

RESEARCH ARTICLE

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In the Footsteps of Sheep Herds: The Neonative *Xeranthemum cylindraceum* Has No Impact but Indicates Ruderalisation of Overgrazed Pastures in the New Range

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ABSTRACT

Aim: Intracontinental range expansion of organisms is expected to be more and more frequent due to anthropogenic climate and land-use changes, but its impact on ecosystems and consequences to nature conservation or economy are not well understood. Our study focuses on a range-expanding neonative annual plant, *Xeranthemum cylindraceum* (Asteraceae, tribe Cardueae), which has become common in pastures. We aimed to assess the potential impact of this species on recipient grassland communities in the new range and to compare its performance between the native and neonative range.

Location: Grasslands in Romania (neonative range) and Bulgaria (native range).

Methods: We surveyed plots from very low to very high abundances of the target species in grassland stands. To compare the vegetation between cover categories of *X. cylindraceum* and between the two study regions, we calculated species richness, Shannon diversity and community weighted mean of Ellenberg and disturbance indicator values. We also compared the vegetation composition based on species life span, habitat preference and guild.

Results: Our results show that species richness and diversity do not decrease with the increasing abundance of *X. cylindraceum* in recipient grasslands. However, the cover of specialist and long-lived species was lower, while that of ruderal and short-lived species was higher in vegetation patches with medium to high *X. cylindraceum* abundance. In the neonative range, this pattern overlapped with an increased disturbance severity and soil nitrogen content indicated by community composition, which bears clear signs of grazing disturbance forcefully transforming plant composition and causing ruderalisation.

Conclusions: We conclude that the range-expanding *X. cylindraceum* does not raise conservation problems, since it is not impacting recipient grassland communities in its neonative range. However, it appears to benefit from grazing disturbance. As a toxic, unpalatable species, it decreases the economic value of intensively used grasslands, pointing out the need for decreasing stocking rates in intensively used pastures.

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1 | Introduction

Human-mediated climate change accelerated the redistribution of species worldwide, challenging society with different impacts on ecosystem health and human well-being (Pech et al. 2017). Latitudinal and elevational range shifts of organisms are well documented, and estimations about the velocity of expansions are also available (Parmesan 2006; Chen et al. 2011; Gottfried et al. 2012; Lenoir and Svenning 2015; Pinsky et al. 2020).

Defining the biogeographical status of species, when multiple anthropogenic factors influence their distribution, has proved to be challenging (Lemoine and Svenning 2022). Essl et al. (2019) proposed a new concept to separate intracontinental range-expanding species, which benefit from indirect anthropogenic impacts on the environment, from the group of non-natives. Based on this concept, ‘neonative’ species track human-induced environmental changes, such as land-use change, climate change, eutrophication, etc., without intentional or unintentional translocation of propagules and use of infrastructure. Species respond to environmental changes at different velocities of range shift (Lenoir et al. 2020; Essl et al. 2024). Studies reported a very slow rate of plant movement in comparison with other taxonomic groups (Corlett and Westcott 2013; Lenoir et al. 2020; Bradley et al. 2024). Many recent examples of neonative species come from the groups of insects and mammals or from marine environments (Lenoir et al. 2020; Stefanović et al. 2024; La Porta and Hardersen 2024; Cillari et al. 2024). The correct delimitation of a species’ native range is another challenging task (Keith et al. 2019), and the detection of a species’ occurrence outside its range margin requires special attention, for example, targeted data collection.

Impacts of range-shifting or range-expanding species on newly inhabited ecosystems are less well understood. Studies report different magnitudes and directions of the impact depending on the taxonomical affiliation, functional traits or biogeographical status (i.e., native or non-native) of the range-expanding species, and the habitat type of recipient communities (Sorte et al. 2010; Gilman et al. 2010; Corlett and Westcott 2013). Thus, case studies addressing species traits, potential drivers of expansion and the impact of these species on the recipient ecosystems would improve future projections (Carey et al. 2012; Wallingford et al. 2020; Seebens et al. 2021).

Neonative species are considered reactive species (Essl et al. 2021), which respond to or follow environmental changes; thus, their impact on the newly colonised ecosystem is assumed to be minor. Still, there are chances that range-expanding species, or at least some of them, have ‘weedy traits’ by means of which they may exert undesirable impacts on native ecosystems, human well-being or even on the economy (Adam et al. 2022). Calculating their potential impacts on native communities is necessary in order to promote pragmatic, species-specific management actions in time, when needed, and to inform stakeholders or even policymakers (Essl et al. 2019). Until recently, there have been no attempts to evaluate the behaviour of neonative plant species in newly colonized plant communities of their neonative range.

