



Effects of surrounding landscape on the performance of *Solidago canadensis* L. and plant functional diversity on heavily invaded post-agricultural wastelands

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Abstract High invasiveness and well-documented negative impact on biodiversity and ecosystem functioning make *Solidago canadensis* L. a species of global concern. Despite a good understanding of the driving factors of its invasions, it remains unclear how the surrounding landscape may shape invasion success of this species in human-transformed ecosystems. In our study, we investigated the impacts of different landscape features in the proximity of early successional wastelands on *S. canadensis* biomass allocation patterns. Further, we examined the relationships between the surrounding landscape, *S. canadensis* cover, and plant functional diversity, used as a supportive approach for the explanation of mechanisms underlying successful *S. canadensis* invasion. We found that increasing river net length had positive impacts on *S. canadensis* rhizome, stem, and total above ground biomass, but negative effects

on leaf biomass, indicating that vegetative spread may perform the dominant role in shaping the competitiveness of this invader in riverine landscapes. A higher proportion of arable lands positively influenced *S. canadensis* above ground and flower biomass; thus promoting *S. canadensis* invasion in agricultural landscapes with the prominent role of habitat filtering in shaping vegetation structure. Concerning an increasing proportion of settlements, flower biomass was higher and leaf biomass was lower, thereby influencing *S. canadensis* reproductive potential, maximizing the odds for survival, and indicating high adaptability to exist in an urban landscape. We demonstrated high context-dependency of relationships between functional diversity components and surrounding landscape, strongly influenced by *S. canadensis* cover, while the effects of surrounding landscape composition per se were of lower importance. Investigating the relationships between the surrounding landscape, invasive species performance, and plant functional diversity, may constitute a powerful tool for the monitoring, controlling, and predicting of invasion progress, as well as the assessment of ecosystem invasibility.

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Introduction

Apart from abiotic habitat properties (Dyderski and Jagodziński 2019), disturbances (Tabacchi et al. 1998; Czortek and Pielech 2020), traits of indigenous vegetation (Dyderski and Jagodziński 2021; Wang et al. 2021a), residence time and history of land-use (Catford et al. 2009; Basnou et al. 2015), landscape characteristics are considered similarly important in shaping invasive plant species abundance, richness, and diversity, as well as their establishment and spread in various ecosystems (González-Moreno et al. 2013a; Boscutti et al. 2018; Guido et al. 2016; Medeiros et al. 2016; see review in Vilà and Ibáñez 2011). The types, rates, and directions of these relationships depend strongly on the spatial scale (Basnou et al. 2015; Guido et al. 2016). For instance, the climate has been identified as a main driver of invasive species occurrence dynamics at continental and regional scales (2000–200 km), while at lower grain sizes (200–1 km) the configuration and complexity of the landscape and land-use play a greater role in shaping the richness and diversity of non-natives (Pearson et al. 2004; Vilà and Ibáñez 2011; Guido et al. 2016). Meanwhile, as an important driver, extensively influencing alien species invasion abilities at the finest spatial scales (~1 km), the composition of the surrounding landscape, ought to be considered (González-Moreno et al. 2013a; Paż-Dyderska et al. 2020a; Lażaro-Lobo and Ervin 2021). For instance, some earlier studies (see review in Medeiros et al. 2016) demonstrated that the distribution patterns of non-natives in the agricultural landscape were shaped predominantly by landscape drivers acting in 0.2–2.0 km buffers, whereas the richness of exotic species in urban parks was influenced by landscape composition in 1.0 km radii (Czortek and Pielech 2020).

The invasion success of numerous exotic species increases in more heterogeneous landscapes with higher connectivity, resource heterogeneity, and the availability of habitats suitable for colonization (Vilà and Ibáñez 2011; Lażaro-Lobo and Ervin 2021; see review in Davis 2009). Alien plants' richness is positively linked with the increasing contribution of communication networks in the surrounding, acting as migration corridors for exotic plants (Vilà and Ibáñez 2011; González-Moreno et al. 2013a; Guido et al. 2016). Another important component of

landscape affecting alien species' invasion success are river networks (Richardson et al. 2007; Czortek and Pielech 2020). Due to irregular, but frequent and severe flooding, these highly connected structures create dynamic mosaics of resource-rich pioneer habitats, suitable for colonization by non-native species (Tabacchi et al. 1998; Czortek et al. 2020a). Urban landscapes, with a high propagule arrival from the surrounding, have been identified as another important predictor, positively influencing alien species naturalizations and spread (Vilà and Ibáñez 2011; González-Moreno et al. 2013b; Basnou et al. 2015; Boscutti et al. 2018). For instance, Wu et al. (2004) demonstrated that introduced ornamental non-natives express higher probabilities to become naturalised in urban landscapes, than species introduced as forage plants. Although there is a positive relationship between the richness of alien species and the human population size of the focal site (McKinney 2004), the richness of exotics tends to be lower in higher-density urban areas than in sites of lower urbanisation levels (Gavier-Pizarro et al. 2010; González-Moreno et al. 2013b). Meanwhile, some earlier authors demonstrated that a higher contribution of agricultural sites in the surrounding landscape may exert similarly positive effects on alien species invasion as urbanisation (Guido et al. 2016). In contrast, other authors discovered that the richness of non-natives is negatively associated with an increasing proportion of arable fields (Medeiros et al. 2016). Additionally, a larger cover of a homogenous agricultural landscape in the surrounding decreases the success of non-natives (Ibáñez et al. 2009), acting as a buffer in preventing invasion (González-Moreno et al. 2013b).

Numerous previous studies have investigated the effects of surrounding landscape composition on the overall richness and diversity of alien plants in urban ecosystems (see reviews: Vilà and Ibáñez 2011; González-Moreno et al. 2013b; Basnou et al. 2015; Silva et al. 2020). However, non-natives differ in terms of residence time, invasion history, dispersal modes, and ecological requirements (Endress et al. 2007; Basnou et al. 2015). Moreover, they represent different strategies for acquisition and utilisation of resources, thus interacting differentially with native vegetation (Catford et al. 2009; Sapsford et al. 2020). Therefore, the development of single-species studies investigating relationships between surrounding landscape and non-natives abundance (e.g. their

percentage cover or biomass), appears to be a sufficient method for formulating effective strategies for invasive species' management (Lundholm and Larson 2004; Endress et al. 2007; Basnou et al. 2015). One useful tool for this task can be the assessment of invasive plants' success, focussing on their performance, i.e., biomass allocation patterns between functionally different organs (Lundholm and Larson 2004). Invasive species' performance, in turn, may be influenced by different components of the surrounding landscape in various ways (Taylor et al. 2016). More specifically, via exerting impacts on trade-offs between the allocation of biomass for organ development, allowing effective acquisition and utilisation of resources, monopolisation of space, and reproduction strategies, the surrounding landscape may influence the non-natives' survival, competitiveness, dispersal, and colonisation abilities (Li et al. 2017).

