Diversity and Distributions

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Hypervolume Trait Spaces Reveal Similarities but Also Functional Differentiation Across Riparian, Roadside and Field Margin Habitats

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ABSTRACT

Aim: To characterize plant species pools and functional diversity of three common linear habitats—riparian corridors, roadsides and field margins—and to evaluate their potential roles in regional biodiversity conservation, particularly regarding invasive and threatened species.

Location: Temperate landscapes in the United Kingdom, France and Spain.

Methods: We compiled vegetation surveys and distinguished species common to multiple habitats and those restricted to a single habitat. We then compared taxonomic and functional diversity (as measured by hypervolumes) across habitats based on traits related to disturbance tolerance, ecological strategy and dispersal.

Results: A quarter of the species pool was shared among the three habitats, and indicator-species overlap was strongest between roadsides and field margins. Riparian corridors had the highest species richness, the greatest number of habitat specialists and the largest functional trait hypervolumes. Roadsides showed comparable richness but substantially lower functional diversity, whereas field margins supported the lowest richness. Although field margins had more disturbance-adapted annuals, all habitats showed similar functional diversity in disturbance tolerance. In contrast, ecological strategies and resource requirements differed strongly, reflecting habitat-specific filtering by hydrology, soil conditions and management regime. Invasive species were most frequent in riparian corridors and roadsides, tended to be large and suited to productive, disturbed environments, while threatened species were more habitat-specific, generally small, sensitive to eutrophication and associated with frequently disturbed but nutrient-poor sites.

Main Conclusions: Riparian corridors emerge as hotspots of both taxonomic and functional diversity, but also as key invasion hotspots, whereas roadsides and field margins support narrower ecological strategies. The co-occurrence of invasive and threatened species in disturbed sites within linear habitats, combined with their contrasting trait syndromes (height and nitrophily),

highlights the need for coordinated management at a broader scale. Protecting vulnerable flora while limiting the spread of invasive species will require controlling nutrient inputs at the catchment scale.

1 | Introduction

In landscapes shaped by human activity, three linear habitats dominate: riparian corridors, roadsides and field margins (Tikka et al. 2001; Marshall and Moonen 2002; Belletti et al. 2020). They act as important local refuges for plant biodiversity in agricultural landscapes (Santibañez et al. 2024) and may also represent complementary habitat compartments that contribute to diversity patterns at broader landscape scales. Yet, the extent to which they differ in terms of species pools and functional diversity remains poorly understood. Do these habitats host similar plant communities due to their shared linear structure and anthropogenic influence, or do local environmental constraints drive functionally distinct assemblages? Moreover, their importance for supporting threatened species and their potential to facilitate the spread of invasive species remain insufficiently explored (Phillips et al. 2020; Auffret and Lindgren 2020).

Riparian corridors, roadsides and field margins share similar configurations in the landscape: they are linear, edge-dominated, strongly influenced by adjacent land use, exposed to natural and anthropogenic disturbances and function as corridors for species dispersal. As such, they can serve as refugia for native flora and fauna by offering shelter from intensive land use (Forman 1995; Sabo et al. 2005; Hilty et al. 2019). At the same time, they can serve as conduits for invasive alien species spread (Kowarik and Von der Lippe 2011; Aronson et al. 2017; Deeley and Petrovskaya 2022). The spatial connectivity between these three linear habitats may further facilitate species movement, potentially leading to overlaps in community composition (Rievrs-Borges et al. 2025). Given these shared attributes and their proximity, we expect some level of functional similarity among plant communities, even if taxonomic differences exist.

However, despite these shared features, the three linear habitats are shaped by distinct ecological filters, including differences in dispersal limitations, environmental conditions, resource availability (e.g., light, water, nutrients) and disturbance regimes. Their capacity to support species movement also depends on their continuity and spatial structure: riparian corridors and roadsides often form more continuous corridors (Vorstenbosch et al. 2020) whereas field margins are typically more fragmented.

Environmental conditions further shape trait composition through habitat filtering. Riparian corridors are shaped by river hydrogeomorphic dynamics, creating strong environmental gradients from the stream channel to the habitat margins (Ward et al. 2002; Naiman et al. 2010; Tabacchi et al. 2024). This heterogeneity fosters the coexistence of diverse plant assemblages, with species distributed along fine-scale gradients of moisture, substrate stability and hydrological disturbance intensity. Environmental gradients tend to be shorter in roadsides and even more in field margins. Roadsides typically have compacted, nutrient-poor soils, episodic exposure to pollutants such as heavy metals, nitrogen oxides, particulate matter and de-icing salts. Stressful conditions near the pavement select for species tolerant of dry, high-light environments (Šerá 2010), while outer roadside zones may vary in moisture (presence of ditches) and may host scattered woody vegetation. In contrast, field margins are generally located in fertile environments where other conditions tend to be moderate, neither excessively wet nor too dry (Brady and Weil 2007). Here, fertilization runoff of adjacent fields is expected to favour nutrient-demanding species with acquisitive strategies (Fried et al. 2018).

Disturbance regimes further differentiate linear habitats, influencing species persistence and turnover. In riparian corridors, these disturbances largely reflect the same hydro-geomorphic dynamics described above—periodic and spatially irregular floods, sediment transport, erosion and deposition—which alter topography and filter species with physiological adaptations to scour, burial, water stress and inundation, such as clonal growth, specialized roots, aerenchyma tissues or floating seeds (Catford and Jansson 2014; Canham et al. 2023). Because disturbance intensity varies across the floodplain, these processes repeatedly reset successional stages and generate high spatial heterogeneity. This promotes the coexistence of early-successional colonizers and disturbance-adapted perennial species (Naiman et al. 2010) and enhances taxonomic diversity (Stanford et al. 2005). In contrast, roadside and field margin vegetation is directly managed by humans, typically through regular mowing (Marshall and Moonen 2002). Soil compaction, maintenance and mowing favour ruderal species with fast growth and strong recovery (Šerá 2010), while herbicide drift can further intensify disturbances in field margins (Fried et al. 2018; Poinas et al. 2023).

Invasive species (i.e., species introduced by humans whose establishment and spread pose ecological risks to ecosystems, habitats, or native species (IUCN 1999)) are known to thrive and spread in linear habitats, potentially outcompeting native species (Simberloff et al. 2013; Vilà and Hulme 2017). Conversely, linear habitats may also act as refuges for threatened species in areas where suitable conditions have disappeared from the surrounding landscape (Auffret and Lindgren 2020). Comparing the traits of invasive and threatened species across these habitats can reveal how habitat characteristics and management influence their spread or persistence.

While several studies have investigated plant diversity and functional traits in these habitats separately (Maskell et al. 2006; Follak et al. 2018; Fried et al. 2024), none have directly compared species pools and functional composition across all three habitat types and at a large spatial extent. In this study, we aim to fill this gap by analysing species pools and selected functional traits in riparian corridors, roadsides and field margins across multiple regions in Western Europe. Similar to Hutchinson's (1957) approach to characterize species niches, we used a hypervolume approach to represent the multidimensional functional traits space occupied by species assemblages (Blonder 2018), based on a dataset integrating plant species occurrences from large-extent vegetation surveys. Specifically, we characterized plant ecological strategies using functional traits related to life-history trade-offs, resource use and disturbance adaptation. We then address

the following questions: (1) How do the species pools of riparian corridors, roadsides and field margins compare in terms of richness and to what extent do they overlap taxonomically? (2) How does functional composition differ across habitats in terms of dispersal, ecological strategies, resource requirements and responses to disturbances? (3) How are invasive and threatened species represented across the three habitats and how do their traits differ between habitats and compared to other species from the same pool? We hypothesize that the greater environmental heterogeneity of riparian corridors will result in higher taxonomic and functional richness. We further expect that field margins and roadsides will share a higher proportion of ruderal and disturbance-adapted species (Gelbard and Belnap 2003; Hovd and Skogen 2005), while riparian corridors will support more functionally distinct assemblages shaped by hydrological variability (Tabacchi et al. 2019). Finally, we hypothesize that invasive species will be more prevalent in roadsides and riparian corridors, due to the combined effects of their corridor function and frequent disturbances and will exhibit generalist traits (Rejmánek et al. 2013). In contrast, we expect threatened species to be more habitat-specific (Kolb and Diekmann 2005) and characterized by more specialized trait values.

2 | Methods

2.1 | Species Occurrence and Abundance Data

To represent the main plant species occurring in riparian corridors, roadsides and field margins across Western Europe, we compiled four major vegetation datasets from northeastern Spain (Catalonia), France and the UK (Table 1).

The 500 ENI Network (*Effets Non Intentionnels*, i.e., unintended effects) (2012–2020) comprises 544 floristic samples collected from approximately 500 field margins across France. Vascular plants were surveyed annually in ten fixed 1 m^2 quadrats per site, providing pseudo-abundance estimates ranging from 1 to 10 quadrats (Andrade et al. 2021; Fried et al. 2024). The TGB dataset (*Trames Grise et Bleu*, i.e., grey and blue infrastructure networks) covers southwestern France (Garonne and Adour catchments), with 1082 roadside and 1197 riparian plots (1 m^2 quadrats, percent cover; (Rievrs-Borges et al. 2025)). The Lleida Plain dataset (Catalonia) comprises 754 plots from 2003 to 2010 across the Segre and Noguera-Ribagorzana rivers and adjacent roadsides and field margins (1–200 m^2 plots; Solé-Senan et al. 2014, 2018; Juárez-Escario et al. 2016). Finally, the UK Countryside Survey 2007 contributed 4641 plots from margins, roadsides and riverbanks (4–10 m^2), with percent-cover estimates (Smart et al. 2003; Carey et al. 2008). Further details on survey protocols, sampling design and harmonization procedures are provided in Appendix S1 and Table 1.

