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Mowing and traditional grazing as a conservation strategy: Fine-spatial scale impacts on the invasion of false indigo bush (*Amorpha fruticosa* L.) in marsh meadows

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Abstract

This study examined the effects of conservation management strategies, including traditional grazing, on marsh vegetation invaded by false indigo bush (*Amorpha fruticosa* L.). Fine-scale methods were employed to analyze vegetation in stands subjected to combined treatments (mowing and grazing) as well as in untreated invaded stands. Vegetation composition and diversity were evaluated using four key metrics: compositional diversity (CD), local distinctiveness (LD), association (AS), and realized species combinations (NRC). Results revealed that the combined treatment led to significantly increased CD (5.366 ± 0.394) and LD (6.41 ± 0.668), despite the presence of the invasive species. Conversely, untreated invaded vegetation exhibited lower CD (3.756 ± 0.755) and LD (4.079 ± 0.93). Additionally, AS and NRC values were higher in treated stands, although the differences were not statistically significant. Notably, the characteristic areas of all functions did not differ significantly between treated and untreated stands. These findings suggest that combining management strategies, such as mowing and traditional grazing, effectively limits *A. fruticosa* invasion and supports marsh ecosystem diversity by promoting the coexistence of native species. Continuous management, particularly grazing, is crucial, as cessation of these practices may lead to rapid reinvasion by the invasive species and a subsequent loss of native biodiversity. Overall, this study highlights the importance of proactive management strategies in combating invasive species and conserving marshland biodiversity.

KEYWORDS

Amorpha fruticosa, fine scale, information theory, land management, plant invasion

1 | INTRODUCTION

Invasive species exert substantial pressure on natural and seminatural habitats and native species. Indeed, their negative ecological impacts primarily affect native species, communities, and ecosystems (Vilà et al., 2024). The most common and severe issues they cause in natural communities include reduced biodiversity, altered interactions and functions, and increased ecosystem vulnerability of other stressors (Vilà et al., 2024; Vilà &

Hulme, 2017). Therefore, comprehensive studies and the development and evaluation of conservation measures are essential to manage invasive species and prevent their spread (Csiszár & Korda, 2015).

The application of fine-scale methods in ecology provides a more detailed understanding of the structure and functions of biological systems. Fine-scale studies of invasive plants can reveal how they alter vegetation composition, spatial arrangement, and interaction patterns (Bakacsy & Szepesi, 2024; Kun et al., 2014; Szentes et al., 2012). Additionally, these studies help assess the effectiveness of conservation treatments against invasion, allowing for more efficient planning and implementation. The spatial patterning methodology and function family developed by Juhász-Nagy Pál (hereafter referred to as the JNP methodology and function family) are applied to examine vegetation communities at smaller spatial scales, that is, in square decimeters or square centimeters (microquadrats), compared with traditional phytosociological surveys (Bartha, Campetella, et al., 2011). Standard JNP methodology sampling procedures employ 52- or 26-m-long circular transects (trainsects) (Bartha, 2008; Bartha, Campetella, et al., 2011; Palmer & van der Maarel, 1995). A transect consists of a series of 5 × 5 cm quadrats, with each quadrat touching the next (Bartha et al., 2004; Palmer & van der Maarel, 1995; Virágh et al., 2006). This arrangement allows placement within smaller vegetation units and facilitates computerized data analysis (Bartha, 2008; Bartha & Kertész, 1998; Palmer & van der Maarel, 1995). Considering spatial scale's importance, JNP function calculations involve spatial series analysis to cover the full spectrum of spatial interactions (Bartha & Kertész, 1998; Horváth, 1998; Virágh et al., 2008). The method is suitable for detecting the internal complexity and organization of communities (Bartha, 2008). The relationship between vegetation diversity and functions can be measured more accurately if the chosen diversity measure reflects not only the number and relative abundance of components but also the community's pattern, that is, its internal structure (Csillag et al., 2001). The method also shows greater sensitivity to spatial and temporal transitions in vegetation and changes in organizational states (Bakacsy & Szepesi, 2024; Bartha, 2008), important indicators during invasion processes, as invasive species' effects on biodiversity initially manifest on small spatial scales (Powell et al., 2011, 2013).