One example of an invasive species with a broad ecological amplitude and well-known spread history in Europe and Asia is *Solidago canadensis* L. (Chmura et al. 2015). Due to its common occurrence and a wide spectrum of negative impacts on the functioning of indigenous ecosystems, understanding *S. canadensis* invasion mechanisms has become an important issue in invasion ecology, reflected in an increasing body of literature on this topic. Some earlier studies have focussed on *S. canadensis* biomass allocation patterns (Szymura and Szymura 2015) and leaf functional traits variation (Dong and He 2019). While some authors highlight the crucial engineering role of this invader in shaping soil biogeochemical cycles (Zhang et al. 2009; Ren et al. 2020a), enzymatic activity (Wang et al. 2018a), as well as the diversity and structure of soil microbes (Dong et al. 2015a), other authors, have focussed on the effects on the species composition of insects (De Groot et al. 2007) and pollination (Sun et al. 2013). Whilst there appears to be relatively sufficient knowledge on *S. canadensis* invasion-driven effects on the taxonomic (Chen et al. 2013; Cheng et al. 2021; Wang et al. 2021a) and functional diversity of vegetation (Wang et al. 2018b, 2019, 2020), it remains unclear as to how landscape drivers in different spatial scales may shape its biomass allocation patterns and invasion success in human-transformed landscapes (Perera et al. 2021).

Apart from *S. canadensis* biomass allocation patterns, our study also examined relationships between

the surrounding landscape, *S. canadensis* cover, and the total functional diversity of vegetation (concerning both native and non-native species), as a supportive approach for the explanation of mechanisms underlying successful *S. canadensis* invasion. The application of this approach, may provide additional information, to demonstrate how surrounding landscape composition and alien species invasion can modulate the importance of different ecological mechanisms (i.e. habitat filtering, competition, or niche partitioning), in shaping the vegetation structure, and how these landscape- and invasion-driven effects on functional diversity can affect ecosystem invasibility (Wang et al. 2018b, 2019, 2020, 2021a, b; Czortek et al. 2020b). However, these relationships remain poorly explored, regarding numerous invasive plant species and ecosystem types (but see Czortek and Pielech 2020; Gutiérrez-Canovas et al. 2020).

In our study, we ask: (i) Does the spatial scale matter for relationships between the surrounding landscape and the biomass allocation patterns of *S. canadensis*, and the functional diversity of vegetation? (ii) How are the biomass allocation patterns of *S. canadensis* on heavily invaded post-agricultural wastelands influenced by the surrounding landscape composition? (iii) How can the surrounding landscape shape the functional diversity of vegetation under *S. canadensis* invasion?

Materials and methods

Plant species studied

Solidago canadensis is an invasive perennial tall herb, native to North America, occurring on the edges of forests, roadsides, abandoned arable lands, meadows, pastures, and urban sites. In the first half of the seventeenth century, it was introduced to England, as an ornamental plant (Chmura et al. 2015). Since the nineteenth century, the expansion of *S. canadensis* in Europe and Asia began, with a high invasion success achieved in natural (e.g. riparian forests and hygrophilous tall herbs vegetation), semi-natural (e.g. lowland dry, mesic, and wet grasslands) and ruderal ecosystems (e.g. wastelands and urban sites). *Solidago canadensis* was first recorded in Poland in 1872 in Cracov and Lublin cities. In subsequent decades, it expanded to almost the entire country (Chmura et al.

2015; Tokarska-Guzik et al. 2012). This invasive plant can occur in various habitat conditions, including soils contaminated by heavy metals (Bielecka and Królak 2019; Czortek et al. 2020b). Due to its fast growth, high production of above ground biomass, and a high propensity for vegetative spread via the production of thick groups of clones, *S. canadensis* is considered to be an effective competitor. Moreover, effective sexual reproduction via the production of huge numbers of small-size anemo-, hydro- and epizoochorous seeds, enables the colonisation of new habitats at large spatial scales (Chmura et al. 2015).

Study area and study design

We performed a vegetation survey and sampling of *S. canadensis* biomass at the end of August, coinciding with the optimal phenological phase of development of *S. canadensis* morphological organs. We conducted our study in 2017, on 50 vegetation plots (100 m² each), located on wastelands invaded by *S. canadensis*, where agriculture had ceased no longer than two to four years before our inventories. Based on the preliminary examination of both study sites, via drive-by surveys, the plots were set randomly, at the places where *S. canadensis* occupied an area of more than 500 m². The minimum distance between vegetation plots was ~120 m, making the potential impacts of pseudoreplication on the results obtained, as low.

Our study covered two urban sites differing in the context of human population density, city size, degree of human transformation, and the contribution of black and grey infrastructure. We established half of the vegetation plots (n=25) in the region of Siedlce city (52° 13' 72"–52° 74' 25" N; 22° 13' 29"–22° 25' 24" E; about 96,000 inhabitants and 141.5 km²), and the other half (n=25) in the region of Olkusz city (50° 15' 83"–50° 23' 39" N; 19° 26' 50"–19° 36' 46" E; about 49,000 inhabitants and 150.7 km²; Fig. 1a–c). In the landscape of the city of Siedlce, fertilised arable lands, as well as, urban suburban and rural sites predominate (Fig. 1b). In comparison with the region of the city of Siedlce, the landscape of the city of Olkusz, is characterised by a slightly larger contribution of pine monocultures than fertilised arable lands, as well as industrial and post-industrial infrastructure (Fig. 1c).

To characterize the structure of the landscape in the surrounding of vegetation plots, we employed the Corine Land Cover data (CLC; Copernicus Land Monitoring Service; 2021). We categorized 14 landscape types into two broadly defined classes covering: settlements (continuous urban fabric (CLC code: 111), discontinuous urban fabric (CLC code: 112), industrial or commercial units (CLC code: 121), road and rail networks associated land (CLC code: 122), mineral extraction sites (CLC code: 131), construction sites (CLC code: 133), green urban areas (CLC code: 141) and sport and leisure facilities (CLC code: 142)) and agricultural areas (non-irrigated arable land (CLC code: 211), permanently irrigated land (CLC code: 212), pastures (CLC code: 231), annual crops associated with permanent crops (CLC code: 241), complex cultivation patterns (CLC code: 242) and land principally occupied by agriculture with significant areas of natural vegetation (CLC code: 243)). Using the Map of the Hydrographic Division of Poland (Polish Geological Institute, National Research Institute; 2021), we calculated river net length (m) (Fig. 1b–d). To investigate the impacts of spatial scales on the percentage cover and biomass of *S. canadensis*, and the components of the functional diversity of vegetation, we calculated the percentage contribution of settlements and agricultural areas, and river net length within buffers of 100, 500, and 1000 m from the study plots (Fig. 1d). Due to the low contribution of rivers in the scale of 100 m, in further analyses, we included only the length of river net in 500 and 1000 m buffers. Furthermore, owing to a relatively low representation level of forests in each of the three spatial scales in both study sites, we did not consider this landscape metric in analyses (Fig. 1b, c).