To fill this gap, we analyzed the impact of a recently discovered neonative species on the recipient plant communities of the new range. *Xeranthemum cylindraceum* Sm., a winter-annual species belonging to the Asteraceae family (tribe Cardueae), with a Mediterranean distribution, was found to expand its range in Romania in the last century; thus, recently, it has been considered neonative in the central part of the country (Euro+Med Plant Base 2006; Ruprecht et al. 2024). In its neonative range, *X. cylindraceum* inhabits not only ruderal and degraded habitats (e.g., annual anthropogenic herbaceous vegetation, dry perennial anthropogenic herbaceous vegetation) but also semi-natural and even high nature value grasslands of community interest (e.g., continental dry grassland, semi-dry perennial calcareous grassland Roleček et al. 2021; Ruprecht et al. 2024 table A.12). Often, it appears in high abundance by establishing from seeds and forming dense patches, especially in grazing lands (Ruprecht et al. 2024). Its affiliation to pastures was found to be attributed to its toxicity to herbivores, cyanogenic glycosides in stems as well as the high dispersal ability in animal fur of its achenes bearing appendages (Schwind et al. 1990; Ruprecht et al. 2024).

Another interesting and not well-explored question regarding neonative species is whether their behaviour in plant communities differ between the native and neonative range. To this end, we compare grassland communities inhabited by *X. cylindraceum* between the native range in Bulgaria with those in the neonative range in Romania. Further, we assess the mass effect of *X. cylindraceum* by analysing differences in community composition and diversity through an abundance gradient from very low to very high abundances of the target species. In order to find out underlying mechanisms, we explore environmental conditions and disturbance history in studied plant communities using the plant indication method.

We formulated two alternative but non-exclusive hypotheses: (1) Since it belongs to the Cardueae tribe of the Asteraceae family with an increased representation of noxious weeds (Susanna and Garcia-Jacas 2009), we suspected *X. cylindraceum* to have a negative impact on the recipient grassland communities of the neonative range, causing diversity loss and decreasing conservation value; (2) *X. cylindraceum* is a reactive species, thus its presence and abundance in grasslands of the neonative range are strongly linked to the frequency and intensity of disturbances affecting the recipient plant communities, in this particular case, the impact by grazing.

2 | Methods

2.1 | Study Area

We studied grassland plant communities inhabited by *X. cylindraceum* in two ranges: in the central part of Romania (Transylvanian Plateau), where the species is considered neonative (Ruprecht et al. 2024), and in Bulgaria (Northern Thrace region), where it is native (Assyov and Petrova 2012, Figure S1 in Appendix S1). The surveyed area in Romania has a temperate continental climate. The mean total annual precipitation falls between 520 and 650 mm, and the mean annual temperature ranges between 8.4°C and 9.7°C

(Kun et al. 2004; Ruprecht et al. 2009). Surveys were made in the Transylvanian Basin, which is a hilly region with elevations between 270 and 600 m a.s.l. Sampled semi-dry grasslands belonged to class *Festuco-Brometea* Br.-Bl. et Tx. ex Soó 1947 (Mucina et al. 2016), which are meadow steppes, where the dominant species were *Festuca stricta* subsp. *sulcata*, with, for example, *Agrimonia eupatoria*, *Achillea millefolium* agg., *Plantago lanceolata*, *Medicago lupulina* and *Elytrigia repens*, frequent species. Sampled sites were grazed mainly by sheep, and more rarely by cattle, with various intensities from extensive to intensive.

The studied area in Bulgaria (Thracian region) has a transitional climate between temperate continental and Mediterranean climate with hot and dry summers (Beck et al. 2018). The mean total annual precipitation of the region falls between 483 and 523 mm and the mean annual temperature ranges between 11.9°C and 12°C (Velev 2010). Surveyed sites are in a low-land area with elevations between 100 and 270 m a.s.l. The most frequent perennial grass species in the studied sites were *Bothriochloa ischaemum*, with a high frequency of *Eryngium campestre*, *Sanguisorba minor*, *Daucus carota* and annual forbs, such as *Trifolium echinatum*, *T. angustifolium*, *T. striatum*, *Sherardia arvensis*, etc. (the species composition of the two study areas is presented in Appendix S3). The studied grassland communities belong to class *Festuco-Brometea*. Four of the sampled sites were extensively grazed by sheep, and five were abandoned from grazing.

2.2 | Study Design and Sampling

In both study regions, we selected dry and semi-dry grassland sites, where we designated one plot series per site: plots with four different abundance (% cover) ranges of the target species: < 25%, 25%–49%, 50%–75% and > 75%. The size of the surveyed plots was 2 m × 2 m, in which we estimated the cover of vascular plant species and the cover of litter using a percentage scale (Dengler and Dembicz 2023). We enabled overlaps in species abundance values; thus, the total cover of the vegetation within a plot could reach values higher than 100%. Sixteen grassland sites were sampled in Romania between 27 June and 25 July 2021 and 9 sites in Bulgaria between 17 and 20 June 2021. In total, we obtained 85 vegetation samples from 25 sites. In Bulgaria, *X. cylindraceum* did not reach higher abundances than 75%; thus, only three plots were sampled at each site, while in Romania, 10 out of the 16 sites were represented by four cover categories. We used the Euro+Med PlantBase (2006) for taxonomical harmonisation.