Invasive alien trees and shrubs pose substantial problems, as they can alter vegetation, landscape structure, soil, and light conditions (Bartha, 2020). For example, false indigo bush (*Amorpha fruticosa* L.), a major invasive woody plant species in the European Union and Hungary (Bartha, 2020; Grabić et al., 2022) belonging to the Fabaceae family, is native to southern and southeastern North America but was introduced to Europe as an ornamental plant in the early 18th century (Szigetvári & Tóth, 2004, 2012). The species was introduced to Hungary before 1907 (Priszter, 1997) and brought to the Tisza River floodplain in the late 19th century to stabilize riverbanks against erosion (Simonkai, 1893). However, frequent flooding and major land use changes over the past 40 years (e.g., abandonment of floodplain farming, reduced grazing, and inadequate forest management) have accelerated the rapid growth of false indigo bush populations (Szigetvári & Tóth, 2012). Its invasion disrupts ecosystem functioning and plant diversity by altering carbon and nitrogen cycles (through N_2 fixation) (Boscutti et al., 2020; Pellegrini et al., 2021) and releasing allelopathic compounds (Csiszár, 2009; Krstin et al., 2021). These traits negatively impact agricultural land, reducing the growth and yield of valuable forage and crops (Bakacsy et al., 2024; Csiszár, 2009; Krstin et al., 2021). From a conservation perspective, it poses a particular threat to scrublands, native wetlands, floodplain vegetation, and grasslands. Its rapid spread forms dense, monodominant stands, challenging floodplain afforestation, arable, and grassland management efforts while complicating flood protection (Szigetvári & Tóth, 2004, 2012). Appropriate management practices can prevent the formation of dense false indigo bush stands in marshes and floodplains, creating more suitable ecological conditions for native communities as well as favorable conditions for flood wave recession. Several studies suggest that cattle grazing could effectively suppress *A. fruticosa* populations (Demeter et al., 2021). In the long term, grazing combined with other pastoral activities could more effectively reduce this species' population (Sallainé Kapocsi & Danyik, 2015).

Despite the conservation challenges caused by *A. fruticose*, the fine-scale changes in invaded vegetation under combined management treatments are not well understood. Therefore, we compared false indigo bush-invaded stands with those treated using a combined method (mowing and grazing), employing fine-scale methods in a wetland setting. Although many studies have documented the positive effects of conservation treatments on invaded vegetation, the fine-scale effects on vegetation structure remain unknown. We hypothesized that the combined treatment would positively influence the structure of invasion associations by sufficiently suppressing the invasive species, thereby increasing the complexity of invaded communities. We believe that this research provides a solid foundation for understanding the ecological consequences of false indigo bush invasion and the effectiveness of conservation treatments in wetland associations.

2 | MATERIALS AND METHODS

2.1 | Description of the study area

Our research was conducted in the Mártély Landscape Protection Area (Figure 1a), located on the left bank of the River Tisza within the floodplain, part of the Kiskunság National Park. The area was designated a protected area in 1971 and has been part of the international Ramsar Convention since 1979. The hydrology of the River Tisza strongly influences the region's flora, fauna, and land use. Two oxbow lakes, Körtvélyesi and the Mártélyi (Ányási), formed by the cutoffs of the river's bends, are present in the area (Kis, 2009) (Figure 1b).

The landscape's key habitats include oxbow lakes, floodplain wet meadows, and natural floodplain forests (Tóth, 1996). Characteristic marsh associations, such as *Carici vulpinae – Alopecuretum pratensis* and *Agrostio – Phalaridetum*, include species such as *Agrostis stolonifera* L., *Phalaris arundinaceae* L., *Alopecurus pratensis* L., *Ranunculus acris* L., and *Symphytum officinale* L. (Bölöni, 2011; Karancsi et al., 2017). Dominant vegetation consists of contiguous floodplain forests and plantation forests, featuring species such as *Salix alba* L., *Populus alba* L., *Populus* × *canescens*, *Populus* × *euramericana*, *Quercus robur* L., and *Populus nigra* var. *Italica*, alongside original constituent species (Karancsi et al., 2017). The characteristic flora of the oxbow lakes includes *Trapa natans* L., *Salvinia natans* (L.) All., *Hydrocharis morsus-ranae* L., *Wolffia arrhiza* (L.) Horkel ex Wimm, and *Potamogeton* spp. (Tóth, 1996).