Biomass collection

Within each 100 m² vegetation plot, we established three subplots (0.16 m² each), located diagonally: two subplots were located ~2 m from two randomly selected opposite edges of the 100m² plot, and the third subplot was located in the middle of the 100m² plot. In each subplot, we harvested and combined all of the above ground ramets of *S. canadensis*, to form one mixed sample, representing each 100 m² vegetation plot. In turn, each sample was used for the measuring the mean dry biomass of flowers, leaves,

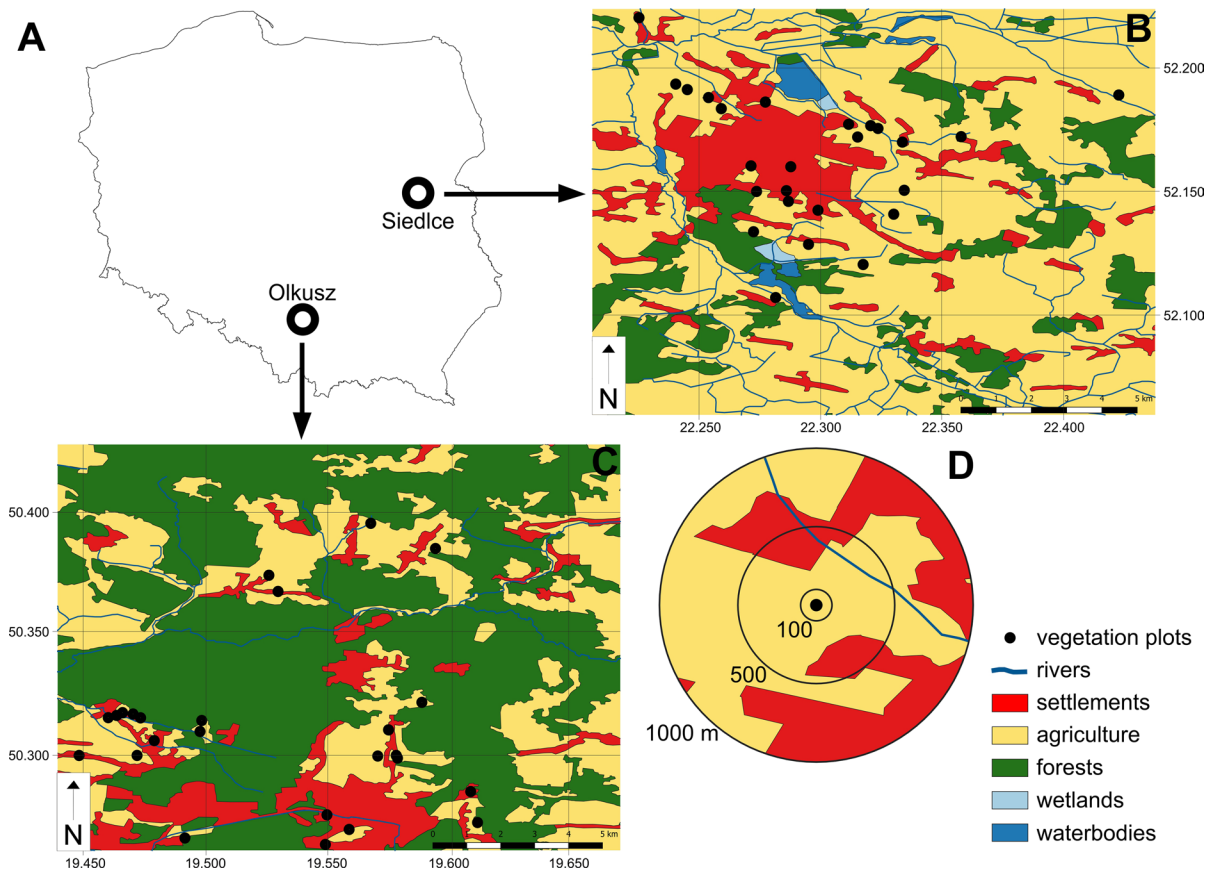


Fig. 1 Map of two study sites located in Poland (a). Location of 50 vegetation plots (25 per study site) are shown by black dots (b, c). Example of one vegetation plot with surrounding

landscape (d). Buffers of 100, 500, and 1000 m used in the landscape analyses are shown by black ellipses

and stems. Regarding the below ground organs of *S. canadensis*, we collected the rhizomes from the same places as the above ground ramets, from a depth of up to 20 cm, rinsing them under running water and again in distilled water. Following on, we combined the samples of rhizomes into one mixed sample, representative of each 100 m² vegetation plot, which was used for the measuring of their mean dry biomass. Finally, we oven-dried the plant material at a temperature of 60 °C to a constant weight. To investigate the trade-offs between the biomass allocation patterns to the different morphological parts of plants, we calculated the percentage contribution of: (i) above ground biomass in total *S. canadensis* biomass (hereinafter referred to as “above ground biomass”); (ii) leaf biomass in total *S. canadensis* above ground biomass (hereinafter referred to as “leaf biomass”); (iii) stem biomass in total *S. canadensis* above ground biomass

(hereinafter referred to as “stem biomass”); (iv) flower biomass in total *S. canadensis* above ground biomass (hereinafter referred to as “flower biomass”) and (vi) rhizome biomass in total *S. canadensis* below ground biomass (hereinafter referred to as “rhizome biomass”), which we used in analyses.

Vegetation survey

For each 100 m² study plot, we recorded all vascular plant species. Using the modification of the decimal scale of Londo (1976), we assessed the percentage cover of each species per plot (including *S. canadensis*): 1%, 5%, 10%, and then at 10% intervals. Three highly experienced botanists (LK, EK, and AB) surveyed vegetation, spending approximately one hour in each plot; thus, minimising the probability of omitting some of the species (e.g. those of low sizes or

existing in a vegetative stage of growth), as well as increasing the reliability (and decreasing the subjectivity) of the correct estimation of species abundance.

To estimate the importance of environmental filtering, interspecific competition, and niche partitioning, in the shaping of species co-existence patterns for each plot, we calculated the four components of functional diversity (using *FD::dbFD()* function), which characterise the distribution of plant functional traits in the community trait hypervolume: functional richness, functional evenness, functional dispersion and functional divergence (following Villéger et al. 2008 and Laliberté and Legendre 2010). Following Hedberg et al. (2014), functional richness measures the size of the niche filled by particular combinations of functional traits. Functional evenness is a measure of the degree of evenness of the distribution of biomass in a niche space (Mason et al. 2005). Both functional divergence and functional dispersion provide information on the richness of functional traits in the plant community hypervolume, but functional divergence focuses more on the importance of plants with extreme trait values, e.g. more specialised species with narrow ecological requirements (Mason et al. 2005; Villéger et al. 2008). A high functional diversity of vegetation indicates a high divergence of life-history strategies of plant species (expressed as high differences between values of functional traits carried by different species), suggesting that numerous plant functional types can co-exist within a community due to the minimal role of interspecific competition in shaping species composition (Carroll et al. 2011). Conversely, a low functional diversity of vegetation indicates a high overlapping of life-history strategies of plant species (expressed as low differences between the values of functional traits assigned to different species), indicating that one or few similar plant functional types co-exist within a community (Chesson 2000; Grime 2006). To summarise, high values of functional diversity components may serve as an indication of the prominent role of niche partitioning, while low values may express the prevalence of environmental filtering or interspecific competition in shaping species co-existence patterns (Mason et al. 2005; Villéger et al. 2008; Le Bagousse-Pinguet et al. 2014; Czortek et al. 2021b).

