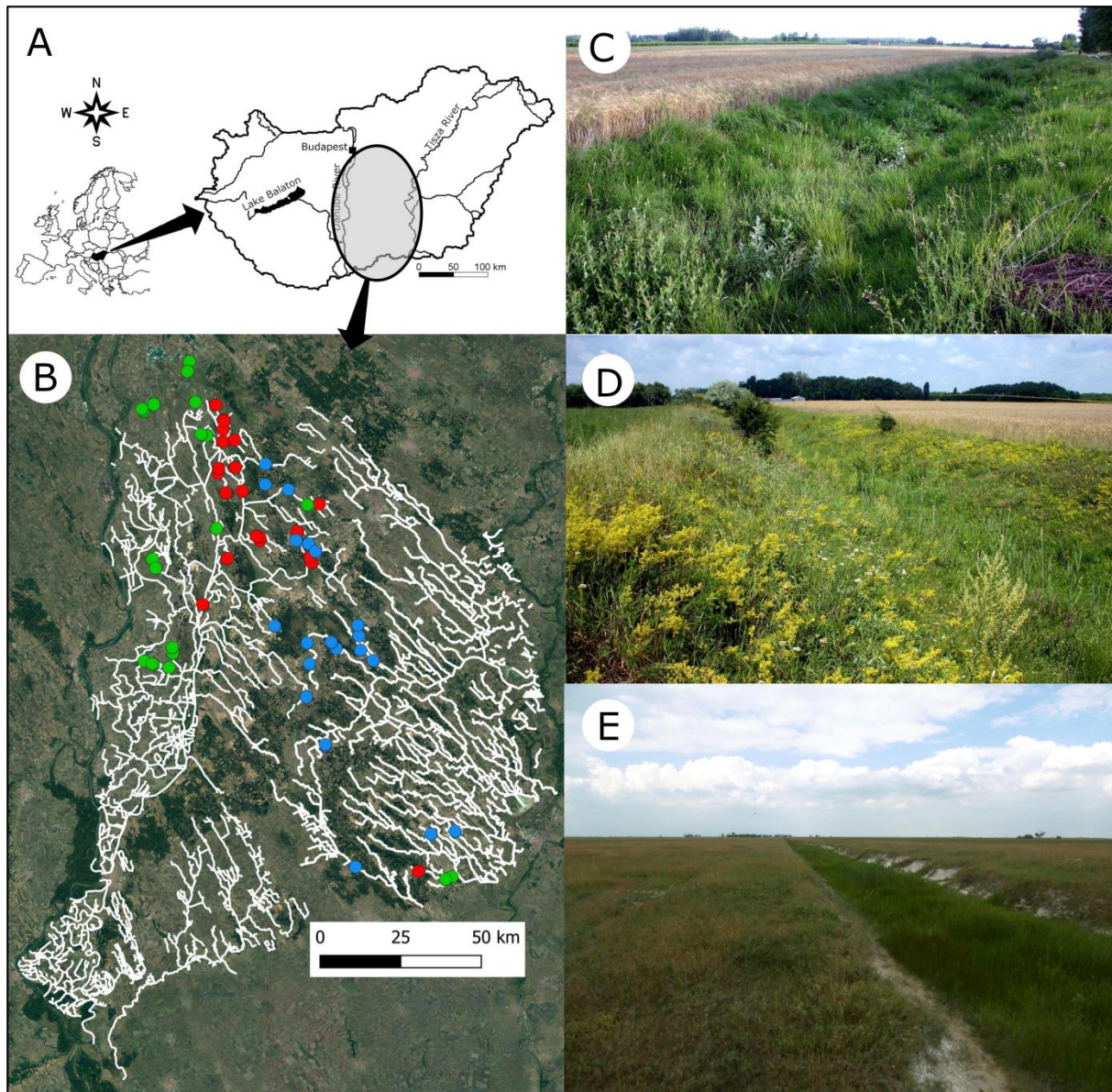
Figure 1 A: Location of the Danube-Tisza Interfluve in Hungary; B: registered drainage canal system of the region (white lines) and the position of the 60 studied canal sections; red: fen canals, green: saline canals, blue: sandy canals; C: small agricultural canal on fen substrate near Tázlár; D: large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

180

To assess the biodiversity of canals, we applied a multi-taxon approach covering various functional groups, including primary producers (vascular plants), pollinating and herbivorous primary consumers (butterflies and true bugs, respectively), predators (spiders) and birds as 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-m^2 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   $$E_i = \frac{(C_i - (\sum_{j=1}^{n} R_j)/n) \times 100}{(\sum_{j=1}^{n} R_j)/n},$$