Fine-scale assessment of the impact of false indigo bush invasion and its management was conducted in the Barci-rét marshland (Figure 1c). Until the turn of the millennium (1989–2000), the marshland was largely untouched, with only sporadic use. The Barci-rét (71.91 ha) was previously used for mowing and grazing by agricultural cooperatives. From 2002 onward, as a part of a KEOP project by the Kiskunság National Park Directorate, efforts began to eradicate invasive vegetation in the floodplains and to rehabilitate areas including the marshland under study, covered by false indigo bush. From the late 2000s onward, the area was leased to tenants, and from 2014 onward, the entire area was leased with the obligation to remove woody invasive species and convert the land into grassland. The Barci-rét is grazed by around 18–25 Hungarian Simmental cattle annually, with a grazing pressure of approximately 0.34–0.36 animals per hectare in the study area (Albert, 2023). Hungarian Simmental cattle are valued in Hungary for their dual-purpose use (i.e., high milk yield and quality beef) and are favored among farmers for their adaptability and productivity. On average, an adult Hungarian Simmental consumes around 2%–3% of its body weight in dry matter daily (considering maize silage and grass hay), which is 12–18 kg for a 600 kg animal (Holló et al., 2012). Rotational grazing units are changed every 2–3 weeks to simulate traditional pastoral grazing. Higher-quality areas are grazed by calves following mowing, whereas lower-quality areas undergo postgrazing cleaning and shredding. Heavily wooded or false indigo bush-covered areas are cleared gradually in small sections each year, with

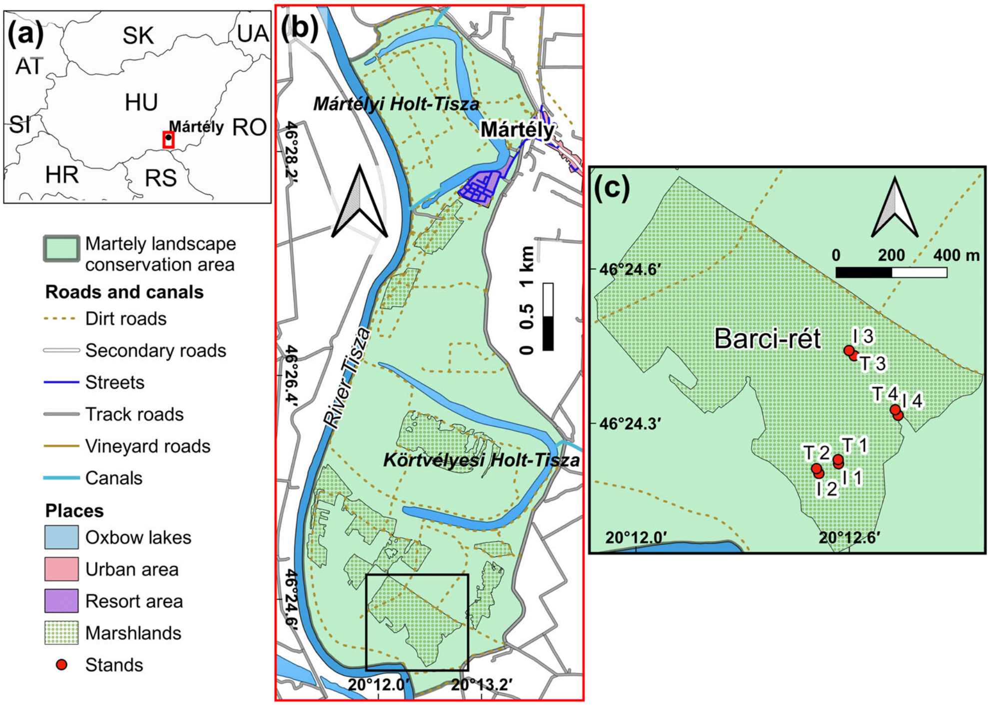

FIGURE 1 Location of the study area in Central Europe. AT, Austria; HR, Croatia; HU, Hungary; RO, Romania; RS, Serbia; SI, Slovenia; SK, Slovakia; UA, Ukraine (a). The Mártély Landscape Protection Area (b), and the marshland within it (Barci-rét). Pairs of treated invaded and untreated invaded vegetation types were selected in Barci-rét (c). T, invaded with combined treatment (mowed and grazed) vegetation type; I, Invaded and untreated vegetation type.

the planning influenced by annual flooding. The National Park designates certain areas, primarily sedge and rush beds, as overwintering sites for hen harriers (*Circus cyaneus* L.) and short-eared owls (*Asio flammeus* Pontoppidan). These sites are primarily managed in spring if not inundated (Albert, 2023). The studied marshland mainly comprises sensitive permanent grasslands (MePAR, 2023). Maps of the study area (Figure 1b,c) and the representation of selected stands were generated using the open-source Quantum GIS software version 3.18.0 (QGIS Development Team, 2021).

2.2 | Sampling methods

The effects of combined conservation treatments on the diversity of natural vegetation impacted by false indigo bush invasion were examined at a fine scale using the JNP methodology and function family (Juhász-Nagy & Podani, 1983; Virágh et al., 2006). The investigation was conducted in July 2023. Four stands of vegetation invaded by false indigo bush were selected in the marshland (Figure 1). This included four stands treated with the combined methods (Treated, T) and four stands invaded but untreated (Invaded, I). The stands were chosen to be relatively close to each other, forming pairs with consistent background vegetation, aside from the combined treatments, to ensure similar environmental conditions (Szentes et al., 2012). We also avoided significant disturbances, such as trails and fallen trees in or near the vegetation stands (Bartha, 2008).