We performed calculations of functional diversity components using the set of eight plant functional

traits (all obtained from the BIEN, BioFlor, LEDA, and Pladias databases), which characterise the strategies of plant species for competition, acquisition, and distribution of resources between different morphological parts: mean canopy height [m], shoot growth form [eight categories], leaf distribution along stem [five categories] and mean specific leaf area; SLA [mm^2/mg], as well as reproduction, seed dispersion, survival and resistance to disturbances: mean seed mass [mg], dispersal mode [14 categories], seed bank longevity [three categories] and mean seed number per shoot. In these calculations, we included all plant species recorded in vegetation plots with available trait values, i.e. both native and non-native species. Apart from *S. canadensis*, the group of non-natives contained other exotic and invasive species, but occurring in study plots in low abundances, e.g.: *Acer negundo*, *Apera spicaventi*, *Armoracia rusticana*, *Cornus alba*, *Erigeron canadensis*, *Juglans regia*, *Partenocissus quinquefolia*, *Prunus serotina*, and *S. gigantea*.

One may assume that the employment of plant functional traits (both qualitative and mean values in the case of quantitative traits), provided by trait databases, in the calculation of functional diversity metrics may lead to the formulation of biased conclusions, regarding the role of different ecological mechanisms in shaping the community structure in our study plots, with respect to the surrounding landscape. More specifically, the same plant species growing under the impacts of a combination of different microhabitat conditions may differ significantly in terms of its performance, expressed by potentially high intraspecific variability of functional traits. Moreover, Paż-Dyderska et al. (2020b) revealed a gross underestimation of intraspecific trait variability of: SLA, total leaf area, and the leaf mass of 167 plant species provided by the LEDA database, when compared to direct field inventories. On the other hand, the same study found that a higher amount of variation in functional traits was explained by species identity rather than site-specific random factors; thus, supporting the application of the database-derived approach as a useful tool in the exploration of relationships between the functional diversity of vegetation and the surrounding landscape composition.

Data analyses

To determine the effects of three landscape predictors, in different spatial scales, on the percentage cover and the six components of *S. canadensis* biomass, as well as the four components of the functional diversity of vegetation (Online Resource 1; Research question 1), we performed preliminary single factor linear models (LM). For each landscape predictor, in each spatial scale (buffer size), we performed one preliminary LM. Based on the Akaike Information Criterion corrected for small sample sizes (AICc), for further analyses, we selected the landscape predictors at the buffer size that best described *S. canadensis* cover, biomass, and the functional diversity components of vegetation (Online Resource 2).

To explore the relationships between landscape predictors in particular spatial scales (chosen as having the greatest predictive power based on AICc provided by preliminary LMs), percentage cover, and the six components of *S. canadensis* biomass (Research question 2), as well as four metrics of functional diversity of vegetation (Research question 3), we built two sets of generalised additive models (GAM; *mgcv::gam()* function). To prevent overfitting of GAMs, expressed by polynomial functions with high local fitness and low ecological significance, we penalised splines. We achieved this by setting a maximum degree level of $k=3$. Initially, we considered the usage of LMs, but based on the LMs outputs inspection, we found a low explanatory power of model estimates compared to the graphical visualisation of models. One solution for this problem is data transformation (e.g. scaling, centering, or Yeo-Johnson power transformations), but it removes real units of variables (and even produces negative values), thus, making the interpretation of results problematical. Therefore, we did not apply this procedure, deciding to use GAMs instead of LMs, which provided a better fit of our data than LMs.

We performed the first set of GAMs to account for the effects of the three landscape predictors on the percentage cover and the six components of *S. canadensis* biomass (Research question 2). To find the subset of GAMs with the highest predictive power, in explaining the variability of *S. canadensis* percentage cover and biomass, as well as address potential issues linked with the situation, when one or more smooth terms may be approximated by other

predictors in the model, we inspected the concurrency of GAMs. For each GAM, we calculated the observed concurrency coefficient (*mgcv::concurrency()* function), which ranges from 0 to 1, where values closer to 0 indicate no concurrency (no correlation between predictors), values around 0.5–0.6 indicate weak concurrency, and values closer to 1 indicate total concurrency (strong correlation between predictors; Amodio et al. 2014; Wood 2022). We found no correlation of river net lengths with the two remaining predictors (concurrency coefficient lower than 0.10). Considering concurrency coefficients calculated for settlements and agricultural area contributions, concurrency coefficient values ranged from 0.14 to 0.69, indicating relatively weak correlations between settlements and agricultural areas cover (Online Resource 3). On this basis, we decided to keep all three landscape predictors in the final GAMs. Initially, we considered including in these GAMs the effects linked with the study region, as our dataset originates from two study sites and differs in terms of transformation levels and urbanisation densities, which could potentially affect our results. Since, the concurrency analysis does not allow the consideration of categorical predictors, for each response variable, we performed one additional GAM, where apart from landscape predictors, we added the study region (Siedlce or Olkusz) as another predictor. A comparison of the AICc values calculated for GAMs, with and without the study region, allowed us to assume that the geographical locality of the study plots had a low impact on the relationships between the majority of response variables and landscape parameters, revealed by ΔAICc values smaller than two between the GAMs (Online Resource 4). On this basis, we decided to exclude the effects linked with the study region in further analyses of *S. canadensis* cover and biomass.

We built the second set of GAMs, to account for the effects of the three landscape predictors in selected spatial scales and *S. canadensis* cover on the four parameters of the functional diversity of vegetation (Research question 3). To explore the joint effects of biological invasion and surrounding landscape composition on functional diversity, apart from the single effects of *S. canadensis* cover and landscape predictors, in this set of GAMs, we included an interaction term between each of the three landscape variables and cover of *S. canadensis*. In addition, in this set of GAMs, we included the study region as another

predictor. Thus, each of the four GAMs consisted of eight predictors. To find the subset of GAMs, with the highest predictive power, in explaining the variability of the four functional diversity metrics, from all the model combinations, we selected models with $\Delta\text{AICc} < 2$ (*MuMIN::dredge* function; Bartoń 2022). On this basis, for each functional diversity component, we performed one final multivariate GAM, consisting of predictors, included in a subset of GAMs with $\Delta\text{AICc} < 2$ (Online Resource 5). Regarding all functional diversity metrics, the final GAMs did not contain the study region as an explanatory variable, which allowed us to assume that the geographical locality of the study plots had a low impact on the metrics of functional diversity (Online Resource 5). Interactions between the landscape characteristics and *S. canadensis* cover included in final GAMs, were visualised by regression slopes predicted for the three levels of *S. canadensis* cover: 25, 50, and 75% (using the *stats::predict()* function).