2.3 | Diversity and Species Composition

We examined the diversity of the vegetation by computing the species richness and the Shannon diversity index of the plots. Further, to assess the vegetation composition, we extracted species habitat preference based on Sârbru et al. (2013). We used three categories for our data analysis: grassland specialist (species occurring exclusively in natural or semi-natural grasslands, for example, in the class *Festuco-Brometea*), generalists (species occurring in natural or semi-natural grasslands and ruderal habitats as well) and ruderal species (species of ruderal habitats).

In addition, we grouped species based on their life span (Sârbru et al. 2013), that is, long-lived species (perennials) and short-lived species (annuals and biennials).

2.4 | Indicator Values

We extracted plant attributes from different databases in order to compare environmental conditions by the indicator values of species, and the disturbance regime also by the indicator values of species. We extracted indicator values from the recently developed comprehensive ecological indicator value system (EIVE 1.0, Dengler et al. 2023), such as the species niche positions of four niche dimensions: soil moisture (M), soil nitrogen (N), light (L) and temperature (T). In order to characterise the disturbance regime in a plot with special emphasis on grazing as the main disturbance type in both study regions, we used the disturbance indicator values developed for European plant species (Midolo et al. 2023): disturbance severity (the magnitude of disturbance), disturbance frequency and soil disturbance. In addition, we used litter cover estimated in our vegetation plots to have a direct assessment about the intensity of grazing in the study sites.

2.5 | Statistical Analysis

In the case of habitat preference and life span, we calculated the sum of species cover values for each species group (grassland specialist, generalist and ruderal species; short-lived and long-lived species) within each plot. We calculated community-weighted mean values (CWM) of ecological indicator values for M, N, L and T and of disturbance indicators (disturbance severity, disturbance frequency and soil disturbance) for each plot. We initially log-transformed species abundance data for CWM calculation in order to treat very large differences between the abundance of dominant and subordinate species (de Bello et al. 2021). We excluded the tree and shrub species in the case of indicator values and plant functional traits. Throughout all our analyses, the abundance of the target species was excluded (Thomsen et al. 2016), thus our results refer strictly to the plant community in which *X. cylindraceum* was established.

We built general and generalized linear mixed effect models to assess the differences in the abovementioned indices between cover categories of *X. cylindraceum* and between the two study regions. Indices computed on plot level were used as dependent variables, and the cover categories of the target species as explanatory variables (a four-level factorial variable) in interaction with the range, that is, native (Bulgaria) or nonnative range (Romania). Study sites were introduced in the mixed effect models as grouping factors. In the case of M indicator value, generalist, ruderal and short-lived species, we performed logarithmic transformation of the dependent variable before the analyses. Square root transformation was applied to litter cover values. Models were built using the ‘lmerTest’ package in R statistical environment (Kuznetsova et al. 2017). We tested the model assumptions using the ‘DHARMA’ package (Hartig 2022). We assessed the importance of the explanatory variables using *Anova* from the ‘car’ package (Fox and Weisberg 2019). For pairwise comparison, we used the ‘emmeans’ package to assess the statistical differences

between plots of different cover categories of the target species (Lenth 2023). Plot-level indices were calculated using the ‘FD’ and ‘vegan’ packages (Laliberté and Legendre 2010; Laliberté et al. 2014; Oksanen et al. 2022). Frequency table with species percentages on range and site scale was made with the “goevig” package (von Lampe and Schellenberg 2024). For visualisation, we used ‘ggplot2’ and ‘ggpubr’ (Wickham 2016; Kassambara 2023). For fast and trustable data organisation, we used the “dplyr” package (Wickham et al. 2023). All analyses were computed in R 4.3.1 (R Core Team 2023).

3 | Results

3.1 | Diversity

Number of plant species per grassland plot was similar between the neonative and native range of the target species ($\chi^2 = 0.11$, $p = 0.740$). Species richness of grasslands in the native range did not differ between cover categories of *X. cylindraceum*, and the same was found for grasslands in the neonative range ($\chi^2 = 2.51$, $p = 0.473$, Figure 1a, results of pairwise comparisons between cover categories are presented in Appendix S1