When merging raw data into a single dataset, species names were standardized using the *Taxonstand* R package (Cayuela et al. 2021). Abundances were standardized to percentage cover using a subset of the '500 ENI' dataset, in which surveys recorded both percentage cover and pseudo-abundance based on presence in 10 quadrats. This subset showed a strong correlation between the two measures (Pearson's $r = 0.82$), allowing the derivation of a conversion function (see Appendix S2 and Figure S1 for details).

2.2 | Functional Trait Data

We characterized plant ecological strategies using key functional traits and ecological indicators (Table 2). Specific leaf area (SLA), plant height and seed mass from the TRY database version 6 (Kattge et al. 2020) captured the main axes of the Leaf-Height-Seed (LHS) scheme (Westoby 1998), reflecting resource use, competitive ability and reproductive strategy (Díaz et al. 2016). Species' environmental preferences were described using Ellenberg indicator values (EIV) for nitrogen, light and moisture derived from the literature (Tichý et al. 2023), as well as through recently derived indicator values of their tolerance to disturbance severity and frequency (Midolo et al. 2023), hereafter referred to as DIS. Information on dispersal mode (animal, gravity, water, wind) and life form (therophytes, hemicryptophytes, geophytes and woody species) was extracted from Baseflor (Julve 2024).

2.3 | How Do Species Richness and Taxonomic Overlap Vary Across Habitats?

To compare species richness among habitats while accounting for differences in sampling effort, we generated species accumulation curves using the *specaccum* function (method = 'random', permutations = 5000) from the vegan R package (Oksanen et al. 2022). Given that the habitat with the lowest sample size (field margins) included $n = 775$ plots, we reported estimated gamma diversity for a standardized sampling size of $n = 600$ plots across all habitats to allow fair comparisons, as values

TABLE 1 | Overview of the number of plots available by habitat and region.

Datasets	Riparian corridors	Roadsides	Field margins	Total
France (500ENI + TGB)	1197	1082	544	2823
500 ENI	0	0	544	544
TGB	1197	1082	0	2279
Spain (Lleida Plain)	604	30	120	754
UK (GB Countryside Survey)	2349	2181	111	4641
Total	4150	3293	775	8218

Abbreviations: 500 ENI, For *Effets Non-Intentionnels* [Unintentional Effects]; GB, Great Britain; TGB, *Trames Grise et Bleue* [Grey and Blue Networks].

TABLE 2 | Functional trait and environmental preference variables used in the analyses, including units/categories, value ranges and data sources.

Traits	Type	Nature	Unit or categories	Range or number of species	Source
Specific Leaf Area (SLA)	Functional trait	Continuous	$mm^2 \cdot mg^{-1}$	2.6–107.6	TRY (Kattge et al. 2020)
Plant height	Functional trait	Continuous	m	0.002–22.5	TRY (Kattge et al. 2020)
Seed mass	Functional trait	Continuous	mg	0.016–9306	TRY (Kattge et al. 2020)
Dispersal mode	Functional trait	Categorical	Animal	203	Baseflor (Julve 2024)
			Gravity	147	
			Water	20	
			Wind	105	
Life forms	Functional trait	Categorical	Woody	68	Baseflor (Julve 2024)
			Geophytes	41	
			Hemicryptophytes	209	
			Therophytes	157	
EIV-Light	Environmental preferences	Continuous	Ordinal scores from 1 to 9	4.7–9	Tichý et al. (2023)
EIV-Moisture	Environmental preferences	Continuous	Ordinal scores from 1 to 12	1–11.9	Tichý et al. (2023)
EIV-Nutrients	Environmental preferences	Continuous	Ordinal scores from 1 to 9	1–8.9	Tichý et al. (2023)
DIS-Frequency	Tolerance to disturbance	Continuous	0–2+	0.905–2.239	Midolo et al. (2023)
DIS-Severity	Tolerance to disturbance	Continuous	0–1	0.124–0.853	Midolo et al. (2023)

closer to the lowest sample size (775) reduced stochastic variation in the resampling procedure.

For taxonomic overlap assessment, we first needed to balance sampling effort between habitats and regions. We used a stratified resampling approach: for each habitat, we randomly resampled 5000 times 500 surveys using a weighting that applies an inverse weight to the number of surveys available from each region (i.e., the probability of drawing a survey in a region with n surveys is 1/n). This procedure minimizes bias that could incorrectly associate a species with a particular habitat due to disproportionate representation of that habitat within a specific region. For each resampling iteration, we computed species frequency (occurrence across surveys) and mean abundance separately, resulting in two parallel data structures (a frequency matrix and an abundance matrix), each with 15,000 rows (5000 resamples × 3 habitats) and 1878 species. We then summarized these resampled matrices by averaging across the 5000 iterations for each habitat, yielding a single matrix of mean species frequency and a second matrix of mean species abundance, both structured as 3 habitats × 1878 species. In the following text, these resampled matrices are referred to as the 'resampled datasets'. To assess the extent of taxonomic overlap among the species pools of the three habitats, we performed a comparison at two levels: (i) using the data based on the presence-absence of species in each habitat (full species pool) and (ii) using only the species identified as habitat indicators. This two-level approach is necessary because relying solely on the full species pool may inflate apparent habitat overlap as it includes species that may occur there by chance due to dispersal, regional pool effects, or uneven sampling. Reducing the number of species allows us to contrast patterns based on the entire regional species pool with those based on a more conservative and ecologically more strongly constrained subset. For the latter, we used the IndVal method (Dufrêne and Legendre 1997) as implemented in the *indicspecies* R package (De Cáceres and Legendre 2009), which identifies species with significantly higher *specificity* (degree of exclusivity to a habitat based on relative abundance) and *fidelity* (frequency within sites of that habitat) than expected by chance. As a conservative approach to avoid including accidental species, we set mean cover abundances below 0.1% to zero in the input matrix before running the IndVal analysis and retained only species with occurrence frequencies above 1% afterward.

Based on the IndVal analysis, we classified species into seven groups: single-habitat specialists (ri: riparian corridors, ro: roadsides, fm: field margins), dual-habitat specialists (riro, fmro, fmri) and generalists (gen), i.e., species that are not indicative of

any particular habitat. We refer to the *species pool* of a habitat as all species observed in it (e.g., the field margin pool includes fm, fmro, fmri and gen) and to species groups as the six groups identified by IndVal (ri, ro, fm, riro, fmro, fmri) and the generalist group. Every species belongs to only one group, e.g., no species can be in both the ri and fmri group.

2.4 | How Do the Functional Traits of Species Pools Differ Across Habitats?

Trait differences among indicator species in each group, as well as in the generalist group (476 species), were assessed using Kruskal–Wallis tests followed by Dunn's post hoc tests with Benjamini–Hochberg correction for multiple comparisons (quantitative traits) and Fisher's exact tests for categorical traits. For the missing trait data (4.9% of species-traits entries), we used the '*mice*' R package algorithm for imputation (van Buuren and Groothuis-Oudshoorn 2011). One species (*Hypecoum procumbens*, a field margin specialist) with too many missing values was excluded because the imputation algorithm cannot reliably handle a high proportion of missing values. For Ellenberg indicator values, 'x' entries, indicating species with no preferences, were replaced with the median value of the observed numeric scores for the corresponding indicator. Next, we assessed the functional diversity of the three habitats using a hypervolume approach implemented in the '*BAT*' R package (Cardoso et al. 2015; Mammola and Cardoso 2020). Unlike convex hulls, hypervolume methods account for irregular trait distributions and are less sensitive to outliers (Blonder 2018), providing a more realistic estimate of functional diversity. We quantified this diversity using two metrics: functional richness, defined as the total volume of trait space occupied by the species pool and functional dispersion, defined as the mean distance between stochastic points within the hypervolume and the hypervolume centroid, using the default implementation in BAT::kernel.dispersion, which corresponds to functional divergence sensu Laliberté and Legendre (2010). Higher functional richness therefore indicates a broader range of functional trait values and a greater diversity of ecological strategies represented in the species pool, whereas higher functional dispersion reflects greater heterogeneity in trait composition, with species more widely spread in trait space rather than clustered around the functional centroid.

We generated three hypervolume types: (1) LHS traits, (2) EIVs (resource requirements) and (3) DISs (tolerance to disturbances). Beyond following best practices formulated by Mammola and Cardoso (2020) that recommended to use a maximum of 3–5 traits per hypervolume, this approach allowed us to disentangle the relative contribution of each functional dimension (ecological strategies, resource requirements, tolerance to disturbances) to the differentiation of the three habitats. To account for variations in the number of habitat-indicator species, we subsampled n species from riparian corridors and n species from roadsides 999 times, where n corresponds to the number of field margin indicator species (the smallest group, $n = 88$ species with sufficient trait data). This resulted in 999 riparian species hypervolumes, 999 roadside species hypervolumes and one field margin hypervolume. Differences in functional richness and dispersion between riparian, roadside and field margin habitat-indicator species were assessed by comparing the frequency distributions of the 999 riparian and 999 roadside hypervolumes with the single field margin hypervolume. The field margin value was considered significantly smaller or larger when it fell outside the 95% range of the simulated hypervolumes (i.e., below the 2.5th percentile or above the 97.5th percentile). Similarly, riparian and roadside hypervolumes were considered significantly different when their 95% distributions did not overlap.

2.5 | Do Invasive and Threatened Species Differ in Distribution and Traits Across Habitats?

We focused on two subsets of species of particular conservation concern: (i) threatened species, based on IUCN Red List status and (ii) invasive alien species. For invasive alien species, we used national and regional sources: the Centre de ressources—Espèces exotiques envahissantes (2025), retaining taxa listed as invasive in at least two French regions; the BSBI list of invasive plants of concern for the UK (Botanical Society of Britain and Ireland 2024) and the Aymerich and Sáez (2019) checklist for Catalonia. For threatened species, we used Red Lists from France (UICN France et al. 2018), the UK (Stroh et al. 2014) and Catalonia (Aymerich and Sáez 2021), including taxa classified as Vulnerable (VU), Endangered (EN), or Critically Endangered (CR). We then examined how trait values of invasive and threatened species differed among the seven habitat groups (fm, ri, ro, fmri, fmro, riro and generalists) and relative to other species within each group, using Kruskal–Wallis and Dunn's post hoc tests on normalized trait values.