223   where E_i is the substrate specific species excess of the ith 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 jth 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 'MOStest' function (*vegan* package) to identify the location of the
257 hump or pit in models with quadratic terms, and the 'fieller.MOStest' 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).
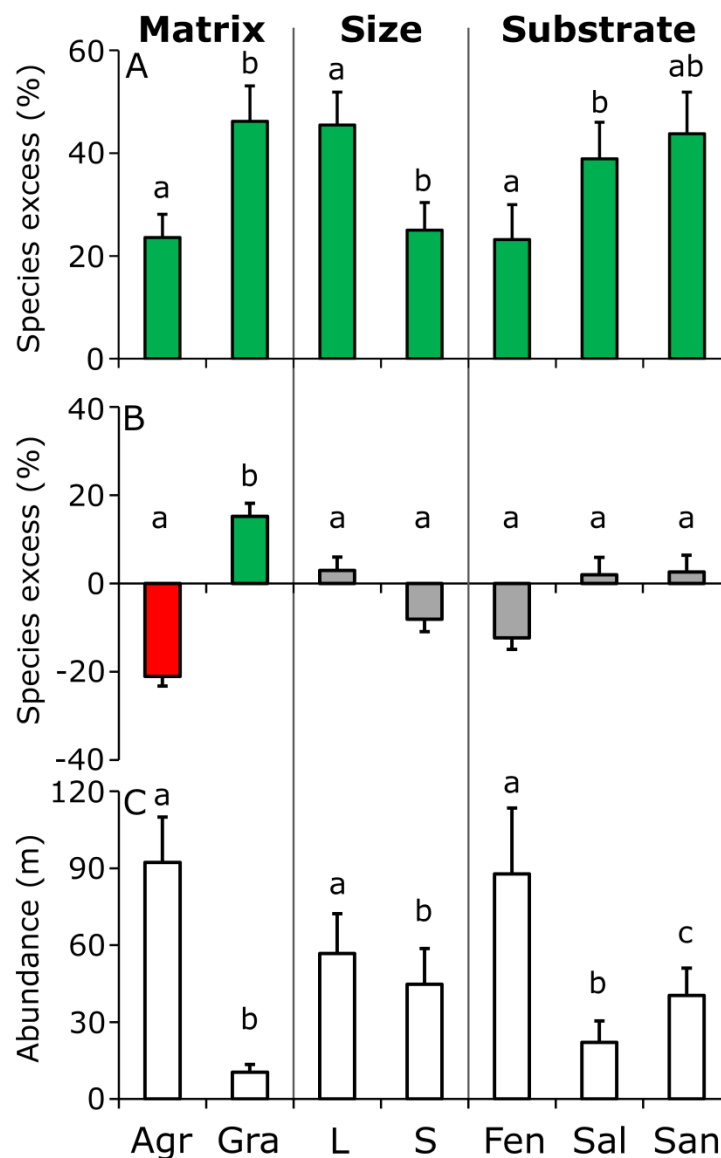
283

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-m^2 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).
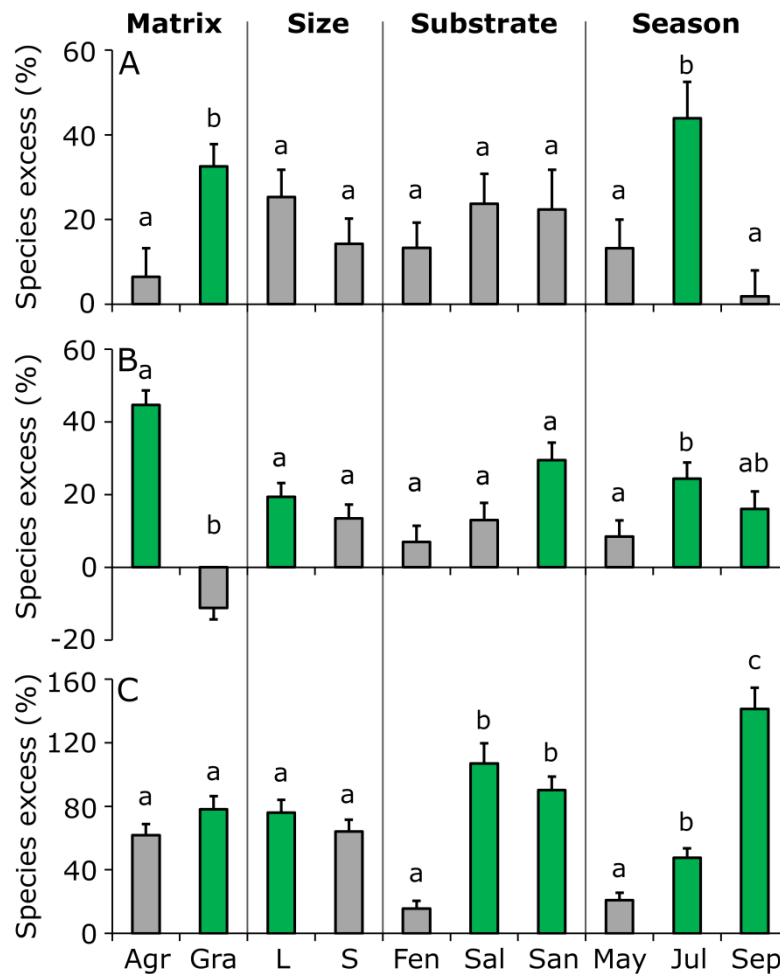
326