Results

The analysed landscape variables differed in their predictive power amongst different buffer sizes. We

found that only some response variables were influenced by the same spatial scale, selected as the best predictors due to the lowest AICc (Online Resource 2). For instance, we identified river net length and the contribution of agricultural areas in a buffer of 500 m as variables with the greatest predictive power for some components of *S. canadensis* biomass, i.e. above ground, leaf, and flower biomass. When considering relationships between the three landscape metrics and the functional diversity indices, functional richness and functional divergence were best explained by a scale of 100 m, while functional evenness and dispersion were best explained by the larger spatial scale of a 1000 m buffer.

Model parameters describing the impacts of landscape characteristics on *S. canadensis* cover and above ground biomass are provided in Online Resource 6. We identified river net length in a buffer of 500 m, as a predictor that significantly and positively influenced *S. canadensis* cover, with a slight increase of this invader's cover when considering the length of river net up to 600 m, and a larger increase when focussing on river net length longer than 600 m in a given buffer (Fig. 2a). The above ground biomass of the studied invader was higher in plots surrounded by a higher cover of agricultural

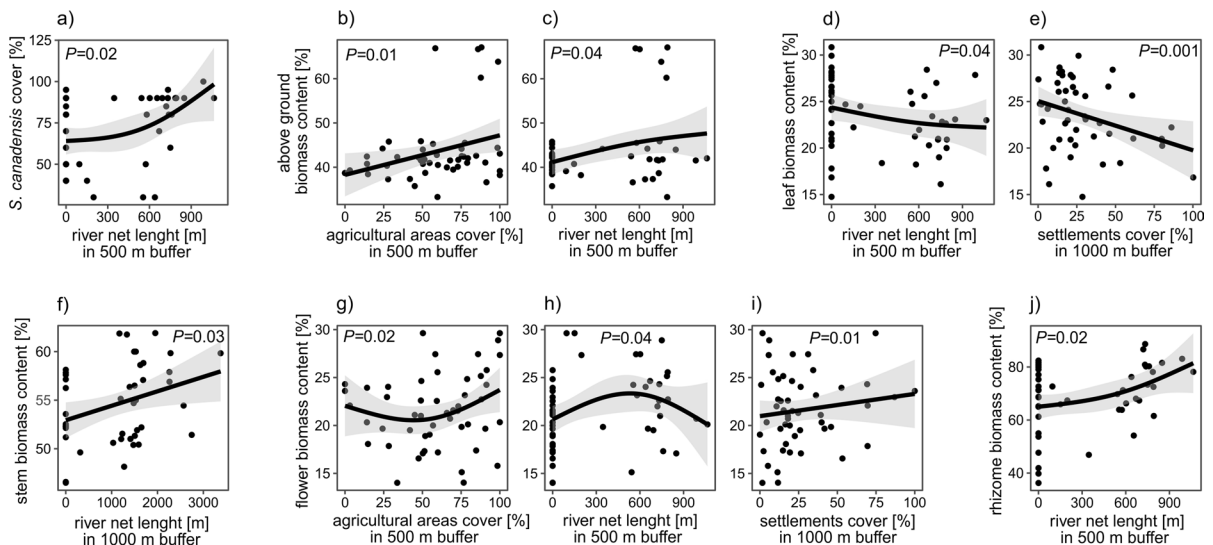


Fig. 2 Partial regressions of the generalised additive models with river net length, cover of settlements, and cover of agricultural areas in different spatial scales (buffer sizes) as predictors influencing the cover (a), total above ground (b, c), leaf (d, e), stem (f), flower (g–i), and rhizome (j) biomass of *Solidago*

canadensis. Predictors in particular spatial scales were selected based on AICc values of preliminary single factor linear models. Note that only significant results are shown. For model parameters see Online Resource 6

areas (Fig. 2b) and longer river nets in the buffer of 500 m (Fig. 2c).

Model parameters describing the impacts of landscape characteristics on *S. canadensis* biomass of leaves, stems, flowers, and rhizomes are provided in Online Resource 6. *Solidago canadensis* leaf biomass decreased significantly in relation to a longer river net in a scale of 500 m (Fig. 2d), and a larger cover of settlements, in a buffer of 1000 m (Fig. 2e). River net length, in a buffer of 1000 m, was a predictor which positively influenced *S. canadensis* stem biomass (Fig. 2f). River net length, in a buffer of 500 m, as well as the contribution of settlements and agricultural areas cover (in 1000 and 500 m buffers, respectively), had significant impacts on the contribution of *S. canadensis* flower biomass (Fig. 2g–i). Although the effect of river net length on flower biomass was difficult to interpret (Fig. 2h), we found that the increasing cover of agricultural areas (Fig. 2g) and settlements (Fig. 2i) influenced flower biomass positively. While the overall relationship between flower biomass and the agricultural areas contribution was positive, focussing on partial relationships, we found that flower biomass decreased slightly when the cover of arable lands was smaller than 50%, but increased substantially when the contribution of arable lands in the surrounding was greater than 50% (Fig. 2g). *Solidago canadensis* rhizome biomass increased significantly with the increasing length of river net in the 500 m buffer, indicating a weak relationship in plots surrounded by a river net less than 600 m, and a stronger effect was observed when the river net was longer than 600 m (Fig. 2j).