For sampling, one 26-m-long circular transect was placed in each stand, a method deemed suitable given the size of the vegetation units (Bartha, Zimmermann, et al., 2011). In this case, the circular transect ensured that the beginning and end of the transect were connected, fitting within a smaller vegetation unit and facilitating data processing (Bartha & Kertész, 1998; Horváth, 1998; Palmer & van der Maarel, 1995). Each transect consisted of 520 sampling units, which were 5 × 5 cm quadrats used to record the presence of rooted plant species. Species identification followed Király (2009).

2.3 | Data processing methods

To understand the fine-scale structure of stands and detect management effects on the invasion of false indigo bush in marsh meadows, we used the models and applications of Juhász-Nagy (1993) and Juhász-Nagy and Podani (1983). The JNP models use several functions to characterize entire associations. Four of these functions were applied in the present study.

Compositional diversity (CD) indicates the internal heterogeneity of the community, measured by the distribution of species combinations. It represents the set of species present in a sampling unit. The value of the CD function reflects the Shannon–Wiener diversity index, calculated from the frequency distribution of species combinations in the sample at the given quadrat size. It provides insight into species coexistence and structural diversity. Compositional diversity is spatial scale dependent, typically forming a curve that reaches a maximum value as spatial scale increases. These maxima indicate the sampling unit size that capture the greatest community diversity. The unit of measurement is the binary digit (bit) (Bartha, 2008; Horváth, 1998; Juhász-Nagy, 1993; Virágh et al., 2008). Compositional diversity can be calculated using the following formula (Equation 1) (Canullo & Campetella, 2005; Horváth, 1998; Juhász-Nagy, 1993).

$$\mathrm{CD_j} = m \log m - \sum_k f_{jk} \log f_{jk}, \tag{1}$$

where f is the frequency of a species combination, j denotes a given step of the spatial series, k is a given species combination, and m represents the number of plots.

Local distinctiveness (LD) measures the uncertainty of the local occurrence of species at a given spatial scale. Shannon entropy is used for the uncertainty of each species' presence, which is then aggregated for the entire community. This function reflects species differences at a given spatial scale and reaches its maximum value when most species achieve their maximum heterogeneity. Local distinctiveness represents the theoretically possible maximum value of CD, assuming species are spatially independent (associatum $[\mathrm{AS}] = 0$) (Bartha, 2008; Horváth, 1998). The value of this function is the sum of local entropies, measured in bits. Local distinctiveness can be calculated using the following formula (Equation 2) (Canullo & Campetella, 2005; Horváth, 1998):

$$\mathrm{LD}_j = sm \log m - \sum_i \left[n_{ij} \log n_{ij} + (m - n_{ij}) \log(m - n_{ij}) \right], \tag{2}$$

where i denotes a given species ($i = 1{-}s$), j represents a given step in the spatial series, m is the number of plots, n denotes species frequency, and s is the number of species.

Associatum quantifies the level of spatial dependence between species within a community. It is calculated as the difference between LD and CD (Equation 3). Associatum reflects the internal structure (orderness) of a community, highlighting constraints that prevent many theoretically possible species combinations from occurring. If there is no spatial dependence between species, LD and CD are equal; thus, AS = 0. However, when spatial dependence exists, AS takes a positive value, indicating relationships between species. The unit of measurement is bit (Bartha, 2008; Canullo & Campetella, 2005; Horváth, 1998).

$$AS_j = LD_j - CD_j, \tag{3}$$

where LD is local distinctiveness, CD is compositional diversity, and j represents a given step of the spatial series.

The number of realized species combinations (NRC) function measures the diversity of species coexistence and the structural complexity within a community. It reflects how the frequency and spatial patterns of individual species contribute to association patterns. The NRC value increases exponentially with the number of species and is dimensionless. Estimating its maximum is useful for measuring fine-scale beta diversity and assessing the relative variance of species combinations across landscape patches (Horváth, 1998; Koncz et al., 2020; Szentes et al., 2012; Virágh et al., 2008). The NRC is calculated using the following formula (Equation 4) (Horváth, 1998, 2006):

$$NRC = 2^s, \tag{4}$$

where s is the number of species.

