RESEARCH ARTICLE

Turning old foes into new allies—Harnessing drainage canals for biodiversity conservation in a desiccated European lowland region

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Abstract

1. Drainage canals are widespread components of agricultural landscapes. Although canals have greatly contributed to biodiversity loss by desiccating wetlands, they have recently attracted conservation attention due to their potential to function as refugia for native species in intensively managed landscapes. However, their conservation role in complex landscapes composed of agricultural fields and desiccated but otherwise untransformed, semi-natural habitats, on which canals still pose a heavy burden, is unknown. Improved understanding of drainage canals and related biodiversity in these landscapes could help unlock their potential and support synergistic land management for nature conservation and water resource management.

2. We applied a multi-taxon approach, including plants, butterflies, true bugs, spiders and birds, to (a) assess the conservation value of drainage canals with temporary water cover in a heavily drained European lowland region, (b) to test landscape-level and local canal parameters for aiding prioritization among canals and (c) to propose a reconciliation-based management framework that suits the interest of all stakeholders.

3. We found that drainage canals and their banks concentrate more species across most taxa than semi-natural, mostly grassland habitats, possibly due to micro-environmental heterogeneity and the absence of low-intensity annual management compared to grasslands. Canals traversing semi-natural grasslands concentrate particularly high numbers of native species, but agricultural canals also support remarkable species richness. However, agricultural canals are important dispersal corridors for non-native invasive plants, which may negatively affect native biodiversity. Canal size has little effect on biodiversity, but habitat stress is an important determinant. The higher the stress (due to sandiness and salinity), the higher the added value of canals to landscape-wide biodiversity.

4. *Synthesis and applications*. We show that drainage canals can harbour high biodiversity and should therefore be recognized as important novel ecosystems with high conservation value, even when cutting through semi-natural grassland habitats. Canals have previously been considered detrimental to nature conservation due to their association with loss of wetlands. However, by reducing water loss with reversible obstructions, controlling invasive species and applying specific conservation measures, they may be turned into conservation allies without compromising long-term interests of water management and agricultural land use.

1 | INTRODUCTION

Drainage and subsequent land cultivation have been a major threat to global wetland ecosystems for centuries (Blann et al., 2009; Davidson, 2016; Herzon & Helenius, 2008). In Europe, most lowland fens have been drained (Hill et al., 2016; Langheinrich et al., 2004); approximately 25% of the arable land of the United States is artificially drained (Herzon & Helenius, 2008); and immense wetlands have recently been drained in tropical Southeast Asia to gain land for agriculture (Aldhous, 2004). Drainage is often performed by excavating artificial water courses, which are referred to as canals (e.g. Dorotovicova, 2013), ditches (Blomqvist et al., 2003) or channels (Tichanek & Tropek, 2015) in the literature. We henceforth use the term 'canal'. Canals are usually retained after the draining process and are regularly managed to sustain low and stable water balance in the cultivated landscape. Drainage canals are thus widespread in heavily modified lowland agricultural landscapes worldwide (Hill et al., 2016; Shaw et al., 2015) and can form dense networks of interconnected artificial waterways. For instance, over 100,000-km canals criss-cross the farmlands of the United Kingdom (Hill et al., 2016), and the total length of canals exceeds 300,000 km in the Netherlands (Blomqvist et al., 2003).

Despite being a widespread instrument of wetland loss, canals and their dry banks represent the only refuges for native biodiversity in many heavily drained and transformed regions (Chester & Robson, 2013; Harvolk et al., 2014; Manhoudt et al., 2007). This paradoxical situation has led to the recognition that conservation value may be assigned to canals in agricultural landscapes, and therefore, canals should be considered in conservation planning and agri-environmental schemes (Blomqvist et al., 2009; van Dijk et al., 2013).

Canals are longitudinally often more homogeneous and have steeper bank and different flow rates compared to natural lowland water bodies or wetlands; their vegetation and associated fauna can thus be considered as novel ecosystems (Hobbs et al., 2009). Management requirements for biodiversity in canals may be substantially different from those of natural wetlands, posing new challenges for conservation planners. Conventional management

prescriptions of agri-environmental schemes have frequently been reported as ineffective (Shaw et al., 2015; van Dijk et al., 2013). The main constraints for biodiversity in canals appear to be the high nutrient load, pollution with pesticides and herbicides and the inappropriate intensity of bed management, including dredging and vegetation cutting (Blomqvist et al., 2009; Herzon & Helenius, 2008). However, when land managers have the tools and incentives to locally optimize management for biodiversity, canals can sustain populations of endangered species and high overall species richness, significantly increasing landscape-level conservation value (Dorotovicova, 2013; Tichanek & Tropek, 2015; Manhoudt et al., 2007). Thus, although remaining natural wetlands habitats should be protected wherever possible, canals offer the potential to help boost the biodiversity that can be supported within highly productive agricultural systems.

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

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

Effective land management becomes more challenging in mosaic landscapes that are composed of both intensive agricultural fields and semi-natural habitats, interconnected with a network of drainage canals. This type of mosaic landscape may become more

common in the future, due to increasing land abandonment and grassland restoration in formerly intensive agricultural landscapes of developed countries (Cramer et al., 2008). Responsible land stewardship in these landscapes requires a complex understanding of the role of drainage canals harbouring novel ecosystems, and comprehensive guidelines must be developed for their management, in order to reconcile conservation purposes and immediate economic needs.

The landscape configuration and land management challenges outlined above perfectly fit the Danube–Tisza Interfluve of central Hungary. This ca. 1-Mha lowland region used to be a mosaic of wetlands and drier habitats, but due to heavy draining in the middle of the 20th century, most wetlands vanished and were transformed into cropland, or gradually turned into drier habitats, mostly wet grasslands, via spontaneous succession (Biró et al., 2007). The promise of higher productivity land after draining proved to be mostly false, as natural ecosystems ceased to provide vital ecosystem services and productivity decreased in some high-lying arable fields due to severe groundwater decline. This landscape history is well reflected in the colloquial name of the main arterial drainage canal of the region: the 'Cursed Channel' (Újházy & Biró, 2018).