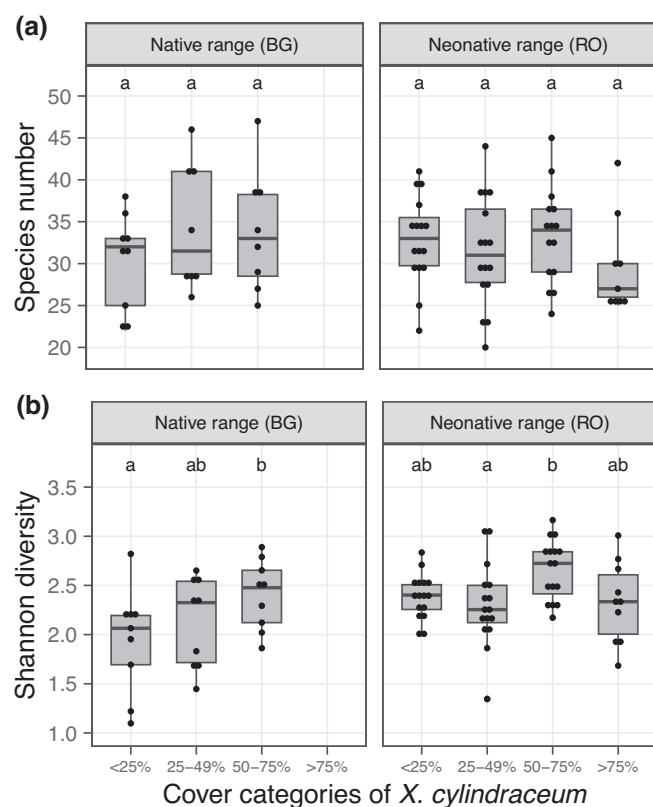


FIGURE 1 | Species number (a) and Shannon diversity (b) of grassland plots in four cover categories of *Xeranthemum cylindraceum*. Left subplots present results of the species' native range (Bulgaria), right subplots present results of the species' neonative range (Romania). Boxes represent values between the first and third quartiles, and whiskers values outside the interquartile range, which are not outliers. Horizontal line in the box shows the median. Black dots show original values of plots. Letters above boxes within each subplot show the results of pairwise comparisons of estimated marginal means ('emmeans') between cover categories of *X. cylindraceum* at $p < 0.05$.

Table 1). In turn, there were differences in the Shannon-diversity between cover categories of the target species. In the native range (Bulgaria), Shannon diversity was the lowest in plots of the first cover category (< 25% cover of the target species), intermediate in the second (between 25% and 49% cover of the target species) and highest in the third (between 50% and 75% cover of the target species). In the neonative range (Romania), plot-level diversity was the highest in the 50%–75% cover category (the same as in the native range) and lowest in plots of 25%–49% cover of *X. cylindraceum* (Figure 1b). In addition, we found differences between the ranges, namely that the native range had lower diversity values than the neonative range (ANOVA results of the range factor: $\chi^2 = 6.58$, $p = 0.010$, of cover category factor: $\chi^2 = 18.34$, $p < 0.001$, for the results of pair-wise comparisons, see Figure 1b and Appendix S1 Table 1).

3.2 | Species Composition

We also examined the species composition of the plots, firstly by the total cover of each habitat preference group (grassland specialist, generalist and ruderal). In the native range (Bulgaria), differences were only found for the grassland specialist group, their total cover being lower in grassland plots of intermediate *X. cylindraceum* abundance (between 26% and 75% cover values) compared to the lower cover category (< 25% cover of the target species, Figure 2a), whereas the cover of generalist and ruderal species was constant through the cover categories. In grasslands of the neonative range (Romania), the total cover of grassland specialist species was lower, and that of ruderal species was higher in plots with a higher cover (> 50% cover) of the target species (Figure 2a). The total cover of generalist species did not differ between cover categories of the target species in grasslands of the native and neonative range (Figure 2a), but the between-range analysis revealed lower cover values of specialist and generalist species in the native, compared to the neonative range (Table 1).

The second examination of the species composition was based on species' life span, which revealed a decreasing pattern of long-lived species through cover categories in both ranges (Figure 2b). In the native range, the cover of short-lived species did not differ between cover categories, whereas in the neonative range, the cover of short-lived species was higher in plots with > 50% cover of *X. cylindraceum* (Figure 2b, Appendix S1 Table 1). Based on the between-range comparison, long-lived species had higher, whereas short-lived species had lower cover values in the neonative range (Table 1).

3.3 | Indicator Values

Ecological indicator values of plant species occurring in the analysed plant communities revealed differences in environmental conditions between sampled grasslands of the two study regions. We found higher values for light and temperature and lower values for soil nitrogen and moisture in the grassland communities of the native range compared to those in the neonative range (Table 1, Figure 3). No difference between cover categories of the target species could be detected in any of the environmental parameters in Bulgarian grassland sites (native range, Figure 3). In the case of

TABLE 1 | Effect of *Xeranthemum cylindraceum* cover (four cover categories) and range (native vs. neonative) on the species composition of grassland plots through certain species groups (grassland specialist, generalist, ruderal species; long- or short-lived species).