3 | Results

3.1 | Taxonomic Comparison of the Three Habitats

Across the resampled dataset, 1878 plant species were recorded: 763 in field margins, 1333 along roadsides and 1419 in riparian corridors. At this stage, 204 species, statistically too rare in the initial matrix (often singletons), were excluded because they were never drawn in the resampling procedure. Species accumulation curves showed that riparian corridors and roadsides had the highest gamma diversity (Appendix S3, Figure S2). For $n = 600$ samples (5000 permutations), computed gamma diversity ± SD was 842 ± 24 for riparian corridors, 838 ± 28 for roadsides and 712 ± 10 for field margins.

Presence–absence data indicated that 29% of species were shared between roadsides and riparian corridors, while 24% occurred in all three habitats (Figure 1A). Overlap between roadsides and field margins was 6% and between field margins and riparian corridors only 3%. Riparian corridors hosted the largest proportion of unique species (19%), followed by roadsides (11%) and field margins (7%).

When focusing on the 429 indicator species (plus 47 generalists), patterns were similar (Figure 1B). Riparian corridors contained the highest proportion of unique indicators (25%), followed by roadsides (20%) and field margins (19%). Shared

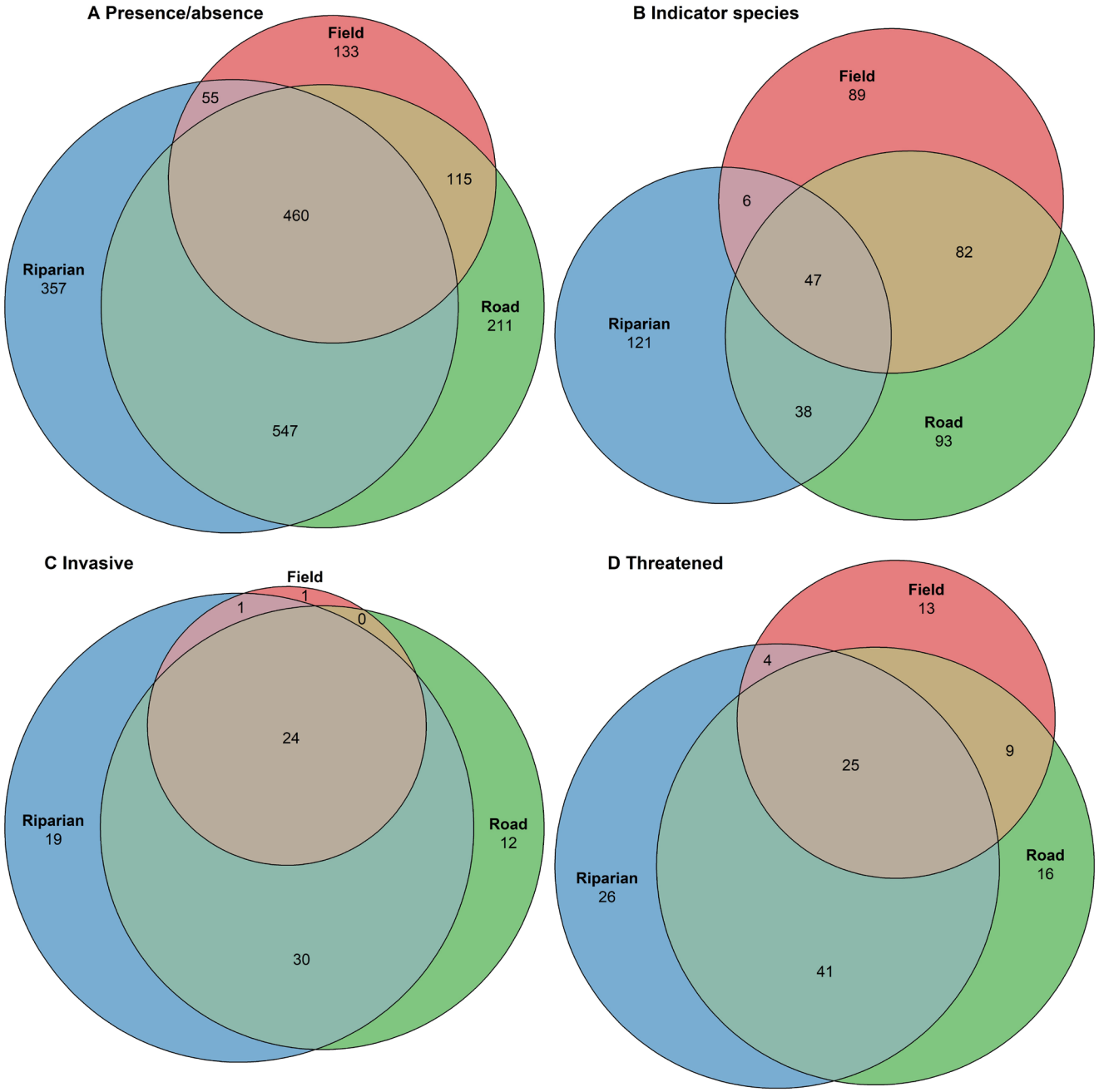

FIGURE 1 | Number of unique species across habitats based on: (a) presence records of all species across the four original sources (resampled dataset); (B) indicator species of each habitat and group of two habitats calculated with IndVal (in this case, the triple interaction zone corresponds to generalist species that are not specialists in any habitat(s) but with a frequency > 1% in all three habitats), (C) presence records of all invasive species across the four original sources (resampled dataset) and (D) presence records of all threatened species across the four original sources (resampled dataset). We used the function euler in the eulerr package (Larsson 2021).

indicators were most common between field margins and roadsides (17%), whereas field margins and riparian corridors shared only 1%. Generalists represented 10% of all species. Based on indicator analysis, 57% of riparian species were single habitat specialists, compared with 40% in field margins and 35% in roadsides.

The five most frequent species overall—*Dactylis glomerata*, *Plantago lanceolata*, *Convolvulus arvensis*, *Agrostis stolonifera* and *Arrhenatherum elatius*—were all generalist and native species (Appendix S4, Table S1). Riparian corridors were characterized by a higher relative contribution of specialist species (e.g., *Phragmites australis*, *Lythrum salicaria*, *Salix alba*), indicating a greater representation of habitat-specific ecological strategies. In contrast, field margins and roadsides were dominated by generalist species (e.g., *Dactylis glomerata*), while specialist species were comparatively less represented, particularly in field margins. See Tables S2–S4 in Appendix S5 for the 40 most frequent species in each habitat.

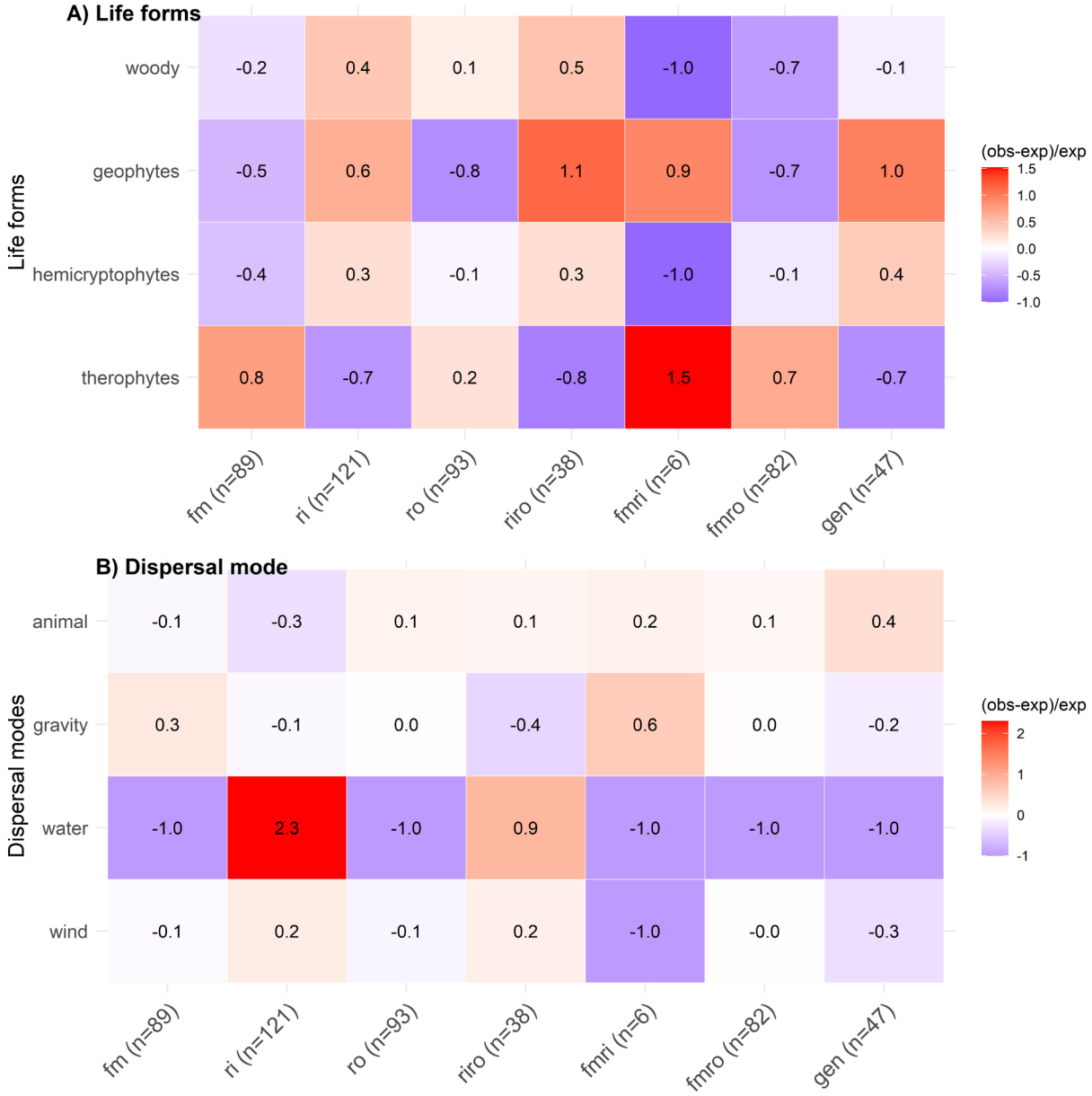

FIGURE 2 | Standardized residual heatmaps from Chi-squared tests showing associations between species traits and species groups. (A) Life forms: Woody plants, geophytes, hemicryptophytes and therophytes across species groups. (B) Dispersal modes: Animal, gravity, water and wind dispersal across habitat combinations. Residuals are expressed as (observed−expected)/expected values; positive values (red) indicate trait overrepresentation in a habitat group and negative values (purple) indicate underrepresentation. Habitat group codes: Fm, field margins; ri, riparian corridors; ro, roadsides; fmri, field margins & riparian corridors; fmro, field margins & roadsides; riro, riparian corridors & roadsides; gen, species common to all three habitats. Residuals are based on Chi-squared contingency tables and follow-up Fisher exact tests for each trait category. Fisher's exact tests indicate whether the observed distribution of values across cells differs from that expected under a model of independence, i.e., whether trait categories are non-randomly distributed among species groups. The colour gradient highlights the magnitude and direction of these deviations from expectation, with more intense colours indicating stronger departures from independence rather than a significance threshold.