In the second half of the 20th century, regional aridification was further increased by climate change (Pongrácz et al., 2011), as well as increased groundwater extraction for irrigation and excessive afforestation (Tölgyesi et al., 2020). As a result, the water table greatly decreased (by up to 7 m in some localities; Ladányi et al., 2010), several wetlands vanished or shrank in size and even a large proportion of the canals became temporary water courses. To date, restoration attempts have been limited to the filling in of some canals inside strict nature reserves and keeping sluices closed for longer periods than earlier, while the majority of canals are still functional and the other causes of aridification have not been addressed. The resulting environmental and biotic changes of irreversible water loss may have pushed the region over a tipping point into the realm of novel ecosystems (cf. Hobbs et al., 2009), in which the appropriate management of drainage canals may have a central role. Presently, the scientific literature offers limited guidance for this endeavour, but the emerging concept of reconciliation ecology (Chapman et al., 2018; Rosenzweig, 2003) offers a promising avenue, as it seeks reconciliation between opposing stakeholders for the mutual benefit of ecosystems and people.

To this end, we aimed to understand the ecological role of the drainage canal network of the region. Specifically, we aimed (a) to identify the extent to which drainage canals contribute to landscape-scale biodiversity conservation, (b) to test the effects of canal characteristics, including the surrounding landscape matrix, canal size, habitat type and reed and woody species abundance on the capacity of canals to sustain biodiversity and (c) to propose reconciliation-based management guidelines, which suite the interests of the presently opposing stakeholders (i.e. nature conservation and water management) at the same time, and thus creating a win–win situation.

2 | MATERIALS AND METHODS

2.1 | Study area

The study region, the Danube–Tisza Interfluve of central Hungary (Figure 1) has a continental climate, with cold winters and warm summers. The mean annual precipitation is 550–600 mm (maximum in early summer) and the mean temperature is 10–11°C (Tölgyesi et al., 2016). The soil substrate is diverse with mostly coarse sand in the central zone, saline loam along the bordering rivers, Danube and Tisza and peaty loam (fen substrate) between the sandy and saline zones. Small isolated pockets of saline and fen areas also occur in the sandy central zone. Since the region is flat and climatically uniform, substrate type is the main determinant of the habitat that can develop in a specific location, leading to three main habitat types, that is, fen, sandy and saline habitats, which also represent a decreasing productivity gradient due to increasing environmental stress.

The total length of registered canals in the region is 4,723 km (Figure 1). Canals are infrequently managed by full-profile dredging, reed cutting and shrub clearing (usually less than once a decade). Mowing once a year and/or extensive grazing are the main management types of adjacent grasslands, but neither mowing nor grazing extends into the canals on a regular basis. Permanent water in the canals is nowadays rare; most contain water only in spring and after periods of heavy rain.

2.2 | Data collection

We selected sixty 200-m long drainage canal sections in the region, covering the two predominant landscape matrices, that is, agricultural and (semi-natural) grassland areas (30 each), the three main habitat types (20 each) and both small and large canals as size classes (30 each), leading to five replicates for each of the 12 category combinations (Figure 1). Agricultural canals were fringed by at least 200 m wide, annually ploughed croplands on both sides. Grassland canals were embedded in extensive grasslands that used to be wetter before draining, but, due to natural successional processes, they still harbour valuable native flora and fauna. All grassland canals were inside protected areas and were part of the Natura 2000 Ecological Network of the European Union. Traditional management is applied in the grasslands, which includes only low-intensity grazing and/or annual mowing. Small canals had a depth of 0.7 ± 0.2 m (mean $\pm$ SD) and a width of 3.6 ± 1.4 m, and large ones a depth of 1.7 ± 0.5 m and a width of 6.8 ± 2.0 m (banks included); very large, arterial canals with constant water cover were avoided. We also assessed the abundance of reed and woody vegetation by measuring their cumulative length along the canals and used them as additional variables to predict biodiversity. Canals dredged within the past 10 years were not considered in the study.