The nature and frequency of JNP functions are scale dependent (Bartha, 2008; Juhász-Nagy, 1972, 1984). By systematically aggregating microquadrats, that is, increasing spatial scale, vegetation changes can be examined using JNP functions, such as the impact of invasion processes, at various spatial scales. As sampling units increase, characteristic curves of JNP functions emerge. At the peak (maximum) of these curves, the greatest coexistence of species is observed, indicating the community's state with high sensitivity. The size of the quadrats at which the function reaches its maximum is known as the characteristic area (CA), measured in cm^2. This concept is further detailed by Bartha (2008) and Campetella et al. (2004). Both the maximum function values and the CA provide insights into community diversity. If species are unconstrained in coexistence, they combine freely during local occurrences, achieving the function's maximum value at the smallest spatial scale. However, disturbances (e.g., mosaic formation or biological invasion) decrease the function's maximum value, shifting the CA toward larger spatial scales. Conversely, during regeneration or succession, the opposite process occurs (Bartha, 2008; Campetella et al., 2004; Juhász-Nagy, 1972, 1984).

The INFOTHEM 3.01 program was employed to calculate JNP functions (Horváth, 1998, 2006). When applying the program, only species with a frequency exceeding 2% (i.e., each species was present in at least 11 quadrats) were included from the species pool (Bakacsy & Szepesi, 2024; Horváth, 1998). This approach prevented rare species from distorting estimations and complicating interpretations of the JNP functions (Tóthmérész & Erdei, 1992). *Amorpha fruticosa* was treated as equivalent to other species and included in the modeling, as it was present in both vegetation types (T and I). To analyze stands, complete randomization was applied as a random reference, based on 5000 randomizations using the Monte Carlo method (Horváth, 1998; Manly, 2006). During this process, occurrence data for species included in the calculations were randomly scattered along transects (Bartha & Kertész, 1998; Horváth, 1998; Palmer & van der Maarel, 1995). Additionally, JNP function values in the INFOTHEM program were standardized with the number of sampling units at each spatial series step, ensuring that different sample sizes per step did not distort the results (Horváth, 1998, 2006).

2.4 | Statistical analyses

We tested for normality in the occurrence frequency values of species, JNP function values, and the CAs using the Shapiro–Wilk tests. For normally distributed data, paired t-tests (two tailed) were used to compare occurrence frequency values in 5 × 5 cm quadrats of stand pairs for the two vegetation types (T and I), as well as JNP function values and CAs. For non-normal distributed data, we used the Wilcoxon matched-pairs signed rank test. Significance levels for these tests were set at $p = 0.05$. Data are presented as means ± standard deviations. Statistical analyses and graph plotting were performed using GraphPad Prism software version 8.0.1.244 (GraphPad Software, La Jolla, California, USA).

3 | RESULTS

A fine-scale methodology was employed to investigate the impact of a combined conservation treatment on the vegetation invaded by false indigo bush in a marshland, focusing on the spatial scales at which these effects manifest.

First, we analyzed the occurrence frequency of species in the transects of vegetation types. The species generally fit into the marshland flora composition, except for invasive species. There was no significant difference ($p = 0.066$) in species numbers between the studied stand pairs. However, T stands showed greater species richness compared with I stands (2 T: 8 species; 3 T: 8 species; 4 I: 4 species; 2 I: 5 species; Table 1). Among species occurring in both vegetation types, only *A. fruticosa* exhibited a significant difference in frequency between the stand pairs, being more frequent in the untreated vegetation than in treated vegetation ($p = 0.003$; Table 1). In untreated vegetation, *A. fruticosa* was present in 132–136 microquadrats out of 520, indicating strong dominance (Table 1).

We compared stand pairs of T and I vegetation types in marshland based on four JNP functions (CD, LD, AS, and NRC) and their CAs. The results are as follows.

The maximum CD values were 5.366 ± 0.394 and 3.756 ± 0.755 bits in the T and I stands, respectively. A significant difference was found between T and I stand pairs ($p = 0.040$). However, there was no significant difference in the CAs of CD between the two vegetation types ($p = 0.875$; Figure 2).

The maximum LD values were 6.41 ± 0.668 and 4.079 ± 0.93 bits in the T and I stand pairs, respectively. Regarding LD, a significant difference was observed between the T and I stand pairs ($p = 0.014$), but no significant difference was found in the CAs of the two vegetation types ($p = 0.875$; Figure 3).