Response	χ^2	df	p	Response	χ^2	df	p	Response	χ^2	df	p	
Grassland specialists												
Cover category	29.834	3	0***	M.EIVE	Cover category	12.297	3	0.006**	Disturbance severity			
Range	5.214	1	0.022*		Range	32.64	1	0***	Cover category	22.079	3	0***
Interaction	2.905	2	0.234		Interaction	4.626	2	0.099	Range	12.072	1	0.001***
Generalist species												
Cover category	1.329	3	0.722	N.EIVE	Cover category	40.248	3	0***	Disturbance frequency			
Range	8.66	1	0.003**		Range	6.133	1	0.013*	Cover category	1.815	3	0.612
Interaction	4.539	2	0.103		Interaction	7.792	2	0.02*	Range	2.242	1	0.134
Ruderal species												
Cover category	22.194	3	0***	L.EIVE	Cover category	2.917	3	0.405	Soil disturbance			
Range	1.391	1	0.238		Range	80.636	1	0***	Cover category	22.191	3	0***
Interaction	10.092	2	0.006**		Interaction	3.951	2	0.139	Range	7.685	1	0.006**
Short-lived species												
Cover category	12.091	3	0.007**	T. EIVE	Cover category	2.584	3	0.46	Interaction			
Range	24.109	1	0***		Range	123.744	1	0***	Cover category	2.378	2	0.305
Interaction	13.972	2	0.001***		Interaction	2.731	2	0.255	Range			
Long-lived species												
Cover category	30.798	3	0***									
Range	56.945	1	0***									
Interaction	3.924	2	0.141									

Note: Differences between cover categories of *X. cylindraceum* and countries in the disturbance severity, disturbance frequency, soil disturbance, moisture (M.EIVE), nitrogen (N.EIVE), light (L.EIVE) and temperature (T.EIVE) conditions of grassland plots indicated by plant species composition. Results of ANOVA analyses (see Methods section). Asterisks indicate the significance level (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

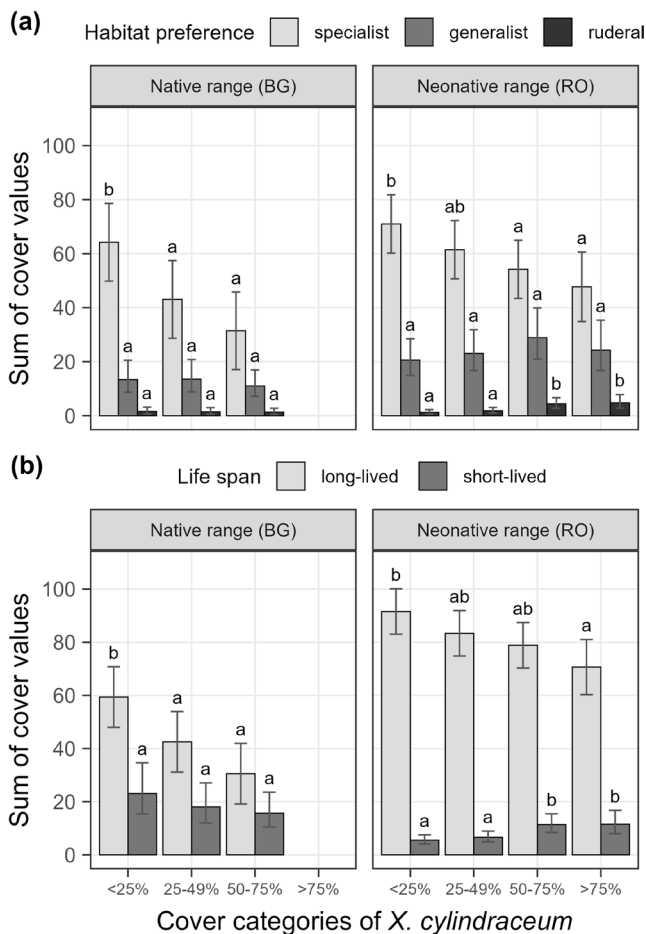


FIGURE 2 | Total cover of species classified in different groups by their habitat preference (a) and life span (b) of grassland plots in four cover categories of *Xeranthemum cylindraceum*. Left subplots present results of the species' native range (Bulgaria), right subplots present results of the species' neonative range (Romania). Bars show average total cover values of different species groups $\pm 95\%$ CI. Letters above the whiskers denote significant differences between cover categories of *X. cylindraceum* at $p < 0.05$, obtained by pair-wise comparisons of estimated marginal means ('emmeans') of each species group.

Romanian grassland sites (neonative range), plots with a higher *X. cylindraceum* abundance (above 50%) had higher soil moisture and higher nitrogen values indicated by plant community composition (Table 1, Figure 3a,b, Appendix S1 Table 1).

Disturbance severity and soil disturbance indices showed significant differences between the two countries, whereas the disturbance frequency index did not. In the native range, values of the disturbance indicators were constant through the studied cover categories (Table 1, Figure 4). In the neonative range, values of the disturbance severity and soil disturbance indices were the lowest in plots with *X. cylindraceum* having <25% cover and the highest in plots with the target species having >75% cover (Figure 4).