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)
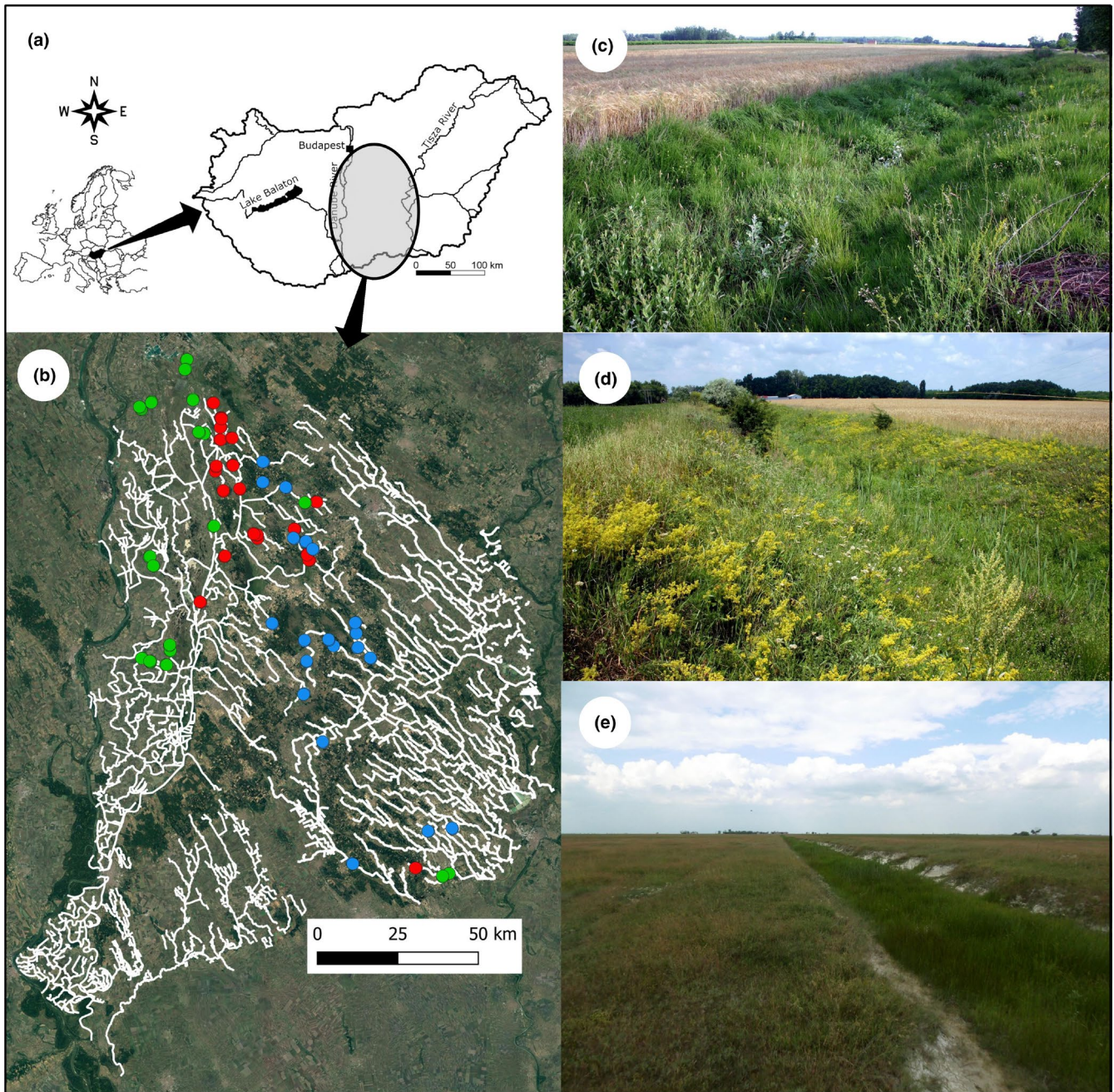
FIGURE 1 (a) Location of the study region in Hungary; (b) registered drainage canal system of the region (white lines) and the position of the 60 studied canal sections (not all are included in the official registry); red: fen canals; green: saline canals; blue: sandy canals; (C) small agricultural canal in fen habitat near Tázlár; (D) large agricultural canal in sandy habitat near Kerekegyháza; (E) small grassland canal in saline habitat near Dunapataj

and birds as representatives of large-bodied vertebrates. Vegetation was sampled in three ways once during the summer of 2018. First, we compiled the total species pool of vascular plants in the 200-m sections (henceforth 'gamma diversity') and second, recorded species in eight evenly spaced 1-m^2 plots to capture plot-scale species richness (henceforth 'alpha diversity'), making a total of 480 plots. Four plots were placed on the dry slopes of the bank and four plots into the bottom of the bed or adjacent to the bottom if water cover was too high. Third, we assessed the abundance of non-native

invasive plants. The measure was the cumulative length of invaded canal bank with a resolution of 1 m. Each bank was measured separately, leading to a maximum invasive plant abundance of 400 m.

Arthropod surveys were repeated three times in 2018: in spring (May), summer (July) and autumn (September), and were performed between 9 a.m. and 6 p.m. in dry, sunny weather without strong wind. We surveyed butterflies in transects along both canal banks. Each transect measured 200 m long and 2.5 m wide. Following the protocol of Nowicki et al. (2008), the observer walked at a slow pace

along the transect and counted and identified to species level all butterfly individuals seen 5 m in front of them. We sampled true bugs and spiders with sweep-netting. Each sample contained specimens from 25 sweeps from four, evenly spaced 25-m long transects along each 200-m long canal section. Samples per section were not pooled. Specimens were stored in alcohol for later identification in the laboratory. We surveyed birds between 5 and 9 a.m. twice during the breeding season of 2019 (May and June). We scanned the area for 10 min from an observation point adjacent to the canals, without disturbing the birds, then slowly walked by the canals to search for hiding individuals. We recorded every bird that landed on the vegetation or the surface of the canals; fly-bys were ignored.

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

2.3 | Data analysis

For analysing the alpha and gamma diversity of the vegetation, we sorted species into ruderal and non-ruderal groups following the Flora Database of Hungary (Horváth et al., 1995). Ruderal species were those that are typical of highly degraded and segetal communities (including non-native invasive species), and thus have little or negative conservation value. The remaining non-ruderal species, comprising species of (semi-)natural grasslands and wetlands, are of conservation interest. We made subsequent analyses first considering all plant species and then reducing the included species to the non-ruderal ones.

In line with the species pool hypothesis of Zobel et al. (1998), we can expect different species pool sizes in different habitats, making comparisons across habitats difficult. Therefore, we standardized the species richness scores of canals to habitat-specific average reference species richness scores. We expressed the resulting species excesses (or deficits, if negative) as percentages. Thus, the use of species excesses, equalling the proportional added value of canals to landscape-wide diversity, allowed us to make between-habitat comparisons by ruling out the effect of the differently sized species pools of different habitats. We used the following equation for the calculations:

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

where E_i is the habitat-specific species excess of the ith sampling unit of a canal (one of eight plots for alpha diversity or the total species count for gamma diversity), C_i is the species richness of this sampling unit, R_j is the species richness of the jth sampling unit of any of the reference transects belonging to the same habitat type as the canal and n is the number of such reference sampling units. The raw species

richness scores we used for the standardization are shown in the Supporting Information (Figure S1).

Invasive plant species were either absent or very scarce in reference transects; therefore, we did not standardize their abundance in the canals but used the raw scores in subsequent analysis. For butterflies, true bugs and spiders, we applied the above method of standardization, but the reference averages we used were specific to both habitat and season. For birds, we used the raw species richness scores for the analysis because there were no reference scores for standardization. Invasive pest species were not encountered among animal taxa; therefore, all species were retained for the analysis.