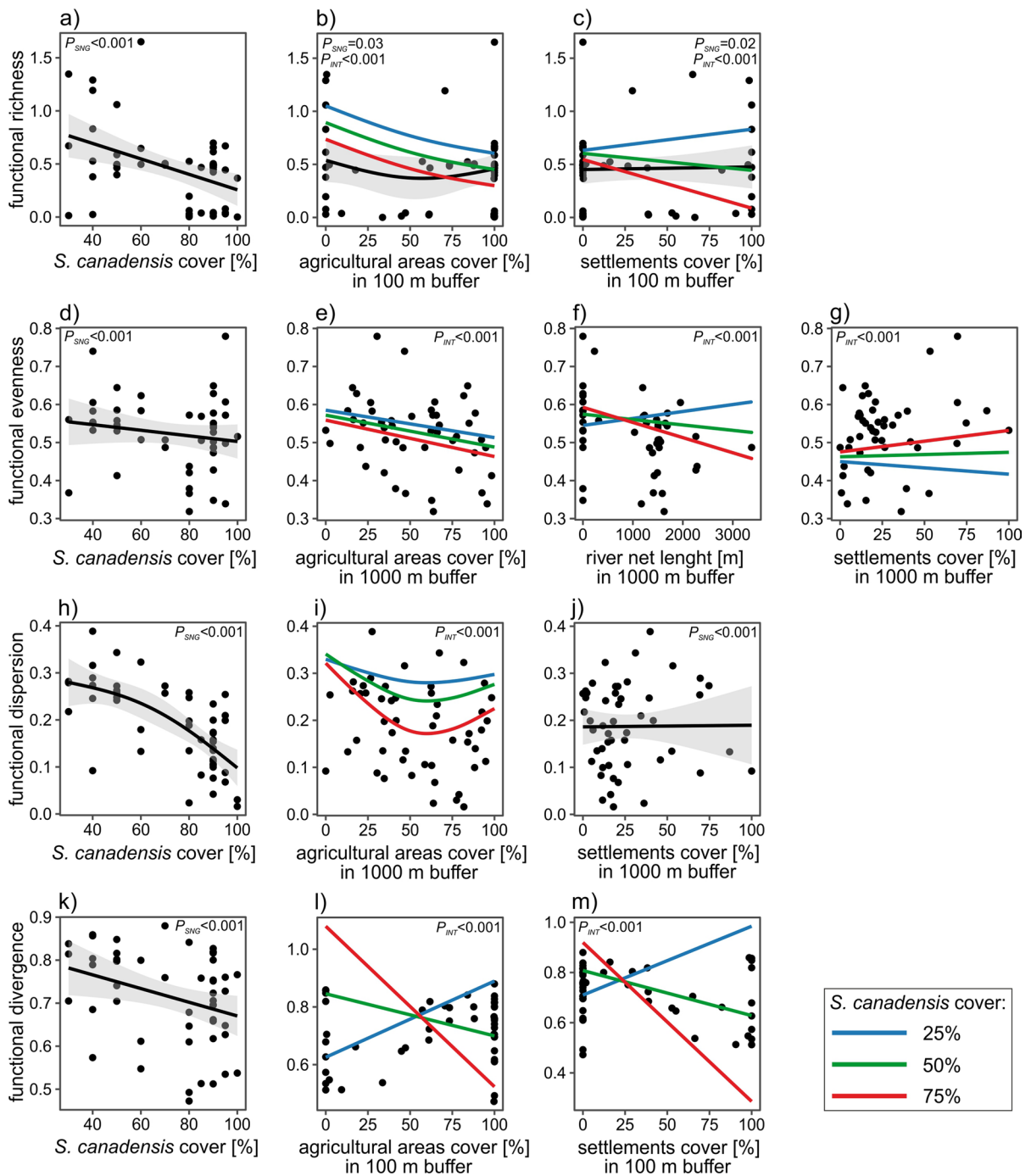
Model parameters describing the relationships between landscape characteristics, *S. canadensis* cover, and the four components of functional diversity are provided in Online Resource 7. Each final GAM contained the cover of *S. canadensis* as a predictor significantly negatively influencing all components of functional diversity (Online Resources 5 and 7), with close-to-linear response revealed for functional richness (Fig. 3a), functional evenness (Fig. 3d) and functional divergence (Fig. 3k), and more pronounced effects of invasion in plots with *S. canadensis* cover higher than 50% in regards of functional dispersion (Fig. 3h). The ecological (in case of functional richness; Fig. 3b, c and dispersion; Fig. 3i, j) or statistical significance (in case of functional evenness; Fig. 3e–g and divergence; Fig. 3l, m) of the effects

of single landscape predictors on functional diversity components was relatively weak (Online Resource 7). However, we identified considerable effects of interactions between the landscape characteristics and *S. canadensis* cover on components of functional diversity, predicted by the three levels of this invader cover, in general, revealing close-to-linear responses (apart from the functional richness and functional dispersion; Fig. 3b, i, respectively). We found strong negative effects of low, moderate and high invasion levels in shaping the relationships between the contribution of agricultural areas (in a 100 m buffer) and functional richness (Fig. 3b). The effect of settled areas contribution (in a 100 m buffer) on functional richness was slightly positive for low invasion levels, becoming more strongly negative for 50 and 75% of *S. canadensis* cover (Fig. 3c). Each level of *S. canadensis* cover similarly negatively shaped the relationship between functional evenness and agricultural areas contribution (1000 m buffer; Fig. 3e). The relationship between functional evenness and the river net length in a buffer of 1000 m was strongly negative under high invasion levels, weaker under 50% of *S. canadensis* cover, and became slightly positive in terms of low levels of invasion (Fig. 3f). Although statistical significance, the effect of settled areas contribution (in a buffer of 1000 m) on functional evenness was weakly influenced by the cover of *S. canadensis* (Fig. 3g). The negative relationship between functional dispersion and agricultural areas contribution (1000 m) became stronger alongside increasing *S. canadensis* cover (Fig. 3i). Relationships between functional divergence, and both agricultural and settled areas contribution (in 100 m buffers) were strongly positive under low invasion levels, but became strongly negative under 50 and 75% of *S. canadensis* cover (Fig. 3l–m).

Discussion

General effects of spatial scale and landscape on *S. canadensis* and functional diversity

Despite some exceptions, we demonstrated that landscape factors at finer spatial scales were more important for shaping *S. canadensis* biomass allocation patterns than those acting at larger scales. This may be confirmed by the significant impacts of river



net length in a 500 m buffer on almost all traits of *S. canadensis* analysed in this study. Further, this indicates that a complex of habitat conditions, acting at ultra-local fine scales may exert a greater influence on *S. canadensis* invasiveness than sub-local factors (Research question 1). Apart from the identification

of some patterns with a possibly weak (or difficult to assess) ecological significance (e.g. non-linear and hump-backed responses of *S. canadensis* cover with river net length or flower biomass with an arable lands contribution), we revealed that different landscape types acted differentially on *S. canadensis*

◀**Fig. 3** Partial regressions of the generalised additive models testing for effects of landscape predictors in different spatial scales (buffer sizes), and *S. canadensis* percentage cover on functional diversity metrics in studied wastelands: functional richness (a–c), functional evenness (d–g), functional dispersion (h–j), and functional divergence (k–m). Predictors in particular spatial scales were selected based on AICc values of preliminary single factor linear models. Interactions between the landscape characteristics and *S. canadensis* cover were visualised by blue, green and red lines, which are the regression slopes predicted for the three levels of *S. canadensis* cover: 25, 50, and 75% (using the `stats::predict()` function). Note that only statistically significant results are presented: P_{SNG} —statistical significance of single predictors (without interaction term); P_{INT} —statistical significance of interaction terms (landscape predictor: *S. canadensis* cover). For model parameters see Online Resource 7

biomass allocation patterns. Thereby, shaping not only its competitiveness but also its reproduction success expressed in its tremendous capacity for persistence, establishment, and spread in extreme environmental conditions generated by agriculture and urbanisation (Research question 2).