We found significant differences in the amount of litter between the two countries ($\chi^2 = 16.75$, $p < 0.001$), but no differences between cover categories ($\chi^2 = 5.58$, $p = 0.134$). The mean value of the estimated cover of litter was $34.7 (\pm 5.41 \text{ SE})$ in Bulgaria and $6.6 (\pm 1.79 \text{ SE})$ in Romania (see also Appendix S2).

4 | Discussion

In this study, we analysed whether the neonative annual, *X. cylindraceum*, is impacting recipient grassland communities in its neonative range, or it is just taking advantage of grazing disturbance without any direct impact on the diversity and composition of recipient grassland communities. To have a broader view, we compared the behaviour of this species in different grassland sites through a gradient of its increasing representation between the native and neonative range.

Our results revealed that species richness does not decrease with *X. cylindraceum* presence, even with greater abundance in both its native and neonative range, while Shannon diversity tends to be even higher in vegetation patches of an intermediate abundance (between 50% and 75%) of the target species in both ranges. With this pattern in mind, we can exclude a direct negative effect of *X. cylindraceum* on species richness and diversity of recipient grassland communities in its neonative range in Romania.

While studies addressing the impact of neonative species on recipient communities are very scarce, there are similar examples among invasive species. Pyšek et al. (2012) have drawn attention to the importance of life form in predicting the impact of an invasive species on resident species, communities or ecosystems, regardless of habitat type or geographical region. The absence of impact, or minor impact, on the species richness of resident communities was reported for a series of short-lived invasive species, such as *Ambrosia artemisiifolia*, *Erigeron* species and *Impatiens* species (Hejda 2012; Fried et al. 2014; Fenesi et al. 2023). Hejda and Pyšek (2006) found that the annual invasive *Impatiens glandulifera* had no impact on the diversity of recipient plant communities by comparing invaded and uninvaded plots; moreover, experimental removal of *I. glandulifera* did not result in altered species composition of the recipient community.

In the next step of our analyses, examining more thoroughly the species composition of recipient plant communities, we detected a decreased cover of grassland specialists in vegetation patches with medium to high abundance of the target species in both the native and neonative range. In the neonative range, this pattern appeared together with an increased representation of ruderal and short-lived species and a decreased representation of long-lived species, which bears clear signs of an external factor forcefully transforming plant composition and causing ruderalisation. Considering that all the studied grassland sites in the neonative range have been grazed, it seems very probable that community composition was affected by grazing disturbance and not by the even high abundance of the annual *X. cylindraceum*. Grazing is known to decrease vegetation cover by consumption, to create open soil surfaces by trampling, and to increase soil nutrients, especially N-levels through excrements (Olff and Ritchie 1998; Lezama and Paruelo 2016). Ruderal species, particularly those of short life span, may first benefit from competition-free gaps within a perennial grassland cover, as well as grassland specialists sensitively indicating growing disturbance levels by their decrease or disappearance (Hofmann and Isselstein 2004; Busch et al. 2019; Kovacsics-Vári et al. 2023). Herben et al. (2018) examined the relationship between key functional plant traits and disturbance intensity along disturbance gradients, concluding