3.2 | Functional Composition of the Species Pools Related to the Three Habitats

Life form and dispersal mode distributions differed significantly among species groups (Fisher exact tests, both $p < 0.001$; Figure 2). Therophytes were strongly overrepresented in field margins (+80% compared to expected) and in their shared groups with riparian corridors (+150%) and roadsides (+70%), whereas hemicryptophytes were moderately more represented among generalists (+40%) and riparian-associated species (+30%). Geophytes were more frequent in riparian-related groups (+60–110%), and woody species were slightly overrepresented in riparian corridors (+40%) and the riparian–roadside group (+50%).

For dispersal modes, water-dispersed species were highly overrepresented in riparian corridors (+230%) and the riparian–roadside group (+90%), while gravity-dispersed species prevailed in field

margins (+30%) and in the field margin–riparian group (+60%). Animal-dispersed species were over-represented among generalists (+40%) but under-represented in riparian corridors (−30%). Wind-dispersed species varied little across groups.

All quantitative traits differed significantly among species groups (Kruskal–Wallis tests, $p < 0.01$; Figure 3). Specific leaf area (SLA) was highest in generalists (+26%) and in field margins (+23%) compared to roadsides (percentages indicate relative

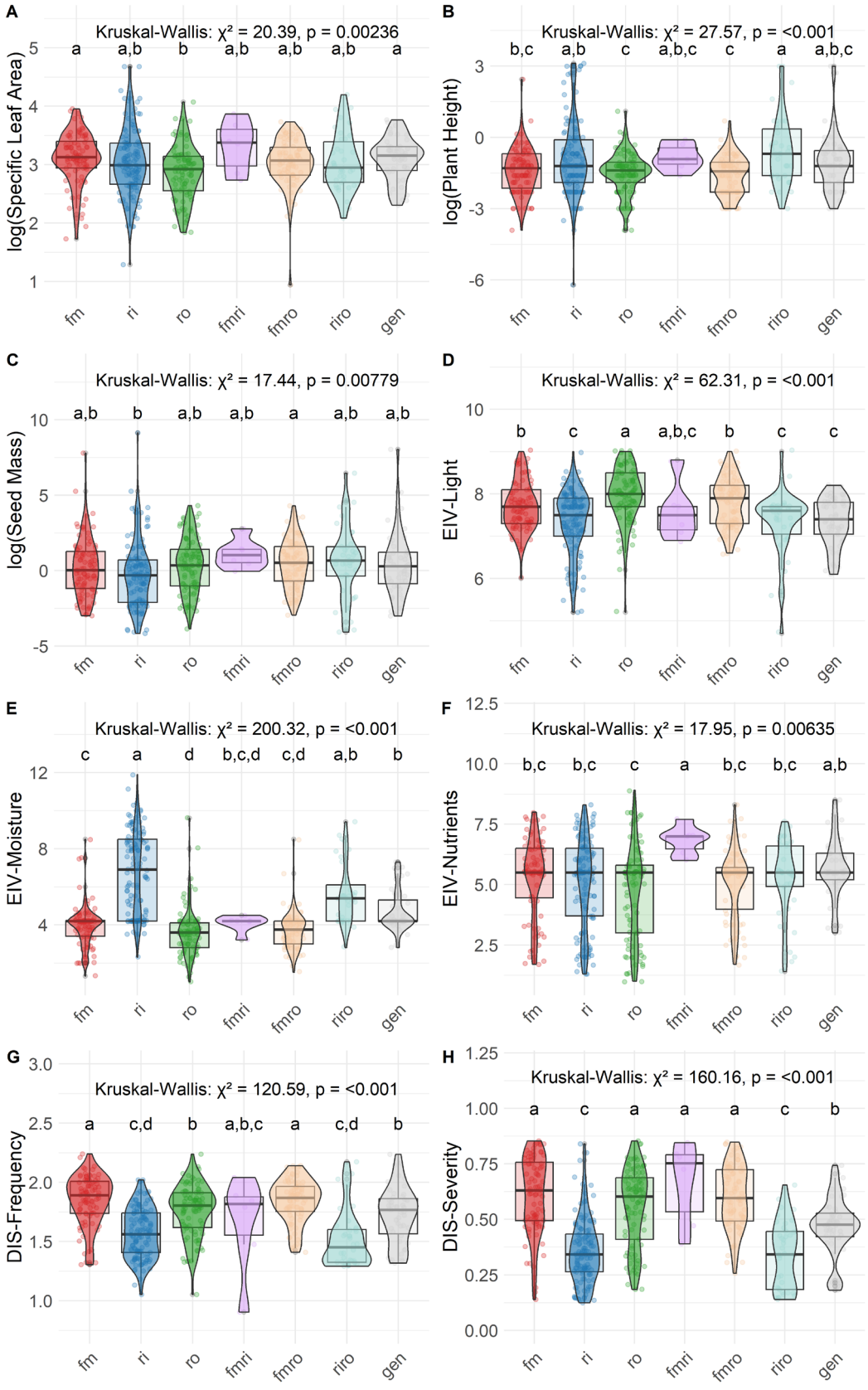

FIGURE 3 | Legend on next page.

FIGURE 3 | Boxplots and violin plots showing the distribution of trait values across species groups for: (A) Specific Leaf Area (SLA; $mm^2 \cdot mg^{-1}$), (B) Plant height (m), (C) Seed mass (mg), (D) Ellenberg indicator values (EIV) for light, (E) EIV for soil moisture, (F) EIV for nutrients, (G) Disturbance indicator values (DIS) for disturbance frequency and (H) DIS for disturbance severity. Species groups are: Fm, field margins; ri, riparian corridors; ro, roadsides; fmri, field margins & riparian corridors; fmro, field margins & roadsides; riro, riparian corridors & roadsides; gen, species common to all three habitats. Different letters indicate significant differences among groups based on Dunn tests ($\alpha = 0.05$), adjusted using the Benjamini–Hochberg procedure, following a global Kruskal–Wallis test. Note that the Y axis in panels A–C are log-transformed (in these cases, KW-tests were done on log-transformed data).

differences based on the values shown in Figure 3). Plant height was twice as high (+100%) in the riparian–roadside group and 20% higher in riparian corridors than in roadsides. Seed mass was greatest in the field margin–roadside group (+131%) compared to riparian corridors (Figure 3A–C).

For ecological indicator values, EIV-Moisture was 64% and 92% higher in riparian corridors relative to field margins and roadsides, respectively, while EIV-Light was slightly higher in roadsides (4% and 7%) compared to field margins and riparian corridors, respectively (Figure 3D,E). EIV-Nutrient was higher in the field margin-riparian group (+45%) and in the generalists (+20%) compared to roadsides (Figure 3F).

For disturbance, DIS-Frequency was highest in field margins and the field margin–roadside group, intermediate in roadsides and lowest in riparian corridors, with field margin-associated groups 20%–21% higher than riparian corridors. DIS-Severity showed a similar pattern, with the highest values in field margin species pools (fm, fmri, fmro) and roadsides and the lowest values in riparian corridors. This corresponds to increases of 74%–120% relative to riparian corridors (Figure 3G,H).

3.3 | Functional Diversity of the Species Pools Related to the Three Habitats

For Leaf-Height-Seed (LHS) traits and Ellenberg Indicator Values (EIVs), functional richness (hypervolume volume) was highest in riparian corridors (Figure 4A,C). For LHS traits, functional richness in riparian corridors was 170% greater than in roadsides and 160% greater than in field margins, with no significant difference between field margins and roadsides. For EIVs, functional richness in riparian corridors was 134% greater than in field margins and 90% greater than in roadsides, while roadsides were 49% greater than field margins. Riparian species also exhibited greater functional dispersion: LHS trait dispersion was 34% and 48% higher than in field margins and roadsides, respectively, and EIV dispersion was 10%–30% higher than in the other two habitats (Figure 4B,D).

For disturbance indicator values (DIS), the pattern differed with slightly higher values for roadsides (Figure 4E,F), but no significant differences were detected among the three habitats for either functional richness or functional dispersion.

3.4 | Invasive and Threatened Species: Differences in Habitat Associations and Trait Values

Our dataset included 87 invasive and 134 threatened species. The most frequent invasives were *Bidens frondosa*, *Paspalum distichum* (both 13% in riparian corridors) and *Veronica persica* (10% in field margins) (Appendix S6, Table S5). *Reynoutria japonica* (1% overall) occurred mainly along roadsides and riparian corridors, while *Ambrosia artemisiifolia* (0.3%) was present in all habitats, mostly in field margins. The most frequent threatened species were *Filago pyramidata*, *Medicago minima* and *Petrorhagia prolifera*, all annual species, which are rare in Great Britain (Endangered (EN), Vulnerable (VU) and Endangered (EN) status, respectively) but still common in France and Catalonia in open habitats including field margins and roadsides (Appendix S6 gives the top ten most frequent invasive (Table S5) and threatened (Table S6) species for the three habitats).