In general, landscape predictors acting at larger scales of a 1000 m buffer, were found to be prominent for shaping the functional evenness and functional dispersion, while ultra-local fine scale (100 m buffer) exerted higher importance for shaping the functional richness and functional divergence (Research question 1). Besides the widely known negative impacts of *S. canadensis* invasion on plant functional diversity (Wang et al. 2019; Wang et al. 2020; but see Cheng et al. 2021), which we identified in regards to all analysed metrics of functional diversity independently from landscape characteristics, the effects of single landscape predictors, however, were of lower significance. Simultaneously, we found that functional diversity was influenced considerably by interactions between the landscape characteristics and *S. canadensis* cover. In general, we revealed that under a low cover of *S. canadensis*, relationships between some components of functional diversity and landscape predictors were positive (e.g., functional divergence and agricultural areas contribution), but became highly negative under high invasion levels (e.g., functional richness and settlements contribution). This illustrates a high context-dependency of landscape-driven effects on functional diversity, to a large extent shaped by biological invasion levels (Sapsford et al. 2020). Moreover, this indicates the relatively low role of surrounding landscape composition per se, but

of the high joint importance of landscape predictors and *S. canadensis* invasion for shaping the functional diversity of the studied wastelands. These negative effects, strengthened under high invasion levels, may be used as a substantiating explanation of the formidable competitiveness of *S. canadensis*, in terms of its vegetative spread and colonisation abilities, as well as the positive role of habitat filtering (generated by rivers-, settled-, and arable lands-driven disturbances) for shaping *S. canadensis* invasion success (Research question 3).

Impacts of river net length on the cover and biomass of *S. canadensis*

Our study demonstrated that the cover of *S. canadensis* increased alongside the increasing length of the river net, in a radius of 500 m. Moreover, a longer length of rivers was a predictor positively influencing total above ground, rhizome (both in a buffer of 500 m), and stem biomass (in a buffer of 1000 m). Presumably, this may be linked with higher nutrient availability in areas with bigger river nets and located closer to rivers (Décamps et al. 1988; Wollheim et al. 2006). This could offer environmental conditions more suitable for colonisation, establishment, and the spread of invasive plants (Tabacchi et al. 1998; Richardson et al. 2007; Czortek and Pielech 2020; Czortek et al. 2020a). More specifically, under the conditions of potentially higher soil humidity and fertility, *S. canadensis* could invest a relatively similar portion of energy in both above and below ground organs (Adomako et al. 2020; Ren et al. 2019, 2020b). Thus, the trade-offs linked with a higher production of below than above ground biomass, under conditions of lower nutrient availability, may be suppressed on more fertile soils (Ren et al. 2019). In this light, a denser river net, via exerting positive impacts on both above and below ground biomass, may increase the competitive abilities of *S. canadensis*. A higher stem and total above ground biomass of *S. canadensis* may indicate its huge propensity for light acquisition and domination in the above ground space (Fenesi et al. 2015). Cheng et al. (2021) and Wang et al. (2021b) demonstrated that *S. canadensis* invasion success depends, *inter alia*, on its total biomass and stem height. Similarly, higher biomass of rhizomes may illustrate a high effectiveness for water and nutrient acquisition, as well as a high tendency of

S. canadensis to dominate in below ground biomass. On the other hand, higher investment in rhizome biomass may be indicative of the positive impacts of river net length on *S. canadensis* vegetative reproduction abilities. This pattern can correspond with the positive relationship between the rivers' contribution in the surrounding landscape and *S. canadensis* cover, its total above ground, and stem biomass. Simultaneously, we found that river net length in a 500 m buffer, had a negative impact on *S. canadensis* leaf biomass. Thus, triggering trade-offs between an investment of energy in the production of leaves, stems, and rhizomes. This may suggest that a higher proportion of river net length in the surrounding could exert negative impacts on photosynthesis effectiveness (reflected in lower leaf biomass), but may positively influence vegetative reproduction (investment in rhizomes) and the abilities of *S. canadensis* for competition for above- (reflected in higher stem biomass) and below-ground space (via higher rhizomes production) (Cheng et al. 2021; Wang et al. 2021b).

Impacts of river net length on the functional diversity of vegetation

One should expect that a higher proportion of rivers may exert positive effects on functional diversity, expressed as a potentially larger contribution of taxonomically rich and diverse riparian plant communities in the surrounding. Rivers may act as plant migration corridors and propagule sources, both for pioneer species, and plants of more advanced successional stages, which could colonize the studied wastelands. A slightly positive relationship between functional evenness and river net length (in a buffer of 1000 m) under low levels of *S. canadensis* invasion may support this area. More specifically, higher values of functional evenness predicted for 25% of *S. canadensis* cover may hint at a higher degree of occupancy of the niche space by functionally-dissimilar plant species, as well as a higher regularity of biomass distribution within a community (Mason et al. 2005; Villéger et al. 2008; Czortek et al. 2021b). However, under the higher cover of *S. canadensis*, the relationship between river net length and functional evenness became negative. Early successional stages of vegetation (as in the case of the studied wastelands), where large parts of niche space could be not occupied or under-utilised by plants, can represent huge

opportunities for exotics, especially when the invading species are competitively superior (Maron and Marler 2007; Dong et al. 2015b; Wang et al. 2018b). In terms of a greater contribution of rivers in the surrounding landscape and a high *S. canadensis* cover, its above ground, stem, and rhizome biomass, the regularity of plants' functional traits distribution within a community could decrease. Thus, identifying *S. canadensis* as a main ecosystem component, prevailing in the utilisation of the entire range of available resources. Therefore, following the invasion paradox (Fridley et al. 2007), this negative relationship may be considered in the context of habitat filtering rather than the niche differentiation hypothesis (Maire et al. 2012). Rivers could favour an increase in the invader's cover and biomass, which in turn, could eliminate native species, that were functionally dissimilar from *S. canadensis* in terms of resource acquisition and utilisation strategies. In this way, longer river length may not only contribute to the higher invasibility of *S. canadensis*, but in a further perspective, may also decrease the role of habitat filtering in shaping the species composition on wastelands.

Effects of agriculture on functional diversity of vegetation and *S. canadensis* biomass

The homogenous and highly disturbed landscape of arable fields in the surrounding may play the role of a buffer in preventing the colonisation of the studied wastelands, by plants from other vegetation types (e.g., mesic meadows) (Ibáñez et al. 2009; González-Moreno et al. 2013b; Medeiros et al. 2016). This buffering role may be demonstrated by negative relationships between functional richness and functional evenness, and the contribution of arable lands (in buffers of 100 and 1000 m, respectively), with a relatively low role of *S. canadensis* cover in shaping these relationships. In this way, a higher contribution of agricultural areas in the surrounding landscape may maintain the studied vegetation in the early stages of succession, illustrated in the prominent role of habitat filtering in shaping the species composition of these pioneer plant communities. On the other hand, a positive relationship between functional divergence and agricultural areas contribution under a low level of *S. canadensis* invasion may be considered as an expression of a presumably high propagule arrival of segetal plant species and ruderal tall herbs

from the surrounding. Apart from *S. canadensis*, this group of species could contain other non-natives (e.g., archaeophytes), differing considerably in traits related to plant size (e.g., height and seed mass) and leaf economical spectrum (e.g., specific leaf area). More specifically, higher values of functional divergence may express larger dissimilarities between functional trait values carried by different species in the community hypervolume, hinting at the high role of pioneer plant species with extreme functional trait values in shaping the vegetation structure (Mason et al. 2005; Villéger et al. 2008; Hedberg et al. 2014; Czortek et al. 2021a). Regarding the importance of habitat filters, a large volume of the niche space may be still underutilised by plant species, thus creating empty microsites unsuitable for colonisation by numerous plant species. At the same time, these empty microsites may be accessible for colonisation by *S. canadensis*, leading to its dominance in plots with a prevalence of agricultural landscape in the surrounding.