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

Effects of canal parameters

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

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

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

Regarding priority order, we conclude that landscape matrix and size are not decisive but substrate type should direct conservation efforts, as the higher the habitat stress (salinity in our model system), the higher the potential added conservation value. If this value cannot 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.
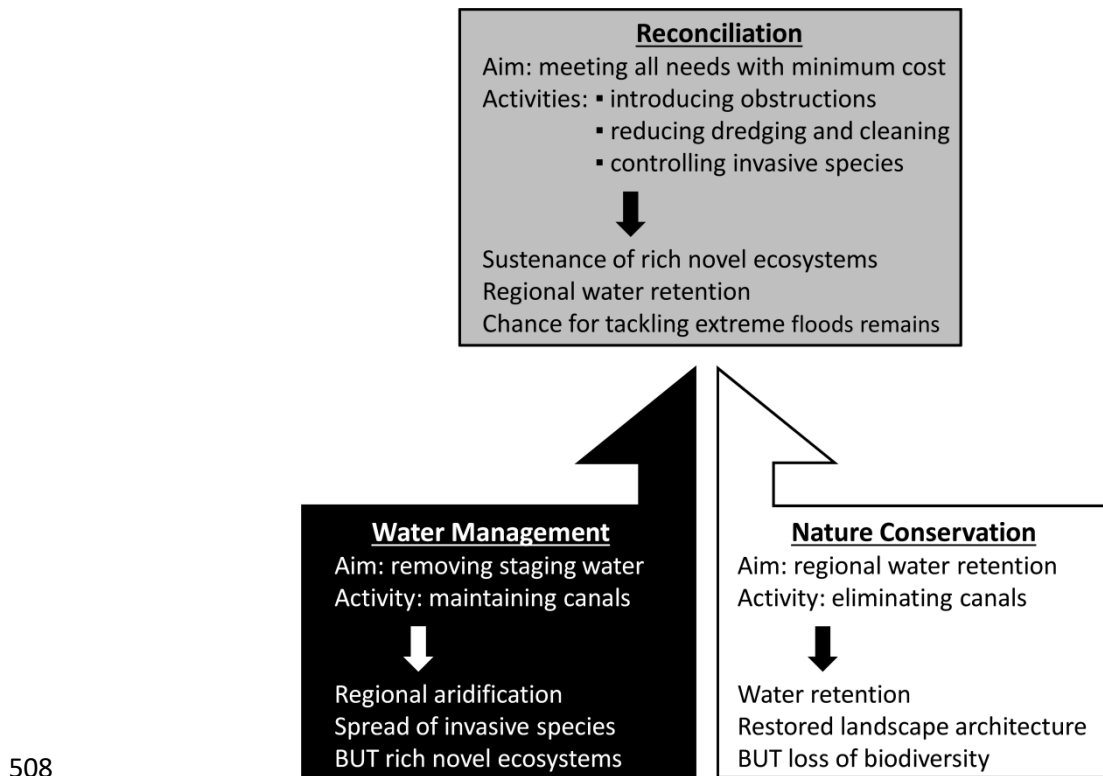
476

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.

Reconciliation
Aim: meeting all needs with minimum cost
Activities: ▪ introducing obstructions
▪ reducing dredging and cleaning
▪ controlling invasive species

Sustenance of rich novel ecosystems
Regional water retention
Chance for tackling extreme floods remains

Water Management
Aim: removing staging water
Activity: maintaining canals

Regional aridification
Spread of invasive species
BUT rich novel ecosystems

Nature Conservation
Aim: regional water retention
Activity: eliminating canals

Water retention
Restored landscape architecture
BUT loss of biodiversity

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

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526

527   Data Availability

528   Data will be stored on the Dryad Digital Repository.

529

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