Distribution patterns differed between the two groups: invasive species included a higher proportion of generalist species occurring in all three habitats (28%) compared to threatened species (19%), whereas threatened species comprised more single-habitat specialists (41% vs. 37%; Figure 1C,D, these values should be interpreted as relative proportions and not as statistically tested contrasts). In riparian corridors, invasive species were more frequent and abundant than non-invasive ones (including both native species and non-invasive non-native species), while other species (non-invasive, non-threatened) were more frequent and abundant than threatened species (Kruskal–Wallis, $p < 0.001$; see Appendix S7 for more details). In field margins, invasive species occurred less frequently than other (non-invasive, non-threatened) species, whereas no significant differences were detected along roadsides.

Compared to other species, invasives were taller and preferred nutrient-rich soils, while threatened species were shorter (Figure 5). Both groups were also associated with higher requirements for soil moisture and greater tolerance to disturbances (Figure 5). Life form and dispersal patterns showed marked contrasts: threatened species exhibited higher proportions of therophytes (+76%) and geophytes (+45%), whereas invasives showed a higher proportion of woody species (+59%, Fisher's exact $p < 0.001$; Appendix S8, Figure S3A). Percentages indicate relative differences in proportional representation among groups. Invasives were also +66% water-dispersed and +25% wind-dispersed, while threatened species had +135% water-dispersed and +21% gravity-dispersed species (Appendix S8, Figure S3B).

4 | Discussion

Our results reveal both similarities and differences in species pool composition, functional traits and conservation value among riparian corridors, roadsides and field margins across Western Europe. At a continental scale, not all functional dimensions contribute equally to habitat differentiation. Some patterns are

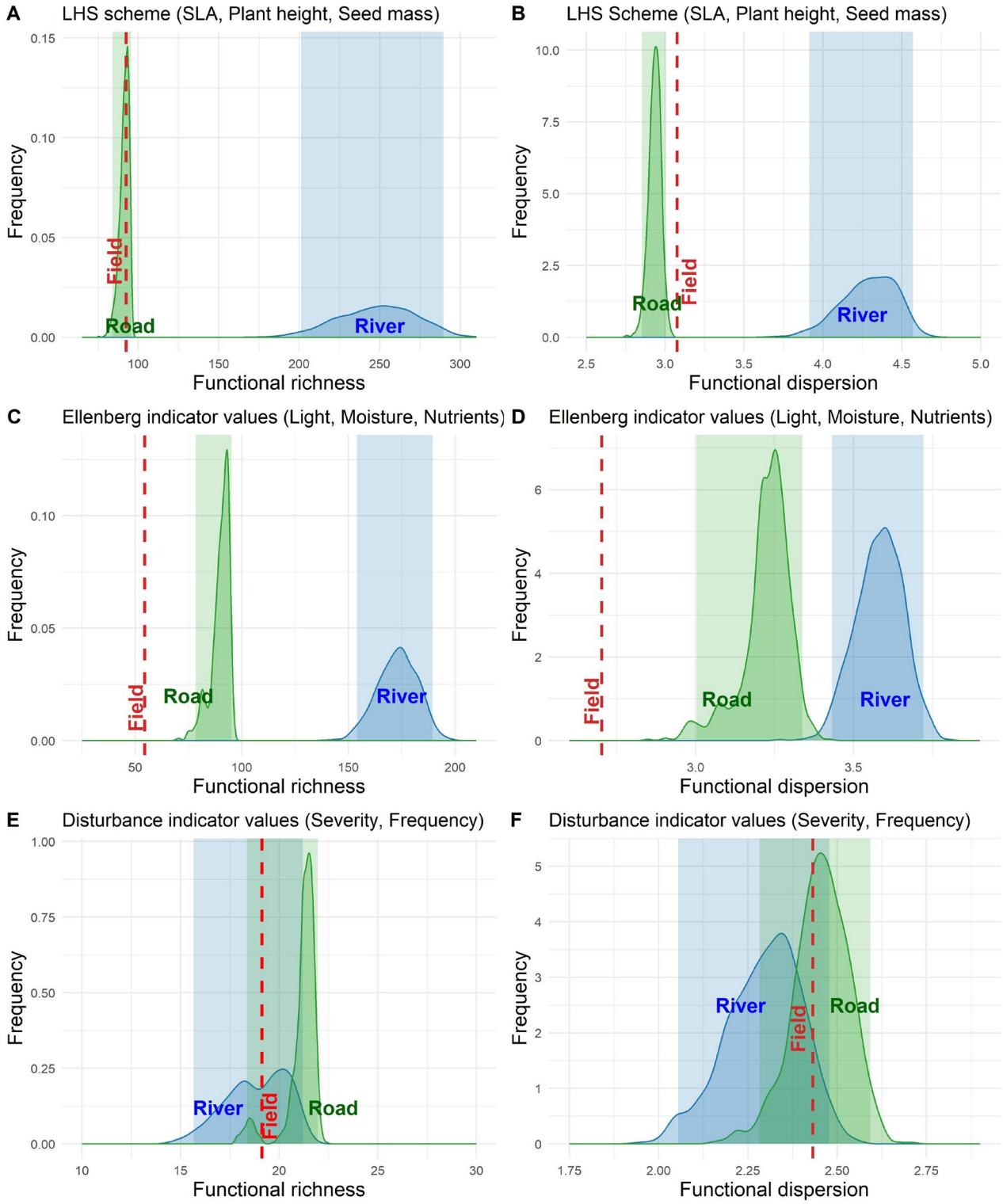

FIGURE 4 | Distribution of functional richness (left) and functional dispersion (right) across 999 simulated hypervolumes of riparian corridor (blue) and roadside (green) indicator species, compared with the observed hypervolume of field margin indicator species (red dashed line) for hypervolumes constructed on LHS traits (top), Ellenberg indicators (middle) and disturbance indicators (bottom). The green and blue background represents the 95% range of values. If the hypervolume of field margins falls outside this range, it indicates that the richness (left panels) or dispersion (right panels) of the hypervolume is significantly different. Similarly, if the 95% range of the hypervolume of roadsides and riparian corridors do not overlap, they are significantly different.

consistent across habitats: they share dominant plant species and show comparable functional diversity related to disturbance tolerance, indicating that all three habitats support a broad range of disturbance responses. In contrast, ecological strategies and resource requirements differ strongly between habitats and help explain the contrasting representation of invasive and threatened species. Gamma and functional diversity were highest in riparian corridors, whereas field margins supported fewer species and showed

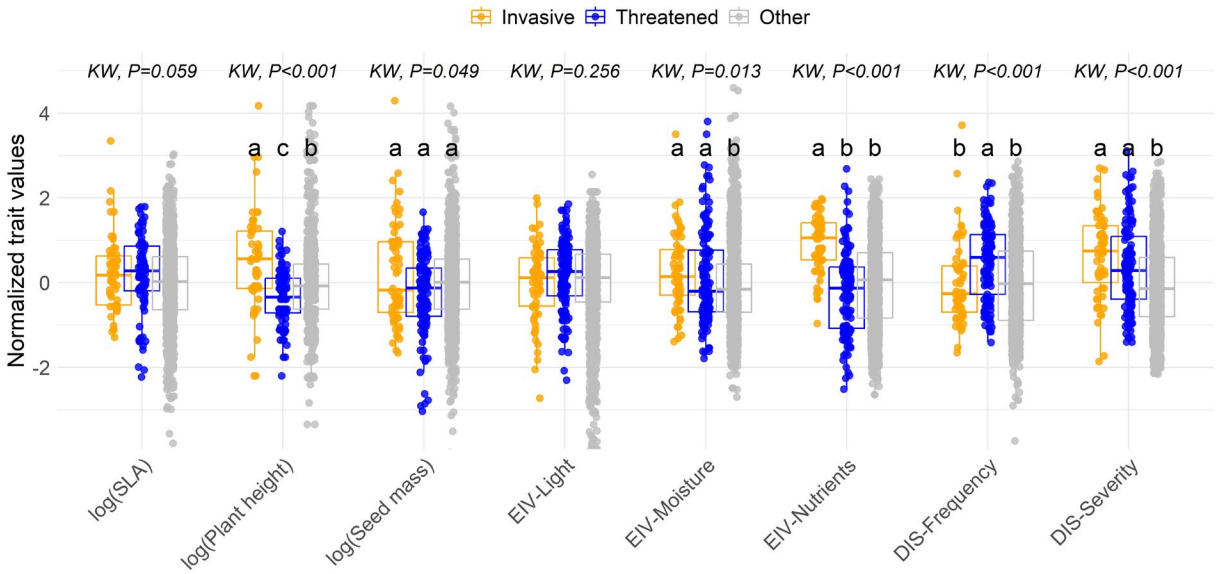

FIGURE 5 | Normalized trait values across species groups for invasive, threatened and other plant species. Trait values were normalized across species groups to allow direct comparison of invasive and threatened species relative to others, accounting for trait differences among species groups. Boxplots show the distribution of values by species status; jittered points represent individual observations. Kruskal–Wallis test results are shown above each trait. Letters indicate homogeneous groups following Dunn post hoc comparisons with Benjamini-Hochberg correction.

trait convergence with roadsides. Despite substantial overlap, each habitat retained distinct assemblages, with riparian corridors supporting most indicator and threatened species. Invasive species were widespread—particularly in riparian corridors—highlighting the contrasting ecological roles of linear habitats and their combined contribution to regional biodiversity.

4.1 | How Do the Species Pools of Riparian Corridors, Roadsides and Field Margins Differ Taxonomically?