We applied a linear modelling approach to evaluate the biotic response variables (species excesses of plant and arthropod species richness, raw invasive plant abundance and bird species richness). We had three categorical (landscape matrix, habitat and size) and two continuous (abundance of shrubs and reed) explanatory variables for plants and birds, while we included season as a fourth categorical explanatory variable for arthropods. We included canal identity as a random factor in models where multiple samples were collected in the canal sections. For birds, we used sampling occasion as a random variable. There was no indication of multicollinearity among the variables (generalized variance inflation factors ranged between 1.00 and 1.62); therefore, all a priori variables were included in the final models and tested their effect on the variation of the biotic variables.

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

Models were prepared in R environment (R Core Team, 2019) using the 'lm' (gamma diversity of plants), 'glm' (invasive plant abundance, Poisson error term), 'lmer' (arthropods and the alpha diversity of plants; LME4 package; Bates et al., 2015) or 'glmer' (birds, LME4 package, Poisson error term) functions depending on the data structures. Generalized variance inflation factors were calculated with the 'vif' function (CAR package, Fox & Weisberg, 2019). The significance of the explanatory variables was tested using the 'ANOVA' function (CAR package). Pairwise comparisons of the levels of habitat and season were performed with the 'emmeans' function (EMMEANS package, Lenth, 2020).

3 | RESULTS

3.1 | Plants

We recorded a total of 512 plant species in the study, but only 388 of these were non-ruderal species (i.e. being wetland or grassland species); the remaining 124 species were ruderal weeds of highly degraded or segetal communities. Considering total species excess on

the gamma level, we found no difference between agricultural and grassland canals but when we omitted ruderal species, significantly lower excess remained in agricultural canals than in grassland ones. Large canals had higher species excesses than small ones and saline canals had higher excesses than fen canals both with and without ruderal species. Fen canals had higher excesses than sandy canals when all species were considered, but the difference was lost after omitting out ruderal species. Compared to the habitat-specific average reference levels, all levels of all categorical variables had significantly positive species excesses for both sets of species. The abundance of reed did not affect the species excess of plants at the gamma level but increasing woody species abundance slightly but significantly increased both sets of species (Figure 2; Tables 1 and 3; Figure S2).

Looking at alpha diversity excess, we found that agricultural canals had lower values than grassland ones considering both sets of species. Large canals had higher total diversity excesses than small ones, but the difference was lost after sorting out ruderal species. Fen canals had lower values than saline and sandy ones when all species were considered but for non-ruderal species, only the difference with saline canals remained significant. Reed abundance slightly suppressed ruderal species but did not affect non-ruderal ones, while woody species did not affect the score for the total set of species but increased for non-ruderal species (Figure 2; Tables 1 and 3; Figure S2).

We encountered several invasive plant species along the canal sections. Their cumulative abundance ranged between 0 (absent) and 400 m. The most abundant invasive species were *Asclepias syriaca*, *Solidago gigantea*, *S. canadensis* and *Aster lanceolatus* agg. Agricultural canals demonstrated a higher level of invasion than grassland canals, and large canals had more invasive species than small ones. Fen canals showed a markedly higher rate of invasive infestation than either

saline or sand canals. Increasing woody species abundance decreased invasive abundance (Figure 3; Table 1; Figure S3).

3.2 | Arthropods

We recorded 58 butterfly species (5,962 individuals) in the study and 55 occurred in the canals, of which 19 were encountered only in the canals and not in the reference transects. Higher species excesses were found in grassland canals than in agricultural ones. Species excesses were higher in summer than in spring and autumn. Neither reed or woody species abundance, nor canal size, nor habitat type had a significant effect on species excess. Compared to the reference levels, grassland canals and canals in summer had significantly positive species excesses (Figure 4; Tables 2 and 3; Figure S4).

We collected a total of 246 true bug species (30,012 adult individuals) in the study, and 219 occurred in the canals, of which 82 were collected exclusively there. Species excesses were affected only by matrix and season, with higher scores in agricultural canals than in grassland ones, and higher scores in summer than in spring. Compared to the reference levels, the statistics confirmed significant species excess in agricultural canals but not in grassland ones, in large canals but not in small ones and on sandy habitat but not on fen or saline habitats. Species excess was highly positive in summer, but significant difference was also confirmed for autumn data (Figure 4; Tables 2 and 3; Figure S4).

We recorded 134 spider species (6,718 adult individuals) in the study; 114 occurred in the canals, of which 38 were found only there. Habitat type and season had significant effects on species excesses, while matrix and size did not. Saline and sandy canals had higher species excesses than fen canals, and the excesses increased as the seasons progressed
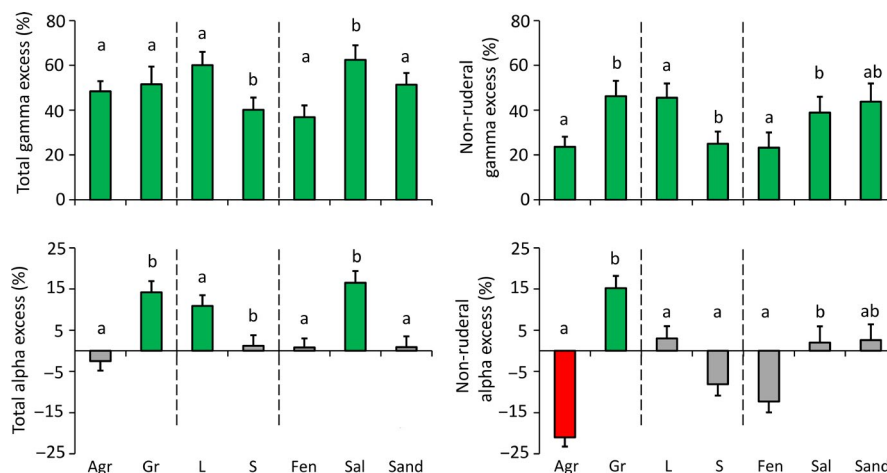
FIGURE 2 The effects of landscape matrix, canal size and habitat type on the species excesses of all and non-ruderal plants separately on the gamma and the alpha levels (i.e. considering total species counts of 200-m long canal sections and 1-m^2 plots respectively). Different lowercase letters within each canal parameter identify significantly different groups. Shading is used to denote differences from the reference level (i.e. from the 0 score). Green and red indicate significantly positive and negative differences, respectively, while grey shading is used when no significant difference was detected from the reference level. Species excess is a proportional difference from the habitat-specific reference averages expressed in per cents. Agr: agricultural matrix, Gra: grassland matrix, L: large canal size, S: small canal size, Fen: fen habitat, Sal: saline habitat, Sand: sandy habitat. Whiskers show standard errors of the means