The agricultural landscape in the surroundings of the two examined study sites is composed mainly of fertilised arable lands, which, due to the potential periodic surface runoff of nutrients, may maintain the fertility of soils on the studied plots. Furthermore, given that the examined wastelands are post-agricultural and have been abandoned for no longer than two to four years, before the conductance of our study, they can still be characterised by high soil fertility, linked with historical land-use (Rejmánek 1989; Davis et al. 2000; Kulmatiski et al. 2006; Boscutti et al. 2018). As in the case of river net length, a higher contribution of fertile agricultural areas in the surrounding landscape had positive impacts on the total above ground biomass of *S. canadensis* (in a buffer of 500 m), thus promoting its colonisation abilities, and increasing the invasion success. This may correspond with strong negative relationships between arable lands contribution (in 1000 and 100 m buffers) and two functional diversity components (functional dispersion and functional divergence) under a high cover of *S. canadensis*. Based on our results, we may consider these effects not only as outcomes, but also as drivers of invasion, maintaining the studied vegetation in the early stages of succession, and influencing the invasion-induced biotic homogenisation of the studied wastelands (Olden et al. 2018). This is in line with results from other studies, revealing the negative

impacts of *S. canadensis* on the functional diversity of recipient communities (Wang et al. 2019, 2020), which was demonstrated also in this study. Thus, this may hint at the important role of agricultural areas in shaping the competitive potential of this invader in the context of competition for above ground space (in our case, expressed by a positive relationship between arable lands cover and total above ground biomass of *S. canadensis*), facilitating its spread, when competition for resources is limited.

Apart from the positive effects on total above ground biomass, an increasing contribution of agricultural areas in a buffer of 500 m, positively influenced the biomass of *S. canadensis* flowers. One should expect that in more fertile soils, plants can produce the biomass being allocated relatively equally to all organs, in our case, expressed in higher flower and total above ground biomass (Ren et al. 2019, 2020b; Adomako et al. 2020). However, a higher contribution of the open and homogenous landscape of arable fields in the surrounding, at the same time, may act as a habitat filter, generating environmental stress linked with higher insolation, higher temperature amplitudes, more pronounced drought events and evaporation, as well as the surface runoff of herbicides (Medeiros et al. 2016). In this context, higher production of flowers may be considered as a response of *S. canadensis* to these extreme habitat conditions (Du et al. 2019). Thus, the production of a higher biomass of flowers under the conditions of a higher proportion of agriculture in the surrounding may demonstrate the astounding abilities of *S. canadensis* for seed production, as well as maintaining long-distance spread and the colonisation of new localities (Boscutti et al. 2018; Chen et al. 2013).

Effects of settlements on functional diversity and biomass of *S. canadensis*

Species composition and the diversity of vegetation developing in urban landscapes can be influenced by a wide range of stress factors, acting not only locally (e.g. intense mowing, trampling, mechanical destruction and soil compaction, sand and gravel exploitation, post-mining heaps and other artificial substrates, fertilisation, nutrient deficiency, and pesticides), but also at larger spatial scales (LaPaix and Freedman 2010; Concepción et al. 2017;

Chollet et al. 2018). This second group of factors can include various availability of habitats suitable for plant colonization and establishment, various connectivity between urban green islands serving as important propagule sources, various landscape heterogeneity, industry-driven pollution, as well as urban heat island effect (Chocholoušková and Pyšek 2003; Zhang et al. 2004; Vilà and Ibáñez 2011; Čepelová and Münzbergová 2012; González-Moreno et al. 2013b; Li et al. 2017; Czortek and Pielech 2020). Thus, the high complexity of habitat filters acting on plant species differentially may promote the occurrence of plants characterised by extreme dissimilarities between functional trait values carried by different species (Mason et al. 2005; Villéger et al. 2008), making the larger volume of niche hyperspace filled by particular combinations of plant functional traits (Hedberg et al. 2014). Positive relationships between the contribution of settled areas and two components of functional diversity (functional divergence and functional richness; both in 100 m buffers) under a low level of *S. canadensis* invasion may support this idea. Contrary, under high levels of *S. canadensis* invasion, relationships between the settlements contribution and the two above-mentioned biodiversity components became strongly negative, hinting at high role of settlements in shaping this invader's success. However, under a high complexity of habitat filters in an urban landscape, *S. canadensis* could invest less energy in mechanisms allowing effective competition for space, light, or photosynthesis effectiveness, exhibited in a negative relationship between leaf biomass and the proportion of settlements in a 1000 m buffer. On the other hand, a positive effect on flower biomass may demonstrate the strategy of *S. canadensis* for maximising the odds of survival and indicate high adaptability to existing under the dominance of black and grey infrastructure in the surrounding (Du et al. 2019). Thus, a higher contribution of settlements in the surrounding could promote reproductive allocation at the expense of a reduction of vegetative growth (Cheng et al. 2021). This strategy may be of crucial importance, at a time of global urban sprawl, which in comparison with current conditions, may lead to an expansion of *S. canadensis* potential geographic distribution under future climate warming (Xu et al. 2014).

Conclusions

Based on the results obtained, we conclude that investigating the relationships between landscape types in different spatial scales, and biomass allocation patterns, may provide a powerful basis for the assessment of *S. canadensis* invasiveness in human-transformed ecosystems. Our study revealed that the composition of the surrounding landscape may shape trade-offs between the allocation of biomass for the development of functionally different organs, exerting impacts on *S. canadensis* acquisition and utilisation of resources, as well as reproduction strategies. We demonstrated that directions of relationships between the surrounding landscape composition and functional diversity were influenced strongly by *S. canadensis* cover, making the results obtained highly context-dependent. Thus, through influencing the importance of habitat filtering in shaping species composition, the structure of the landscape in the surrounding can facilitate the spread of *S. canadensis* and increase its invasion success. Therefore, the surrounding landscape may not only shape *S. canadensis* invasiveness, but simultaneously, can also influence ecosystem invasibility; thus, providing a comprehensive explanation of the mechanisms underlying successful *S. canadensis* invasion. Although we formulate our conclusions based on an indirect approach, we assert that the assessment of the relationships between invasive species biomass, plant functional diversity, and surrounding landscape composition may be considered as a useful tool for predicting the invasion risks and in the formulation for proper strategies of invasive species management in transformed ecosystems.

Author contributions PC, EK and LB conceived the ideas and designed methodology; EK, LB and AB collected the data; PC analysed the data. The first draft of the manuscript was written by PC and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability Raw data is stored in repository of the Białowieża Geobotanical Station of the University of Warsaw (Sportowa 19, 17-230 Białowieża, Poland) and may be available on reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval The study did not involve human or animal participants as a study subjects.

Consent to participate The authors agreed to be included as co-authors of the manuscript.

Consent to publication The authors declare agreement for publication of the manuscript in the Biological Invasions journal.

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