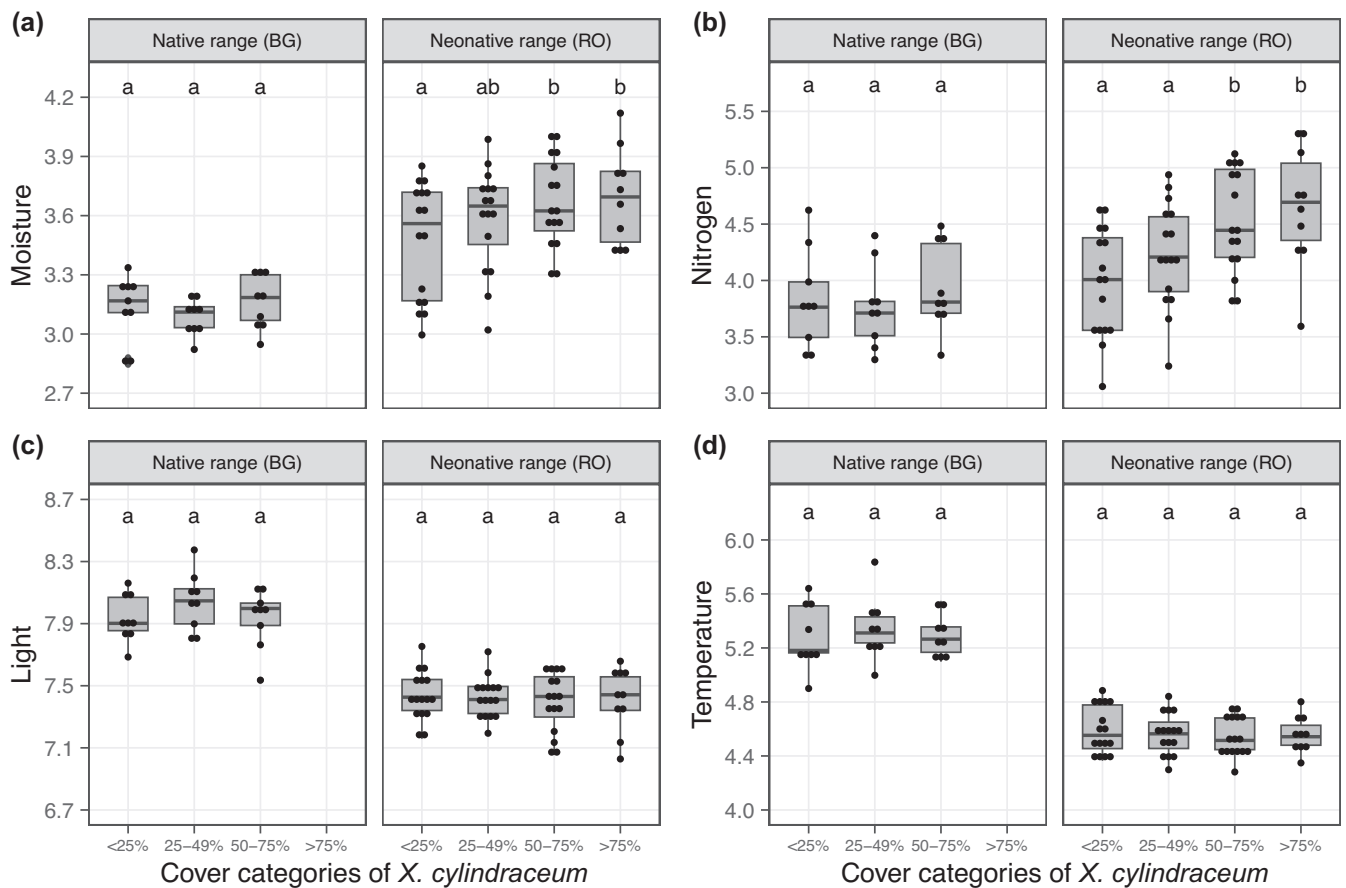


FIGURE 3 | Community-weighted means of ecological indicator values, moisture (a), nitrogen (b), light (c) and temperature (d) of grassland plots in four cover categories of *Xeranthemum cylindraceum*. Left subplots present results of the species' native range (Bulgaria), right subplots present results of the species' neonative range (Romania). Boxes represent values between the first and third quartiles, and whiskers values outside the interquartile range, which are not outliers. Horizontal line in the box shows the median. Black dots show original values of plots. Letters above boxes with in each subplot show the results of pair-wise comparisons of estimated marginal means ('emmeans') between cover categories of *X. cylindraceum* at $p < 0.05$.

that the annual life span was the single trait with the strongest relationship with the severity of disturbance. The positive response of short-lived species along with the negative response of long-lived perennials to grazing disturbance was concluded in a global synthesis by Díaz et al. (2007). Kovácsics-Vári et al. (2024) found a high abundance of ruderal species and short-lived forbs with increasing grazing intensity on sand pastures, which are very similar to our findings.

In line with the above scenario, also in the neonative range, vegetation patches with a medium to high abundance of *X. cylindraceum* were found to indicate higher disturbance severity and soil disturbance arising most probably from trampling by livestock, compared to patches of lower cover of the target species.

During the last decades, the short-lived generalist *X. cylindraceum* is one of the candidates to occupy open, disturbed, nutrient-rich patches in grasslands of its neonative range in Romania, as we found an increased abundance of this species in patches with high indicated soil nitrogen content (high CWM for nitrogen indicator values). Cyanogenic glycoside content of the shoots (Schwind et al. 1990; Ruprecht et al. 2024), which protects the plant from being consumed by grazing animals, makes *X. cylindraceum* a successful pasture weed; thus, its abundance

in grasslands is very probably linked to the intensity of grazing (Kelemen et al. 2019). Drawn by warming climates north to its native range and successful dispersal of its fruits in animal fur, this species expands its range tracking disturbances caused by intensive grazing (Ruprecht et al. 2024).

In Romania, intensive grazing is considered one of the major threats affecting grassland vegetation, which has led to the degradation of approximately 50% of the permanent grassland sites between 2000 and 2010 (Roman et al. 2019). Opposite to this, in Bulgaria, livestock farming has declined after 1990, which resulted in the abandonment of many grasslands from being grazed (Velev and Vassilev 2014). Our survey sites in Bulgaria clearly mirrored this lack of grazing or low grazing pressure since litter cover was much higher compared to the Romanian study sites. The absence of or very low disturbance pressure may explain the lack of grassland patches with a very high abundance (> 75%) of *X. cylindraceum* in Bulgaria. Further, there was no difference in the environmental and disturbance parameters between low, medium and high cover patches of the target species in the native range.