TABLE 1   Test results of the fixed factors of the full models we prepared for plants. Pairwise comparisons of factor levels are shown for factors with more than two levels and with significant effect. The type of test statistics depends on the design of the models (for details see main text). Significant results ($p < 0.05$) are indicated with boldface

	Plants—gamma (total)		Plants—alpha (total)		Plants—gamma (non-ruderal)		Plants—alpha (non-ruderal)		Invasive plants	
	F	p	χ^2	p	F	p	χ^2	p	χ^2	p
Reed	3.85	0.055	**4.48**	**0.054**	3.82	0.056	2.23	0.135	0.016	0.686
Woody (log scale)	**8.50**	**0.005**	1.98	0.159	**10.27**	**0.002**	2.46	0.117	**290.77**	**<0.001**
Matrix	0.95	0.334	**7.49**	**0.006**	**13.88**	**<0.001**	**27.24**	**<0.001**	**1965.11**	**<0.001**
Size	**7.31**	**0.009**	**4.74**	**0.030**	**8.07**	**0.006**	3.31	0.069	**8.80**	**0.003**
Habitat	**8.63**	**<0.001**	**10.93**	**0.004**	**5.84**	**0.005**	**6.14**	**0.046**	**611.51**	**<0.001**
	t ratio	**p**	**t ratio**	**p**	**t ratio**	**p**	**t ratio**	**p**	**t ratio**	**p**
Fen-Saline	**−4.11**	**<0.001**	**−2.82**	**0.018**	**−3.39**	**0.004**	**−2.44**	**0.046**	**16.99**	**<0.001**
Fen-Sand	−0.69	0.770	0.78	0.716	−1.45	0.325	−1.44	0.492	**18.86**	**<0.001**
Saline-Sand	**3.07**	**0.009**	**3.13**	**0.008**	1.82	0.171	1.23	0.439	−1.71	0.201

TABLE 2   Test results of the fixed factors of the full models we prepared for animal taxa. Pairwise comparisons of factor levels are shown for factors with more than two levels and with significant effect. Significant results ($p < 0.05$) are indicated with boldface

	Butterflies		True bugs		Spiders		Birds	
	χ^2	p	χ^2	p	χ^2	p	χ^2	p
Reed	3.34	0.068	1.65	0.199	**5.19**	**0.023**	**17.65**	**<0.001**
Woody (log scale)	2.73	0.098	2.82	0.093	0.01	0.935	**26.21**	**<0.001**
Matrix	**7.42**	**0.006**	**37.85**	**<0.001**	0.38	0.451	0.38	0.537
Size	2.39	0.122	1.86	0.172	2.62	0.097	4.27	0.058
Habitat	3.55	0.170	2.07	0.356	**19.10**	**<0.001**	2.48	0.289
Season	**24.72**	**<0.001**	**9.87**	**0.007**	**136.21**	**<0.001**	—	—
	t ratio	**p**	**t ratio**	**p**	**t ratio**	**p**	**t ratio**	**p**
Fen-Saline	—	—	—	—	**−4.14**	**<0.001**	—	—
Fen-Sand	—	—	—	—	**−2.59**	**0.032**	—	—
Saline-Sand	—	—	—	—	1.56	0.273	—	—
July–May	**3.51**	**0.002**	**3.14**	**0.005**	**2.45**	**0.038**	—	—
July–Sept	**4.80**	**<0.001**	1.65	0.224	**−8.66**	**<0.001**	—	—
May–Sept	1.29	0.403	−1.50	0.294	**−11.11**	**<0.001**	—	—

from spring through summer to autumn. Species excess was negatively affected by reed abundance, but woody cover had no detectable effect. Compared to the habitat- and season-specific reference levels, grassland canals had positive excesses but agricultural ones did not. Both large and small canals tended to have significantly positive scores, and among different habitat types, we could confirm positive species excesses for saline and sandy canals. Species excesses were significantly positive in summer and autumn but not in spring (Figure 4; Tables 2 and 3; Figure S4).

3.3 | Birds

We observed 38 bird species (892 individuals) during the study. We found that birds similarly frequented agricultural and natural canals

and there was no difference among canal size classes and habitat types (Figure 3; Table 2). However, the abundance of woody species and reed had significantly positive effects on species richness (Figure 5; Table 2).

4 | DISCUSSION

4.1 | Biodiversity of drainage canals

Drainage canals are widespread components of managed lowland landscapes worldwide (Hill et al., 2016; Shaw et al., 2015). Although drainage is among the primary causes of the loss of the original biodiversity, there is growing evidence that canals can act as refuges for a variety of native species in transformed landscapes (Chester &