The higher richness observed in riparian corridors and roadsides may be explained by their more complex habitat structure. Riparian corridors and to a lesser extent roadsides, often comprise multiple sub-habitats (Tabacchi et al. 2024), from the immediate riverbank or road verge—typically bare or sparsely vegetated due to erosion or disturbance—to more external elements such as riparian forests or tree lines (Rievrs-Borges et al. 2025). In contrast, field margins are generally simpler and narrower (Marshall and Moonen 2002). Higher connectivity along riparian and roadside networks likely also contributes to richness, enhancing dispersal and recolonization of disturbed sites (Tonkin et al. 2018).

On the one hand, the substantial overlap of species—with nearly two-thirds occurring in at least two habitats, including one quarter shared by all three—may partly reflect similar ecological conditions, particularly those shaped by disturbance regimes. For instance, the high number of frequent species shared between field margins and roadsides can likely be attributed to their similar management regimes, particularly regular mowing (Hovd and Skogen 2005). Spatial proximity and connectivity may also contribute to species sharing, as field margins often adjoin or even overlap with roadside verges (Chaudron et al. 2016).

On the other hand, more than one third of all species and two thirds of indicator species occurred exclusively in a single habitat. As expected, the riparian corridor species pool contains the highest number of specialists and shares the fewest indicator species with the other two habitats. Moreover, riparian corridors stood out by supporting a substantially higher number of habitat specialists with high frequency—13 among the 40 most common species—compared to just one and three in field margins and roadsides, respectively. Based on the identity of these specialist species (e.g., *Phragmites australis*, *Lythrum salicaria*, *Salix alba*, *Populus nigra*) and the characteristics that most differentiate riparian corridors from the other two habitats, this greater distinctiveness is likely due to the wetter conditions of alluvial soils. These conditions result from a combination of closer groundwater levels and periodic overbank flooding, which distinguish riparian corridors from field margins and roadsides. This emphasizes the importance of riparian corridors in maintaining habitat-specific biodiversity at the landscape level (Naiman et al. 1993; Bennett et al. 2014) and how it contributes to increasing regional diversity (Sabo et al. 2005).

4.2 | How Do Species Pools in Riparian Corridors, Roadsides and Field Margins Compare Functionally?

Riparian habitats show greater functional diversity than roadsides and field margins, reflecting higher habitat heterogeneity and dynamic conditions—fluctuating water levels, erosion and sediment deposition—that create diverse ecological niches at a local scale (Naiman et al. 2005; Biswas and Mallik 2010; Hough-Snee et al. 2015; Lawson et al. 2015). Riparian species generally have higher soil moisture and lower light requirements (reflecting successional processes) but encompass a wide range of values, including drought-tolerant species, indicating numerous microhabitats with varying moisture regimes (Janssen et al. 2021). The higher functional diversity in riparian corridors

may also result from more spatially structured environmental filtering. Flooding as a disturbance force is spatially and temporally heterogeneous or patchy and creates 'gaps' in ecological filters, enabling a wider range of trait combinations to persist. Roadsides and field margins, however, experience more uniform anthropogenic pressures (regular mowing along strip habitats), enforcing stronger, more consistent environmental filters that limit functional trait variation.

Abiotic filtering is stronger in roadsides, where species show narrower light and moisture preferences—high light and low moisture—reflecting drier, poorer soils (Šerá 2010). Field margins support more ruderal species, with more annuals, higher specific leaf area (SLA) and elevated nutrient indicator values (EIV-N), typical of arable weeds with acquisitive strategies (Grime 1974; Bourgeois et al. 2019), likely driven by fertilization runoff from croplands (Hovd and Skogen 2005; Fried et al. 2018).

The lack of differences among habitats in the functional richness and dispersion of disturbance tolerance suggests that all three habitats host a wide range of species, from disturbance-tolerant to disturbance-sensitive. This coexistence may result from contrasting conditions between the inner, more disturbed edges and the outer, less disturbed edges of these linear habitats (Rievrs-Borges et al. 2025).

4.3 | How Are Invasive and Threatened Species Represented Across the Three Habitats and How Do Their Traits Compare to Other Species From the Same Pool?

Our findings reveal a strong contrast in the distribution and trait profiles of invasive versus threatened plant species across linear habitats. Two-thirds of invasive species occurred in multiple habitats, particularly shared between riparian corridors and roadsides, whereas nearly half of threatened species were restricted to a single habitat. Invasive species were more frequent and abundant in riparian corridors, consistent with their role as dispersal corridors due to high connectivity and frequent disturbance (Richardson et al. 2007). They are disproportionately wind- and water-dispersed, facilitating long-distance spread along and beyond these corridors (Thiele et al. 2018).

The hypothesis that invasive and threatened species differ in their trait profiles from other species is supported (Bradshaw et al. 2008): invasive species were taller and preferred moist, nutrient-rich soils, consistent with competitive dominance in productive environments (MacDougall et al. 2009; Dostál et al. 2013). Such functional divergence from co-occurring species can allow invasive species to access novel niches, use available resources more efficiently and translate these advantages into dominance over native taxa (Divíšek et al. 2025). Threatened species were smaller and associated with frequently disturbed but nutrient-poor habitats, placing them at the opposite end of the ecological gradient and making them vulnerable to eutrophication and vegetation encroachment. However, invasive and threatened species do not differ much in terms of dispersal mode or response to disturbances, likely because the selective pressures of linear habitats shape these traits. This emphasizes a management challenge: some disturbance is necessary to maintain threatened species, but it must not favour invasive generalists, which can create shading and competitive pressure (Staude et al. 2023).

Riparian corridors emerged as the most species-rich and functionally diverse habitats, supporting numerous specialists and a substantial share of threatened species across temperate Europe (Naiman et al. 1993; González et al. 2017; Graziano et al. 2022). Although roadsides supported a comparable number of species, generalists dominated their communities and functional diversity was lower. Even so, these artificial habitats host almost as many threatened species as riparian corridors and field margins, in turn, contain fewer invasive species while supporting several threatened arable weeds (e.g., *Asperula arvensis*, *Bifora testiculata*) (Fried et al. 2009). By combining taxonomic metrics with functional hypervolume analyses, our approach identifies habitats that contribute unique or underrepresented portions of trait space at a biogeographic scale. This integrative framework strengthens conservation prioritization by highlighting habitats that safeguard not only local species richness but also regional functional strategies essential for ecosystem resilience across landscapes (Lee et al. 2025).

Beyond describing these patterns, our results have direct implications for management of widespread linear habitats. First, by identifying which invasive or threatened species are shared across all habitat types versus those restricted to specific ones, our framework can help prioritize monitoring and control efforts towards species that consistently occur across multiple habitat types and may therefore require coordinated management strategies at the landscape scale. Second, our findings can inform the design of targeted monitoring programs by highlighting habitats with higher proportions of invasive or threatened species, thereby supporting decisions on where monitoring effort should be concentrated. Third, this type of information can contribute to the selection of species pools for restoration or sowing schemes, by helping practitioners anticipate which species are most suitable or most likely to persist under site-specific conditions, in line with practitioner priorities for site suitability in restoration planning (Henry et al. 2024). More generally, similar approaches have been shown to support management and policy-relevant decisions in linear and anthropogenically mediated ecosystems (e.g., Asth et al. 2021; Montero-Castaño et al. 2023), particularly when used to guide monitoring design and early detection of invasive species in dispersal corridors.

5 | Conclusion

Our study provides the first comprehensive characterization of the most widespread linear habitats—riparian corridors, roadsides and field margins—in industrialized landscapes, highlighting their key functional and taxonomic traits and associated conservation challenges. Using hypervolume metrics, we show that vegetation in the three habitats exhibits similar responses to disturbances, with all hosting a wide range of disturbance-tolerant and -sensitive species, yet differs more strongly in ecological strategies and, in particular, resource requirements. Invasive species occur predominantly in riparian corridors and roadsides, while threatened and specialist species are primarily

concentrated in riparian corridors. Riparian corridors emerge as hotspots of taxonomic and functional diversity but they also represent key invasion hotspots. Trait-based analyses show that invasive species, generally larger, thrive in resource-rich, disturbed environments, whereas threatened species, smaller, tolerate disturbances but are sensitive to eutrophication and competitive exclusion. This contrast provides a framework for targeted management, including catchment-scale nutrient control, to reconcile conservation of vulnerable flora with invasion control in multifunctional landscapes.

Author Contributions

G.F.: Conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, writing – original draft, review and editing. E.R.B.: Conceptualization, methodology, writing – review and editing. A.J.E.: Conceptualization, methodology, data curation, writing – review and editing. L.M.: Data curation, writing – review and editing. B.B.: Methodology, writing – review and editing. M.C.: Conceptualization, methodology, writing – review and editing. E.G.S.: Conceptualization, methodology, writing – review and editing. A.M.T.: Writing – review and editing. E.T.: Conceptualization, data curation, funding acquisition, methodology, project administration, supervision, writing – review and editing. All authors contributed substantially to the conception and design of the study and/or the acquisition, analysis or interpretation of the data. All authors critically revised the manuscript for important intellectual content, approved the final version and agree to be accountable for all aspects of the work.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Zenodo at https://zenodo.org/records/17732277.

References

Andrade, C., A. Villers, G. Balent, et al. 2021. "A Real-World Implementation of a Nationwide, Long-Term Monitoring Program to Assess the Impact of Agrochemicals and Agricultural Practices on Biodiversity." *Ecology and Evolution* 11: 3771–3793.

Aronson, M. F., M. V. Patel, K. M. O'Neill, and J. G. Ehrenfeld. 2017. "Urban Riparian Systems Function as Corridors for Both Native and Invasive Plant Species." *Biological Invasions* 19: 3645–3657.

Asth, M. D. S., R. G. Rodrigues, and R. D. Zenni. 2021. "Canals as Invasion Pathways in Tropical Dry Forest and the Need for Monitoring and Management." *Journal of Applied Ecology* 58: 2004–2014. https://doi.org/10.1111/1365-2664.13950.