The AS values were 1.323 ± 0.507 and 0.479 ± 0.132 bits in the T and I stands, respectively. No significant difference in AS was observed between the two groups

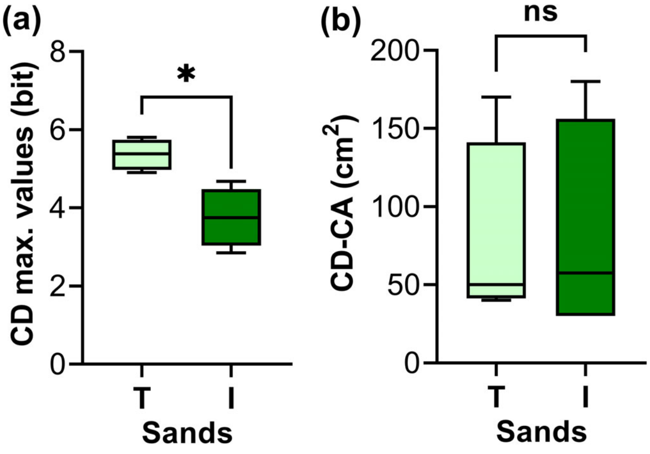

FIGURE 2 Impact of the *Amorpha fruticosa* invasion and combined nature treatment (mowing and grazing) on compositional diversity (CD) (a) and characteristic areas (CAs) (b) is examined; CA represents the spatial scale at which CD reaches its maximum value. I, invaded and untreated vegetation type; T, invaded with combined treatment (mowed and grazed) vegetation type. Significance levels: $*p < 0.05$; ns, nonsignificant. Two-tailed paired *t*-test ($n = 4$).

TABLE 1 Species and their respective numbers observed in 520 5 × 5 cm microquadrats in the transects.

		Stands							
Family	**Species**	**1 T**	**2 T**	**3 T**	**4 T**	**1 I**	**2 I**	**3 I**	**4 I**
Asteraceae	*Bidens frondosa*	0	0	0	0	12	0	0	0
Boraginaceae	*Symphytum officinale*	17	0	15	0	13	0	15	18
Brassicaceae	*Erysimum hieracifolium*	0	0	0	0	207	25	0	177
Cyperaceae	*Carex melanostachya*	89	47	22	76	0	50	44	0
Euphorbiaceae	*Euphorbia lucida*	0	0	21	20	0	0	0	0
Fabaceae	*Amorpha fruticosa*	82	67	39	67	135	136	132	132
Iridaceae	*Iris pseudacorus*	31	13	15	41	0	0	33	0
Oleaceae	*Fraxinus pennsylvanica*	0	0	0	0	0	0	0	20
Poaceae	*Agrostis stolonifera*	0	0	0	0	0	214	0	0
	Alopecurus aequalis	43	114	0	68	0	27	0	0
	Glyceria maxima	0	0	0	0	0	0	14	0
	Phalaris arundinacea	85	96	181	111	19	0	0	0
Primulaceae	*Lysimachia vulgaris*	0	19	13	0	0	0	18	0
Ranunculaceae	*Ranunculus acer*	0	18	17	0	0	0	0	0
Rosaceae	*Rubus caesius*	0	23	0	19	0	0	0	0
Urticaceae	*Urtica dioica*	0	0	0	0	11	0	0	0
	Species number	6	8	8	7	6	5	6	4

Note: One to four stand pairs. Species present in <2% of the microquadrats in each transect are not included in the table.
Abbreviations: I, invaded and untreated vegetation type; T, invaded with combined treatment (mowed and grazed) vegetation type.

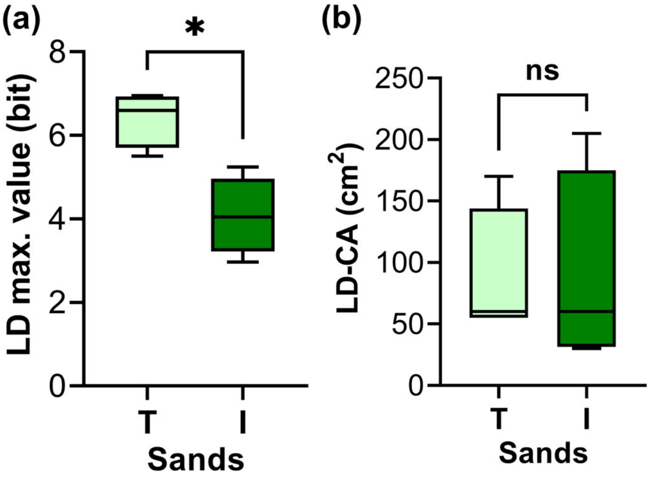

FIGURE 3 Impact of *Amorpha fruticosa* invasion and combined treatment (mowing and grazing) on local distinctiveness (LD) (a) and characteristic areas (CAs) (b); CA represents the spatial scale at which LD reaches its maximum value. I, invaded and untreated vegetation type; T, invaded with combined treatment (mowed and grazed) vegetation type. Significance levels: $*p < 0.05$; ns, nonsignificant. Two-tailed paired *t*-test ($n = 4$).