TABLE 3 Test results of the reduced models with which we tested whether the levels of the categorical variables differ from the reference levels. Biotic variables without reference levels were not analysed this way and are not included below. Significant results ($p < 0.05$) are indicated with boldface

|	Plants—gamma (total)		Plants—alpha (total)		Plants—gamma (non-ruderal)		Plants—alpha (non-ruderal)		Butterflies		True bugs		Spiders	
	t	P	t	p	t	p	t	p	t	p	t	p	t	p
Matrix														
Agricultural	8.05	**<0.001**	−0.54	0.592	4.07	**<0.001**	−4.09	**<0.001**	0.93	0.357	6.38	**<0.001**	2.00	**0.049**
Grassland	8.71	**<0.001**	3.24	**0.002**	8.07	**<0.001**	3.02	**0.004**	4.75	**<0.001**	−1.58	0.120	3.09	**0.003**
Size														
Large	10.51	**<0.001**	2.36	**0.022**	7.74	**<0.001**	0.50	0.620	3.47	**<0.001**	2.14	**0.037**	3.04	**0.003**
Small	7.13	**<0.001**	0.28	0.777	4.33	**<0.001**	−1.35	0.184	1.99	0.051	1.50	0.139	2.01	**0.048**
Habitat														
Fen	5.36	**<0.001**	0.16	0.874	3.23	**0.002**	−1.68	0.098	1.51	0.137	0.49	0.625	0.86	0.393
Saline	8.89	**<0.001**	2.95	**0.005**	5.28	**<0.001**	0.27	0.789	2.62	**0.011**	0.91	0.369	1.44	0.153
Sand	7.31	**<0.001**	0.18	0.857	5.94	**<0.001**	0.39	0.698	2.48	**0.016**	2.86	**0.006**	4.97	**<0.001**
Season														
May	—	—	—	—	—	—	—	—	1.84	0.068	1.22	0.22	1.80	0.074
July	—	—	—	—	—	—	—	—	6.11	**<0.001**	3.58	**<0.001**	4.09	**<0.001**
September	—	—	—	—	—	—	—	—	0.26	0.792	2.35	**0.019**	12.17	**<0.001**

Robson, 2013; Golubovic et al., 2017; Torma et al., 2018), reinforcing the importance of moist micro-environments in the face of local and global environmental changes (Keppel et al., 2012; McLaughlin et al., 2017). Our findings go one step further, as we show that canals not only function as secondary habitat for a certain subset of the native biodiversity but also they concentrate more species than adjacent semi-natural habitats, being typically grasslands, across a wide range of taxa. One reason for this diversity may be the micro-environmental heterogeneity offered by the canals (Stein et al., 2014). A wide moisture gradient is traversed from the dry top zone of the canal banks down to the bottom, enabling plant species with contrasting moisture demand to coexist in close proximity, whereas the flat surrounding areas are characterized by more homogeneous environmental conditions. As a result, both grassland and agricultural canals could harbour more plant species, including those of conservation interest (i.e. non-ruderal species), at the gamma level than semi-natural grasslands. Grassland canals had higher species richness at the alpha level, despite the lack of annual management, which usually enhances the fine-scale coexistence of species (Klimek et al., 2007; Vadász et al., 2016).

The high diversity of plants, in turn, seems to cascade up to the level of primary consumers (butterflies and true bugs) and predatory arthropods (spiders). Nevertheless, some structural and functional

FIGURE 3 The effects of landscape matrix, canal size and habitat type on the abundance of invasive plant species and the species richness of birds. Different lowercase letters within each canal parameter identify significantly different groups. Agr: agricultural matrix, Gra: grassland matrix, L: large canal size, S: small canal size, Fen: fen habitat, Sal: saline habitat, Sand: sandy habitat. Whiskers show standard errors of the means [viewed at wilcom]

features of the canals may have also contributed to the high arthropod richness we detected. Canals, which are local depressions in flat landscapes, can provide wind shelter for flying insects, including butterflies (Dover, 1996). Furthermore, canals provide overwintering opportunities for arthropods in the soil, litter and standing vegetation such as hollow stems, whereas soil disturbance in arable land impedes successful overwintering (Herzon & Helenius, 2008). Semi-natural grasslands and grassland canals may be similar in suitability for overwintering in the soil, but the management (i.e. mowing or grazing) of grasslands leaves little standing vegetation and litter into the winter. A variety of other non-cropped linear landscape elements, such as road verges, flower-rich field margins or hedgerows, have also been shown to be important for overwintering (Gallé et al., 2018; Ramsden et al., 2015), and canals are also likely to fulfil this function.