As an interesting aspect of the range expansion, *X. cylindraceum* occurs in more open (higher CWM for light), warmer (lower

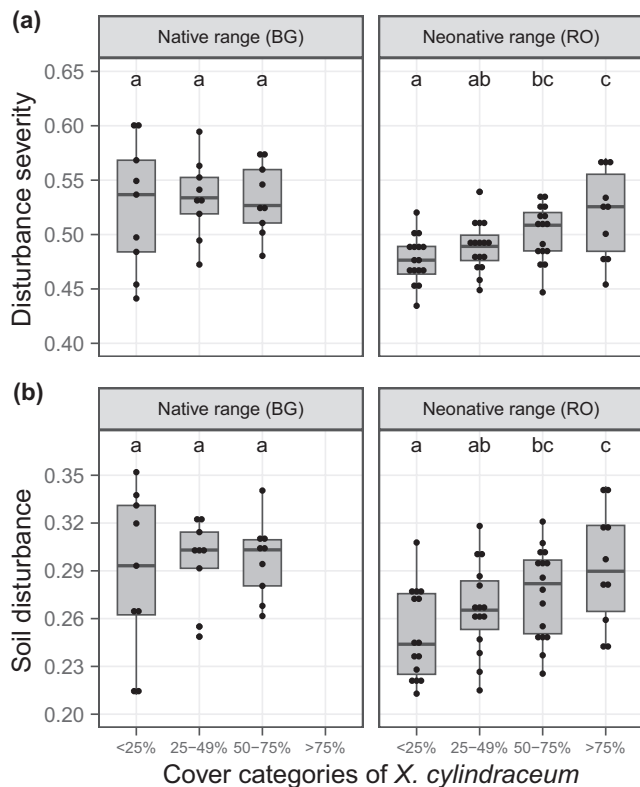


FIGURE 4 | Community-weighted means of disturbance indicator values, disturbance severity (a) and soil disturbance (b) of grassland plots in four cover categories of *Xeranthemum cylindraceum*. Left subplots present results of the species' native range (Bulgaria), right subplots present results of the species' neonative range (Romania). Boxes represent values between the first and third quartiles, and whiskers values outside the interquartile range, which are not outliers. Horizontal line in the box shows the median. Black dots show raw values of plots. Letters above boxes within each subplot show the results of pair-wise comparisons of estimated marginal means ('emmeans') between cover categories of *X. cylindraceum* at $p < 0.05$.

CWM for temperature) and drier (lower CWM for moisture) grassland communities in its native range in Bulgaria compared to its neonative range in Romania. Grasslands sampled by us in the native range were naturally more open even without grazing disturbance, thus proper for the permanent subsistence of short-lived species establishing from seed, as the target species. In the native range, *X. cylindraceum* is limited by the abundance of perennial species, on grassland scale and also on patch scale, as we found that high abundance patches of the target species were characterized by a low abundance of perennial species. The transition of *X. cylindraceum* from the native range to more mesic but closed grassland communities in the neonative range is very probably helped by vegetation structural changes caused by grazing (e.g., lower perennial cover), which precondition its successful establishment in open soil surfaces created by trampling erosion. Further, the transition to cooler sites towards the north of this Mediterranean species is promoted by climate change, which gradually creates more and more proper conditions for the germination of its seeds, winter survival of its seedlings and successful reproduction during the summer. Water availability seems to certainly favour the growth of *X. cylindraceum*, since

medium to high abundance patches were found to have higher moisture values indicated by the resident plant community. In addition, based on our former experimental study on this species, increased soil water availability accounted for an expressed fitness advantage in this species (Ruprecht et al. 2024).

Our sampling encompassed a single year, thus we cannot state with certainty to what extent the results obtained in the present study show a sustainable pattern in the behaviour of the target species and solid differences between the ranges (native and neonative). Our permanent plot observations, which we initiated in the studied grassland sites in Romania, will hopefully shed light on the broader validity of the results referring to the neonative range, which are presented here.

Based on our results, *X. cylindraceum* does not raise conservation problems in grasslands of the neonative range. However, due to its unpalatability and high abundance presence in pastures, it decreases the foraging value, resulting in economic loss. Mass presence of this species in grasslands managed by grazing is not a problem for biodiversity conservation per se, but indicates the overuse of pastures; by this means, it should raise concerns both among land managers and nature conservation authorities. Resting the pastures for a few years or decreasing stocking rates can be easily implemented management solutions to restore grassland vegetation and, by this means, control the excessive presence of *X. cylindraceum* in grazing lands.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Vegetation plots are stored in the Romanian Grassland Database (plot numbers: 45126-45183) and in the Balkan Dry Grassland Database (plot numbers: 13586-13604), available upon request (semi-restricted status, <https://edgg.org/index.php/databases/Regional-databases>).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Map of the studied sites and results of pairwise comparisons between cover categories of *Xeranthemum cylindraceum*. **Appendix S2:** Sampling site characteristics. **Appendix S3:** Frequency table of species.