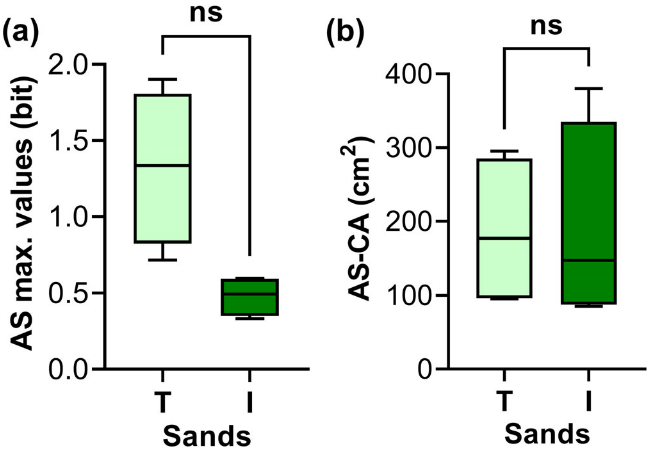

FIGURE 4 Impact of *Amorpha fruticosa* invasion and combined treatment (mowing and grazing) on association (AS) (a) and characteristic areas (CAs) (b); CA represents the spatial scale at which AS reaches its maximum value. I, invaded and untreated vegetation type; T, invaded with combined treatment (mowed and grazed) vegetation type. Significance levels: ns, nonsignificant. Two-tailed paired *t*-test ($n = 4$).

($p = 0.052$) or in the CAs of the stand pairs ($p = 0.976$; Figure 4).

The maximum NRC values were 0.127 ± 0.035 and 0.055 ± 0.025 bits in the T and I stands, respectively, with no significant difference between the two vegetation types ($p = 0.072$). Similarly, there was no significant difference in the CAs of the stand pairs ($p = 0.666$; Figure 5).

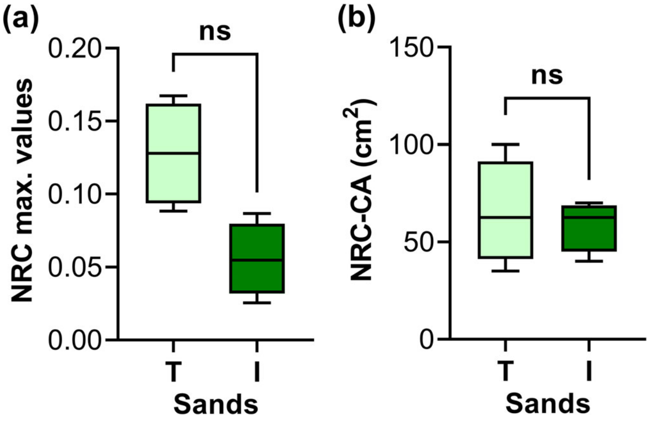

FIGURE 5 Impact of *Amorpha fruticosa* invasion and combined treatment (mowing and grazing) on the number of realized species combinations (NRC) (a) and characteristic areas (CAs) (b); CA represents the spatial scale at which the NRC reaches its maximum value. I, invaded and untreated vegetation type; T, invaded with combined treatment (mowed and grazed) vegetation type. Significance levels: ns, nonsignificant. Two-tailed paired *t*-test ($n = 4$).

4 | DISCUSSION

The objective of this study was to investigate the coexistence diversity of treated and untreated invaded marshland vegetation at fine spatial scales. This analysis aimed to provide insight into the relationship between grazing and invasion and their effects on the local ecosystem, ultimately informing the development of more effective management strategies to control *A. fruticosa* invasion.

Results indicated that the abundance of invasive species was lower in stands subjected to combined treatment (mowing and grazing) compared with untreated stands. This finding aligns with previous studies showing that untreated areas are characterized by the presence of false indigo bush (Demeter et al., 2021; Fehérváry & Kiss, 2021; Kiss & Fehérváry, 2023). The occurrence frequency of species within transects revealed that the invaded but treated vegetation exhibited greater species richness compared with untreated invaded stands (Table 1). Similar findings were reported by Demeter et al. (2021), who investigated the diversity of differently grazed riparian planted forests. In grazed forests, false indigo bush covered less area, allowing for a higher representation of native species. Conversely, in ungrazed riparian forests, as observed for the I vegetation type in the present study false indigo abundance was high, resulting in fewer and less frequent native species. This effect may be due to false indigo bush shading native herbaceous species as it grows over them, coupled with its potential negative allelopathic effects (Bakacsy et al., 2024; Grabić et al., 2022; Xiao et al., 2016).