Arthropods greatly benefited from canals also in summer, as the highest species excesses were found in this period. Summers in the region are dry; thus, canals can be important sources of water and fresh vegetation for true bugs and floral resources for butterflies. Furthermore, several studies emphasize that agricultural areas usually have 'hunger periods' for arthropods in summer when there is a mismatch between resource demand and supply due to the synchronized phenology of cropped plants (Timberlake et al., 2019; Wintermantel et al., 2019). At the same time, canals are rich in resources throughout the vegetation period, including times when agricultural areas experience supply gaps. Although less commonly studied, this may also apply to managed grasslands. Grassland vegetation after being mown with powerful machinery provides little resource for either pollinators or other herbivorous insects. Grassland canals are usually avoided during mowing, and thus represent continuity in food supply, similar to intentionally uncut vegetation strips in hay meadows (Buri et al., 2013; Kühne et al., 2015). Thus, canals are not just locally species-rich strips but are potentially important functional cornerstones of landscape-wide arthropod diversity.
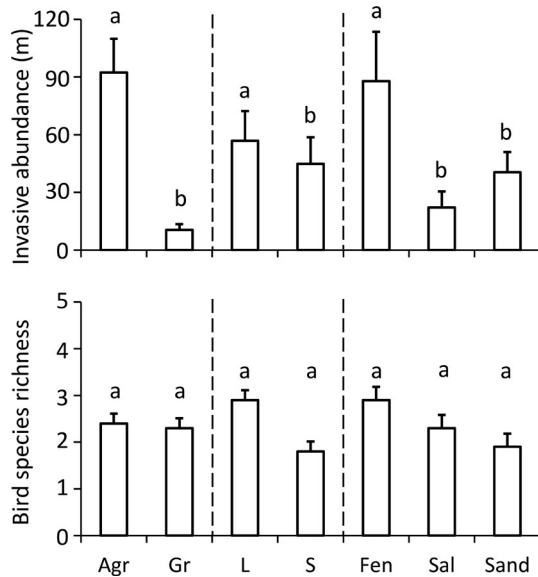
Besides the local and landscape-level effects of canals on biodiversity, they may have consequences on even larger spatial scales. Canals often form continuous networks, overarching large regions and connecting isolated habitat fragments, similar to other linear landscape elements such as road verges, river embankments and hedgerows (Bátori et al., 2020; Vanneste et al., 2020). Canals, if longitudinally permeable for native species, can act as green corridors of dispersal, increasing regional connectivity and alleviating deficiencies of meta-population dynamics (van Dijk et al., 2013; van Geert et al., 2010), or can even act as conduits of climate change-mediated range shifts, which would otherwise be hindered by extensive hostile areas, such as arable lands or exotic tree plantations (Robillard et al., 2015; Saura et al., 2014). Our findings, however, highlight that invasive plant species may also use canals as dispersal corridors, especially in agricultural areas (see also Maheu-Giroux and de Bois, 2007). As a result, canals can facilitate the invasion of otherwise intact and isolated habitats, and highly invaded canal sections may represent points of high resistance for native dispersal. Thus, controlling invasive species, particularly in agricultural canals, is a pressing issue that should be included in regional conservation strategies.
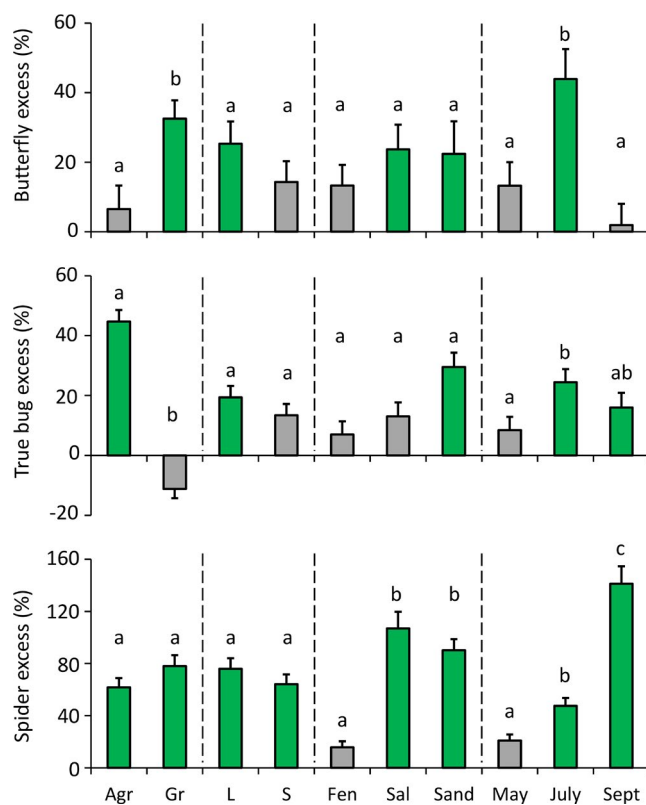
4.2 | Effects of canal parameters

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 than agricultural ones for most taxa, both types deserve our attention, as grassland ones exceed adjacent semi-natural grassland richness and agricultural canals represent one of those rare landscape elements in hostile agricultural

landscapes that have considerable conservation value. 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. Plant species excess was higher in large canals both on the alpha and gamma levels, but on the alpha level, this was only due to a higher prevalence of ruderal species. Furthermore, large canals hosted a higher abundance of invasive species, indicating that large canals may be stronger conduits of plant invasion than small canals.

Conversely, habitat type provides more guidance for prioritization among canal types. Fen canals proved to be the least valuable as (a) the rate of invasion was the highest in them, (b) they had lower plant species excess than saline canals on both levels and in both sets of species and (c) had lower spider species excess than the two other habitats. 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 coexisting species in canals (Houlahan & Findlay, 2004) compared to canals in other habitats. At the same time, traditional management in adjacent fen grasslands effectively suppresses competitors and sustains 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 in sandy habitats (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 microtopography (Kelemen et al., 2013).

Regarding priority order, we conclude that landscape matrix and size are not decisive but habitat type should direct conservation efforts, as the higher the habitat stress (sandiness or salinity in our model system), the higher the potential added conservation value. If this potential value is not realized due to local conditions in certain canals (e.g. because of high local disturbance), these conditions

FIGURE 4 The effects of landscape matrix, canal size, habitat type and season on the species excesses of butterflies, true bugs (Heteroptera) and spiders. Different lowercase letters within each canal parameter identify significantly different groups. Green shading indicates significantly positive difference from the reference level (i.e. the 0 score), while grey shading is used when no significant difference was detected from the reference level. Species excess is a proportional difference from the habitat- and season-specific reference averages. Agr: agricultural matrix, Gra: grassland matrix, L: large canal size, S: small canal size, Fen: fen habitat, Sal: saline habitat, Sand: sandy habitat. Whiskers show standard errors of the means
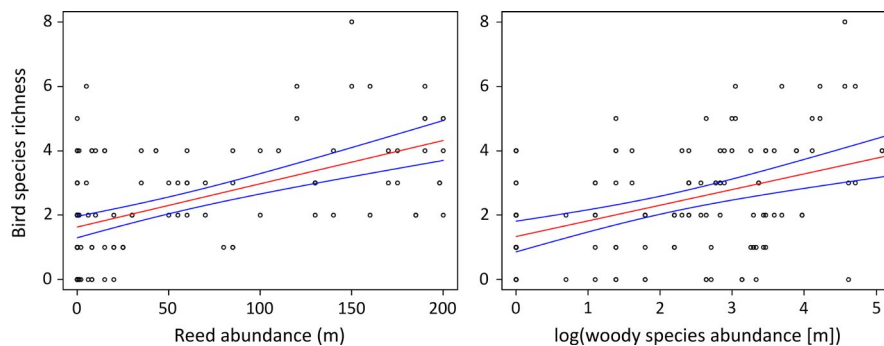
FIGURE 5 Relationship between the species richness of birds and the abundance of reed and woody plant species along the studied canal sections. Woody abundance is considered on log scale to account for its heavily right-skewed distribution. The repeated measures design of the data is not reflected in the plots but considered in the full models. Blue curves mark the 95% confidence limits of the model lines; both models were significant ($p < 0.05$)

should be identified and mitigated to assist reaching the predicted biodiversity levels. Our findings also provide guidance on the net conservation effects of restoration projects, in which the filling in of canals is considered unavoidable, as the highest accompanying biodiversity loss is expected in saline habitat and the lowest in fen habitat during such interventions.