Auffret, A. G., and E. Lindgren. 2020. "Roadside Diversity in Relation to Age and Surrounding Source Habitat: Evidence for Long Time Lags in Valuable Green Infrastructure." *Ecological Solutions and Evidence* 1: e12005.

Aymerich, P., and L. Sáez. 2019. "Checklist of the Vascular Alien Flora of Catalonia (Northeastern Iberian Peninsula, Spain)." *Mediterranean Botany* 40: 215–242.

Aymerich, P., and L. Sáez. 2021. *Llista Vermella de la Flora Vascular de Catalunya. Actualització Any 2020*. Vol. 2. Monografies de la Institució Catalana d'Història Natural.

Belletti, B., C. Garcia de Leaniz, J. Jones, et al. 2020. "More Than One Million Barriers Fragment Europe's Rivers." *Nature* 588: 436–441.

Bennett, A. F., D. G. Nimmo, and J. Q. Radford. 2014. "Riparian Vegetation Has Disproportionate Benefits for Landscape-Scale Conservation of Woodland Birds in Highly Modified Environments." *Journal of Applied Ecology* 51: 514–523.

Biswas, S. R., and A. U. Mallik. 2010. "Disturbance Effects on Species Diversity and Functional Diversity in Riparian and Upland Plant Communities." *Ecology* 91: 28–35.

Blonder, B. 2018. "Hypervolume Concepts in Niche- and Trait-Based Ecology." *Ecography* 41: 1441–14550.

Botanical Society of Britain and Ireland. 2024. "NNSIP GB Invasive Species List".

Bourgeois, B., F. Munoz, G. Fried, et al. 2019. "What Makes a Weed a Weed? A Large-Scale Evaluation of Arable Weeds Through a Functional Lens." *American Journal of Botany* 106: 90–100.

Bradshaw, C. J. A., X. L. Giam, H. T. W. Tan, B. W. Brook, and N. S. Sodhi. 2008. "Threat or Invasive Status in Legumes Is Related to Opposite Extremes of the Same Ecological and Life-History Attributes." *Journal of Ecology* 96: 869–883.

Brady, N. C., and R. R. Weil. 2007. *The Nature and Properties of Soils*. 14th ed. Pearson.

Canham, C. A., C. Woods, S. A. Setterfield, et al. 2023. "Functional Traits of Riparian Trees in the Lower Fitzroy River, Western Australia." *Ecohydrology* 16: e2488.

Cardoso, P., F. Rigal, and J. C. Carvalho. 2015. "BAT - Biodiversity Assessment Tools, an R Package for the Measurement and Estimation of Alpha and Beta Taxon, Phylogenetic and Functional Diversity." *Methods in Ecology and Evolution* 6: 232–236.

Carey, P., S. Wallis, P. Chamberlain, et al. 2008. *Countryside Survey: UK Results From 2007 NERC*. Centre for Ecology & Hydrology CEH Project.

Catford, J. A., and R. Jansson. 2014. "Drowned, Buried and Carried Away: Effects of Plant Traits on the Distribution of Native and Alien Species in Riparian Ecosystems." *New Phytologist* 204: 19–36.

Cayuela, L., I. Macarro, A. Stein, and J. Oksanen. 2021. "Taxonstand: Taxonomic Standardization of Plant Species Names. R Package Version 2.4".

Centre de ressources—Espèces exotiques envahissantes. 2025. "Liste d'espèces par territoire." https://especes-exotiques-envahissantes.fr/base-documentaire/liste-despeces/.

Chaudron, C., R. Perronne, S. Bonthoux, F. Di Pietro, and R. Ohlemuller. 2016. "Influence of Management Practices on Plant Assemblages

of Road–Field Boundaries in an Agricultural Landscape." *Applied Vegetation Science* 19: 644–654.

De Cáceres, M., and P. Legendre. 2009. "Associations Between Species and Groups of Sites: Indices and Statistical Inference." *Ecology* 90: 3566–3574.

Deeley, B., and N. Petrovskaya. 2022. "Propagation of Invasive Plant Species in the Presence of a Road." *Journal of Theoretical Biology* 548: 111196.

Díaz, S., J. Kattge, J. H. C. Cornelissen, et al. 2016. "The Global Spectrum of Plant Form and Function." *Nature* 529: 167–171.

Divíšek, J., P. Pyšek, D. M. Richardson, et al. 2025. "Naturalized and Invasive Species Integrate Differently in the Trait Space of Local Plant Communities." *Ecology Letters* 28: e70235.

Dostál, P., W. Dawson, M. van Kleunen, L. H. Keser, and M. Fischer. 2013. "Central European Plant Species From More Productive Habitats Are More Invasive at a Global Scale." *Global Ecology and Biogeography* 22: 64–72.

Dufrêne, M., and P. Legendre. 1997. "Species Assemblages and Indicator Species: The Need for a Flexible Asymmetrical Approach." *Ecological Monographs* 67: 345–366.

Follak, S., M. Eberius, F. Essl, A. Fürdös, N. Sedlacek, and F. Trognitz. 2018. "Invasive Alien Plants Along Roadsides in Europe." *EPPO Bulletin* 48: 256–265.

Forman, R. T. 1995. "Some General Principles of Landscape and Regional Ecology." *Landscape Ecology* 10: 133–142.

Fried, G., S. Petit, F. Dessaint, and X. Reboud. 2009. "Arable Weed Decline in Northern France: Crop Edges as Refugia for Weed Conservation?" *Biological Conservation* 142: 238–243.

Fried, G., I. Poinas, L. Henckel, and A. Alignier. 2024. "Major Field Margin Vegetation Types in France and Their Relationships With Climate, Agricultural Landscapes and Management Intensity." *Botany Letters* 171: 235–252.

Fried, G., A. Villers, and E. Porcher. 2018. "Assessing Non-Intended Effects of Farming Practices on Field Margin Vegetation With a Functional Approach." *Agriculture, Ecosystems & Environment* 261: 33–44.

Gelbard, J. L., and J. Belnap. 2003. "Roads as Conduits for Exotic Plant Invasions in a Semiarid Landscape." *Conservation Biology* 17: 420–432.

González, E., M. R. Felipe-Lucia, B. Bourgeois, et al. 2017. "Integrative Conservation of Riparian Zones." *Biological Conservation* 211: 20–29.

Graziano, M. P., A. K. Deguire, and T. D. Surasinghe. 2022. "Riparian Buffers as a Critical Landscape Feature: Insights for Riverscape Conservation and Policy Renovations." *Diversity* 14: 172.

Grime, J. P. 1974. "Vegetation Classification by Reference to Strategies." *Nature* 250: 26–31.

Henry, A. L., R. Robinson, K. Sinnott, E. Tarsa, M. W. Brunson, and K. M. Kettenring. 2024. "Lay of the (Wet) Land: Manager Practices and Challenges in Wetland Revegetation." *Restoration Ecology* 32, no. 5: e14167.

Hilty, J. A., A. T. Keeley, W. Z. Lidicker Jr., and A. M. Merenlender. 2019. *Corridor Ecology: Linking Landscapes for Biodiversity Conservation and Climate Adaptation*. Island Press.

Hough-Snee, N., B. G. Laub, D. M. Merritt, et al. 2015. "Multi-Scale Environmental Filters and Niche Partitioning Govern the Distributions of Riparian Vegetation Guilds." *Ecosphere* 6: 1–22.

Hovd, H., and A. Skogen. 2005. "Plant Species in Arable Field Margins and Road Verges of Central Norway." *Agriculture, Ecosystems & Environment* 110: 257–265.

Hutchinson, G. E. 1957. "Concluding Remarks." *Cold Spring Harbor Symposia on Quantitative Biology* 22: 415–427.

IUCN, W. 1999. "IUCN Guidelines for the Prevention of Biodiversity Loss due to Biological Invasion." *Species* 31: 28–42.

Janssen, P., R. Chevalier, A. Evette, and F. Archaux. 2021. "The Closer the Better? Relative Influence of Forest Continuity and Distance to Water on the Taxonomic and Functional Structure of Riparian Plant Communities Along Headwater Streams." *Applied Vegetation Science* 24: e12591.

Juárez-Escario, A., J. A. Conesa, and X. O. Solé-Senan. 2016. "Identifying Alien Plants Linkages Between Irrigated Orchards and Adjacent Riparian Habitats From a Trait-Based Approach." *Agriculture, Ecosystems & Environment* 225: 173–183.

Julve, P. 2024. "baseflor. Index Botanique, écologique et chorologique de la Flore de France. Version [juin 2024]. Programme Catminat." https://www.tela-botanica.org/ressources/donnees/telechargements/.

Kattge, J., G. Bönisch, S. Díaz, et al. 2020. "TRY Plant Trait Database–Enhanced Coverage and Open Access." *Global Change Biology* 26: 119–188.

Kolb, A., and M. Diekmann. 2005. "Effects of Life-History Traits on Responses of Plant Species to Forest Fragmentation." *Conservation Biology* 19: 929–938.

Kowarik, I., and M. Von der Lippe. 2011. "Secondary Wind Dispersal Enhances Long-Distance Dispersal of an Invasive Species in Urban Road Corridors." *NeoBiota* 9: 49–70.

Laliberté, E., and P. Legendre. 2010. "A Distance-Based Framework for Measuring Functional Diversity From Multiple Traits." *Ecology* 91: 299–305.

Larsson, J. 2021. "eulerr: Area-Proportional Euler and Venn Diagrams With Ellipses, R Package Version 6.1.1." https://CRAN.R-project.org/package=eulerr.

Lawson, J. R., K. A. Fryirs, T. Lenz, and M. R. Leishman. 2015. "Heterogeneous Flows Foster Heterogeneous Assemblages: Relationships Between Functional Diversity and Hydrological Heterogeneity in Riparian Plant Communities." *Freshwater Biology* 60: 2208–2225.