The observed differences in species occurrence were mirrored in the applied functions, indicating variations in the fine-scale organization and internal structure of the vegetation. Untreated vegetation exhibited significantly lower values of the CD and LD values compared with the treated vegetation, likely due to the dense presence of false indigo bush (Figures 2a and 3a). Despite the presence of invasive species, combined treatment allowed numerous native species to coexist, leading to higher internal structural complexity in T vegetation. This suggests that the combined treatment maintains a high diversity of species coexistence modes in invaded stands. These findings are consistent with those of Kun et al. (2014), who also demonstrated through microecological studies that the CD of marshlands densely invaded by *Solidago gigantea* Aiton is significantly reduced. However, intense mowing decreased the mass of false indigo bush, subsequently increasing marshland diversity.

Regarding the association between vegetation and the NRC, the values for treated stands tended to remain higher than those for untreated stands, although not significantly (Figures 4a and 5a). This may be attributed to the mitigating influence of integrated treatments on invasive species' negative impacts, whereas in the absence of treatment, false indigo bush nearly completely displaces other species (Table 1).

Contrary to our initial expectations, we did not detect any significant differences in the CAs between the two vegetation types, indicating that the invaded and untreated marshland vegetation types organize at the same spatial scales (Figures 2b, 3b, 4b, and 5b). Nevertheless, several studies have indicated that invasion affects CA values by increasing competition among species (Kun et al., 2014; Szentes et al., 2012), implying more intense competition for space. Conversely, some studies document instances where, for example, vegetation invaded by *Asclepias syriaca* L. exhibited no discernible difference in CD and NRC values compared with invasion-free vegetation, yet species coexistence occurred at larger spatial scales, indicating a negative impact of invasion on biodiversity (Bakacsy, 2019). The function values of untreated invaded vegetation types clearly demonstrate a strong negative impact of the invasive species on species coexistence, even while they organize at the same spatial scales as treated T vegetation types. These findings highlight the complex, species- and community-specific nature of invasive plant species' impacts on vegetation, occurring along characteristic spatial scales. Moreover, they underscore the effectiveness of applied treatments against false indigo bush invasion at fine spatial scales.

The findings of this study suggest that grazing, when supplemented with mowing as a combined conservation treatment, is an effective method for controlling the invasion of *A. fruticosa* in marshlands. This effectiveness is evidenced by the retreat of the invasive species in treated areas, resulting in positive outcomes for invaded vegetation, such as increased coexistence diversity and internal complexity. These results align with those of Demeter et al. (2021), who highlighted the multifaceted benefits of grazing in floodplains, including the reduced frequency and cover of invasive false indigo bush, leading to greater native species diversity. Nevertheless, Sallainé Kapocsi and Danyik (2015), along with Kiss et al. (2019), emphasize the necessity of continuous treatment. Grazing combined with other management activities, such as mowing, can enhance the efficiency of invasive species control; however, grazing is pivotal. Mechanical removal of invasive species alone is insufficient; without grazing, the invasive species rapidly reestablishes itself (Sallainé Kapocsi & Danyik, 2015). Within 2–3 years after grazing ceases, dense shrubs form, which are typically avoided by grazed animals (Varga et al., 2020). Therefore, it is recommended that grazing should precede mechanical interventions (Schindler et al., 2016). Additionally, long-term financial support is crucial for sustaining effective and environmentally friendly management methods, such as grazing.

5 | CONCLUSION

This study provides valuable insights into the effects of management practices on the structure and complexity of riparian vegetation invaded by *A. fruticosa* in the Mártély Landscape Protection Area. By analyzing fine-scale vegetation patterns, we identified significant differences in species composition and coexistence among two vegetation types subjected to varying levels of invasion and management interventions. Our findings underscore the importance of comprehensive management strategies in combating plant invasions and sustaining riparian biodiversity. Understanding how invasive species alter community dynamics and responding with targeted management actions can help preserve the ecological integrity of riparian ecosystems. These findings have practical implications for conservation practitioners and land managers involved in riparian habitat restoration and invasive species control efforts. Invasive species pose a major threat to riparian ecosystems, but proactive management strategies, such as targeted grazing, can help to mitigate their negative impacts and promote native species diversity. By implementing research-based management approaches, we can work toward restoring and conserving the biodiversity of riparian habitats, ensuring their resilience in the face of environmental change.

AUTHOR CONTRIBUTIONS

NKN: investigation, ata curation, ormal analysis, iscussion, revision, writing—original draft preparation. LB: conceptualization, methodology, experimental design, nvestigation, reviewing and editing, supervision. The final manuscript has been read and approved by all authors.

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CONFLICT OF INTEREST STATEMENT

The authors have no competing interests or conflict of interest.

DATA AVAILABILITY STATEMENT

Data will be made available on request.

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