We also tested the effects of parameters that can be modified by management (i.e. the abundance of woody species and reed). The presence of woody species had positive effects on biodiversity (birds and the gamma diversity of plants). This finding was expectable, as sparse woody cover has been shown to introduce heterogeneity into micro-environmental conditions and vegetation structure (López-Pintor et al., 2006), both of which are known to boost biodiversity (Herzon & Helenius, 2008; Teleki et al., 2020). At the same time, the encroachment of woody species tended to correlate with the abundance of invasive plants, so periodic woody species clearing should be coupled with interventions to control invasive species, or techniques that can simultaneously tackle both groups of plants should be applied.

The effect of reed abundance is more difficult to evaluate because it was contrasting among taxa: positive for birds but negative for spiders). It had a positive effect on the gamma diversity of plants but only when all species were considered, meaning that reed increased only the richness of ruderal species. In fact, reed was the only parameter that showed taxon specificity in the direction of the effects, suggesting that conservationists may need to choose which taxon to favour. Some authors have come to the conclusion that reeds should regularly be cut along canals for the

benefit of biodiversity (e.g. Tichanek & Tropek, 2015), but these were mostly single-taxon studies, none of which considered birds. Since birds are declining rapidly in human-modified landscapes (Donald et al., 2001), the complete suppression of reed should be avoided to ensure that canals function as good quality refuge sites for them.

4.3 | Reconciliation between conservation and water management

Our findings highlight the high conservation value of drainage canals, but we need to emphasize that canals in their present form are not yet true allies in nature conservation. They still remove significant amounts of water from the surrounding landscape in wet periods, contributing to water shortage both in (semi-)natural habitats (Ladányi et al., 2010; Pongrácz et al., 2011) and in agricultural production systems (Szinell et al., 1998). To make canals net positive contributors to conservation, the draining effect should be minimized (without compromising necessary agricultural production), while maintaining the canal profile with all the diverse microhabitats, flora and fauna. This can be achieved by introducing more sluices and semi-permanent obstructions, such as earthen plugs (see also Tichanek & Tropek, 2015 for similar recommendations). Canals that are permanently dry require no modification of the bed.

To date, conservationists have aimed to reverse engineer entire canal sections in Hungary to fight against their draining effect (Valkó et al., 2017). This is extremely labour- and cost-intensive and, according to our results, can also entail a considerable loss of local biodiversity. As an illustration, a single project between years 2013 and 2015 aiming to fill up a wet saline and a permanently dry sandy canal section cost approx. 600,000 USD and required the movement of 67,000 m^3 of soil (Kiskunság National Park Directorate, 2021). Our recommendation does not require such intensive interventions and retain the microhabitats for plants and animals. If financial resources can be spared by lowering the intensity of intervention, they should be reallocated to identifying and mitigating weak points of the canal network where the potential habitat-specific biodiversity concentrating effect is hindered by local factors, such as disturbance, pollution and invasive infestation.

We suppose that the introduction of more sluices and earthen obstructions would be more acceptable for water management authorities than removing the canals, since canals would thus remain available for reopening if extreme water levels require. However, we also discourage intensive dredging of the entire canal profiles, as it means the removal of the rich flora and fauna we described in this study. Furthermore, we encourage the retention of moderate amounts of woody plants and reed as they can increase the quality of canals as refuge sites for biodiversity. Implementation of these proposed guidelines would constitute a viable alternative to presently applied practices (Figure 6). However, the actual protocol of our recommendations, such as
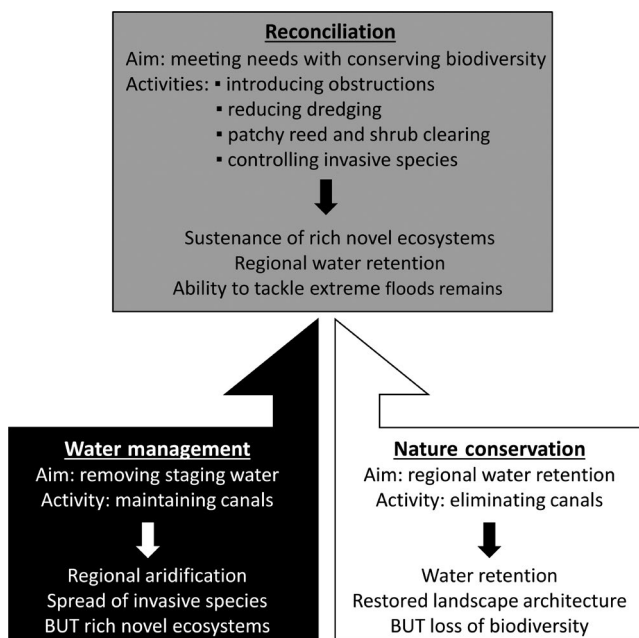
FIGURE 6 The main components of our management framework for drainage canals, showing the presently differing aims and activities of stakeholders and the related environmental impacts (bottom left and right), and our proposed cost-effective management alternatives (top)

the number and spacing of obstructions and the spatio-temporal pattern of low-intensity dredging, should be tested in the future for optimal outcome.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHORS' CONTRIBUTIONS

C.T. conceived the ideas and designed the methodologies; C.T., J.Š., A.T., R.G., N.G.-S., M.P., T.V., Z.B. and A.K. participated in data collection; C.T. analysed the data and all authors contributed critically to the writing of the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.cvdncjt52 (Tölgyesi et al., 2021).

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