Lee, J. S., J. Brazill-Boast, W. Cornwell, and R. Gallagher. 2025. "Accounting for Functional Diversity in Biodiversity Protection Measures." *Plants, People, Planet* 8: 1–11. https://doi.org/10.1002/ppp3.70126.

MacDougall, A. S., B. Gilbert, and J. M. Levine. 2009. "Plant Invasions and the Niche." *Journal of Ecology* 97: 609–615.

Mammola, S., and P. Cardoso. 2020. "Functional Diversity Metrics Using Kernel Density n-Dimensional Hypervolumes." *Methods in Ecology and Evolution* 11: 986–995.

Marshall, E. J. P., and A. C. Moonen. 2002. "Field Margins in Northern Europe: Their Functions and Interactions With Agriculture." *Agriculture, Ecosystems & Environment* 89: 5–21.

Maskell, L. C., J. M. Bullock, S. M. Smart, K. Thompson, and P. E. Hulme. 2006. "The Distribution and Habitat Associations of Non-Native Plant Species in Urban Riparian Habitats." *Journal of Vegetation Science* 17: 499–508.

Midolo, G., T. Herben, I. Axmanová, et al. 2023. "Disturbance Indicator Values for European Plants." *Global Ecology and Biogeography* 32: 24–34.

Montero-Castaño, A., M. A. Aizen, P. González-Moreno, L. Cavallero, M. Vilà, and C. L. Morales. 2023. "Influential Factors and Barriers Change Along the Invasion Continuum of an Alien Plant." *Biological Invasions* 25, no. 9: 2977–2991.

Naiman, R. J., J. S. Bechtold, D. C. Drake, J. J. Latterell, T. C. O'Keefe, and E. V. Balian. 2005. "Origins, Patterns, and Importance of Heterogeneity in Riparian Systems." In *Ecosystem Function in Heterogeneous Landscapes*, 279–309. Springer.

Naiman, R. J., H. Decamps, and M. E. McClain. 2010. *Riparia: Ecology, Conservation, and Management of Streamside Communities*. Elsevier.

Naiman, R. J., H. Decamps, and M. Pollock. 1993. "The Role of Riparian Corridors in Maintaining Regional Biodiversity." *Ecological Applications* 3: 209–212.

Oksanen, J., G. L. Simpson, F. G. Blanchet, et al. 2022. "vegan: Community Ecology Package".

Phillips, B. B., J. M. Bullock, J. L. Osborne, and K. J. Gaston. 2020. "Ecosystem Service Provision by Road Verges." *Journal of Applied Ecology* 57: 488–501.

Poinas, I., G. Fried, L. Henckel, and C. Meynard. 2023. "Spatial Scale Dependence in Agricultural Drivers of Field Margin Plant Communities".

Rejmánek, M., D. M. Richardson, and P. Pyšek. 2013. "Plant Invasions and Invasibility of Plant Communities." In *Vegetation Ecology*, 387–424. Wiley.

Richardson, D. M., P. M. Holmes, K. J. Esler, et al. 2007. "Riparian Vegetation: Degradation, Alien Plant Invasions, and Restoration Prospects." *Diversity and Distributions* 13: 126–139.

Rievrs-Borges, E., E. González-Sargas, N. Casajus, et al. 2025. "Road-River Intersections (Bridges) Negatively Affect Plant Species Diversity and Ecological Attributes." *Applied Vegetation Science* 28: e70011.

Sabo, J. L., R. Sponseller, M. Dixon, et al. 2005. "Riparian Zones Increase Regional Species Richness by Harboring Different, Not More, Species." *Ecology* 86: 56–62.

Santibañez, F., M. Sabatino, and L. A. Garibaldi. 2024. "Searching to Improve Connectivity in Fragmented Landscapes: Road Verges as Complementary Habitats." *Applied Vegetation Science* 27: e12773.

Šerá, B. 2010. "Road-Side Herbaceous Vegetation: Life History Groups and Habitat Preferences." *Polish Journal of Ecology* 58: 69–79.

Simberloff, D., J. L. Martin, P. Genovesi, et al. 2013. "Impacts of Biological Invasions: What's What and the Way Forward." *Trends in Ecology & Evolution* 28: 58–66.

Smart, S., R. Clarke, H. Van De Poll, et al. 2003. "National-Scale Vegetation Change Across Britain; an Analysis of Sample-Based Surveillance Data From the Countryside Surveys of 1990 and 1998." *Journal of Environmental Management* 67: 239–254.

Solé-Senan, X. O., A. Juárez-Escario, J. Conesa, and J. Recasens. 2018. "Plant Species, Functional Assemblages and Partitioning of Diversity in a Mediterranean Agricultural Mosaic Landscape." *Agriculture, Ecosystems & Environment* 256: 163–172.

Solé-Senan, X. O., A. Juárez-Escario, J. A. Conesa, J. Torra, A. Royo-Esnal, and J. Recasens. 2014. "Plant Diversity in Mediterranean Cereal Fields: Unraveling the Effect of Landscape Complexity on Rare Arable Plants." *Agriculture, Ecosystems & Environment* 185: 221–230.

Stanford, J. A., M. Lorang, and F. Hauer. 2005. "The Shifting Habitat Mosaic of River Ecosystems." *SIL Proceedings, 1922–2010* 29: 123–136.

Staude, I. R., J. Segar, V. M. Temperton, et al. 2023. "Prioritize Grassland Restoration to Bend the Curve of Biodiversity Loss." *Restoration Ecology* 31: e13931.

Stroh, P., S. Leach, T. August, et al. 2014. "A Vascular Plant Red List for England." *BSBI News* 9: 1–193.

Tabacchi, E., E. Gonzalez, D. Corenblit, V. Garófano-Gómez, A. Planty-Tabacchi, and J. Steiger. 2019. "Species Composition and Plant Traits: Characterization of the Biogeomorphological Succession Within Contrasting River Corridors." *River Research and Applications* 35: 1228–1240.

Tabacchi, E., A.-M. Planty-Tabacchi, and R. J. Naiman. 2024. "Riparian Landscapes." In *Encyclopedia of Biodiversity*, 3rd ed., 646–656. Elsevier.

Thiele, J., J. Schirmel, and S. Buchholz. 2018. "Effectiveness of Corridors Varies Among Phytosociological Plant Groups and Dispersal Syndromes." *PLoS One* 13: e0199980.

Tichý, L., I. Axmanová, J. Dengler, et al. 2023. "Ellenberg-Type Indicator Values for European Vascular Plant Species." *Journal of Vegetation Science* 34: e13168.

Tikka, P. M., H. Högmander, and P. S. Koski. 2001. "Road and Railway Verges Serve as Dispersal Corridors for Grassland Plants." *Landscape Ecology* 16: 659–666.

Tonkin, J. D., F. Altermatt, D. S. Finn, et al. 2018. "The Role of Dispersal in River Network Metacommunities: Patterns, Processes, and Pathways." *Freshwater Biology* 63: 141–163.

UICN France, FCBN, AFB, and MNHN. 2018. "La Liste rouge des espèces menacées en France – Chapitre Flore vasculaire de France métropolitaine. Paris, France".

van Buuren, S., and K. Groothuis-Oudshoorn. 2011. "Mice: Multivariate Imputation by Chained Equations in R." *Journal of Statistical Software* 45, no. 3: 1–67.

Vilà, M., and P. E. Hulme. 2017. *Impact of Biological Invasions on Ecosystem Services*. Springer.

Vorstenbosch, T., F. Essl, and B. Lenzner. 2020. "An Uphill Battle? The Elevational Distribution of Alien Plant Species Along Rivers and Roads in the Austrian Alps." *NeoBiota* 63: 1–24.

Ward, J., K. Tockner, D. B. Arscott, and C. Claret. 2002. "Riverine Landscape Diversity." *Freshwater Biology* 47: 517–539.

Westoby, M. 1998. "A Leaf-Height-Seed (LHS) Plant Ecology Strategy Scheme." *Plant and Soil* 199: 213–227.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Full description of the datasets used. **Appendix S2:** Standardization of abundance data. **Figure S1:** Relationship between the frequency of occurrence across 10 quadrats and the mean cover within those same 10 quadrats. Note that the data were log-transformed. **Appendix S3:** Species accumulation curves for the three linear habitat types based on random permutations of species presence across sampling sites. **Figure S2:** Species accumulation curves for the three linear habitat types based on random permutations of species presence across sampling sites. The figure shows the cumulative species richness (y-axis) as a function of sampling effort (x-axis) for field margins (red), roadsides (green) and riparian corridors (blue). Curves represent mean richness values calculated using 5000 random permutations. Shaded ribbons indicate ±1 standard deviation around the mean. The vertical dashed line at 600 samples marks a common threshold for comparative analyses across habitats. **Appendix S4:** Mean frequency and mean abundance of the most frequent species in the three habitats. **Table S1:** The most frequent species in the dataset and their mean frequency and mean abundance (percentage cover) in the three habitats as well as their frequency rank (rank order based on mean frequency in a given habitat). **Appendix S5:** Top 40 most frequent species in the three linear habitats. **Table S2:** Top 40 most frequent plant species along field margins. **Table S3:** Top 40 most frequent plant species along roadsides. **Table S4:** Top 40 most frequent plant species along riparian corridors. **Appendix S6:** List of invasive and threatened species. **Table S5:** Top 10 most frequent invasive species per habitat. **Table S6:** Top 10 most frequent threatened species per habitat. **Appendix S7:** Invasive vs. threatened species: frequency, abundance and traits across habitats. **Appendix S8: Figure S3** Standardized residual heatmaps from Chi-squared tests showing associations between species traits and species status (invasive, threatened, other). (A) Life forms: woody plants, geophytes, hemicryptophytes and therophytes across habitat combinations. (B) Dispersal modes: wind, water, gravity and animal dispersal across habitat combinations. Residuals are expressed as (observed – expected)/expected values; positive values (red) indicate trait overrepresentation in a habitat group and negative values (blue) indicate underrepresentation. Residuals are based on Chi-squared contingency tables and follow-up Fisher exact tests for each trait category.