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RESEARCH ARTICLE

Larval diet breadth and wingspan mediate landscape–richness relationship in butterfly communities

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Abstract

1. Landscape structure and species traits both shape butterfly assemblages, but their joint effects, and how landscapes restructure trait space independently of richness, remain less understood.
2. We surveyed butterflies at 50 semi-natural grasslands (Serbia) and modelled species richness (SR) with GAMs using two sets of landscape predictors within 2-km buffers: composition (% cover of grassland, forest, complex agriculture) and configuration (distance to the nearest natural patch, nearest natural-patch size, edge density). We included community-weighted mean (CWM) of two traits: wingspan (WS) and host-plant specificity (HPS) and fit landscape-only models, trait-additive models and pre-specified trait–landscape interactions per set (HPS and complex agriculture; WS and distance to the nearest natural patch). To test whether these gradients restructure trait space, we modelled functional divergence (FDiv) as a complementary response.
3. The only landscape predictor of SR was complex agriculture, which increased richness but reduced FDiv. Beyond landscape composition, HPS consistently improved SR models in both sets, with richness peaking at intermediate-to-narrow diet breadth and declining towards extremes. Isolation increased SR only in large-winged communities (WS × distance to the nearest natural patch), and FDiv increased with isolation, evidencing greater representation of trait extremes. Crucially, landscape effects on FDiv persisted after conditioning on SR, showing that landscapes filter which traits persist, not just how many species occur.
4. Butterfly assemblages are driven by resource-based and movement-based filtering rather than landscape structure alone. Our key novelty shows that the same landscape gradients decouple taxonomic from functional diversity; agricultural complexity adds species while compressing trait breadth, whereas isolation benefits large-winged communities and expands trait dispersion. Conservation should therefore track functional structure as well as counts,

maintaining diverse larval host-plants and stepping-stone connectivity to sustain both species richness and the functional breadth that underpins resilience.

KEYWORDS
butterfly community, larval diet breadth, species richness, trait–environment interactions, wingspan

1 | INTRODUCTION

Understanding how landscape structure affects biodiversity is a central question in ecology. Both habitat composition (types and proportions of land cover) and configuration (spatial arrangement) shape species richness and community structure (Guderjan et al., 2023; Holzschuh et al., 2010; Öckinger & Smith, 2006; Pendl et al., 2022; Schmitt et al., 2021). However, landscape features rarely act in isolation but often interact with species' functional traits, landscape structure, topography and disturbance gradients, making biodiversity patterns context-dependent (Gámez-Virués et al., 2015; Henriques et al., 2022; Perović et al., 2015).

By shifting trait distributions, landscapes determine not only which species persist (taxonomic composition), but also which ecological strategies prevail, affecting functional diversity (Le Provost et al., 2020; Lecoq et al., 2021; McGill et al., 2006; Wong & Candolin, 2015). Functional traits are thus a key mechanistic link between landscape and drivers of community stability, including diversity outcomes (Allan et al., 2015; Pla-Narbona et al., 2022; Simons et al., 2016; Sperandii et al., 2025). Central to trait-based framework is the concept of environmental filtering, whereby abiotic conditions selectively favour certain trait combinations and exclude others (Keddy, 1992; Weiher et al., 1998).

In butterflies, environmental filtering often operates via two proximate pathways; resource filtering acting via the availability and continuity of larval host plants, and movement filtering acting via matrix permeability and isolation (Deppe et al., 2024; Kőrösi et al., 2022; Pla-Narbona et al., 2022). Accordingly, we focus on two trait proxies aligned with these mechanisms, wingspan as an indicator of dispersal capacity (Kuussaari et al., 2014; Öckinger et al., 2010), and host-plant specificity as larval diet breadth along the generalism–specialism spectrum. Although wingspan is an imperfect proxy for dispersal capacity, it is a useful correlate of dispersal capacity at regional scales where species share similar constraints (Sekar, 2011).

This framing has clear implications for animal functional ecology. Low-mobile species tend to be restricted to high-quality, localized patches and are more vulnerable to habitat fragmentation (Hanski & Ovaskainen, 2000), whereas highly mobile species can traverse larger distances, exploit scattered resources and maintain metapopulation dynamics that buffer fragmentation effects (Kőrösi et al., 2022; Thomas & Hanski, 1997). Likewise, broad diet breadth often confers resilience in altered or fragmented habitats, while narrow breadth can heighten sensitivity (Börschig et al., 2013; Brückmann et al., 2010; Komonen et al., 2004; Warren et al., 2021).

Analytically, we distinguish additive effects, where traits and landscape influences richness independently, from non-additive (interactive) effects, where one predictor's effect depends on another, potentially yielding synergy (interaction effect greater than expected under additivity), antagonism (weaker than expected) or sign reversal (direction of a predictor's effect changes across levels of the other predictor) (Gelman & Hill, 2007; Seltman, 2018). Thus, additive effects describe independent contributions of composition, configuration and community traits, whereas interactive effects arise when landscape–richness relationships vary with trait composition.

As few studies quantify the independent contributions of traits versus landscape on pollinator richness, we address this gap by comparing three model structures: a landscape-only model, an additive model including traits and an interaction model including trait–landscape terms. We therefore ask the following: (1) do traits add independent explanatory power for species richness beyond landscape structure alone, (2) do trait–landscape interactions further improve richness models and (3) are the directions of these effects consistent with resource and dispersal mechanisms?

We tested the following hypotheses:

H1 (landscape): landscape structure, both habitat composition and configuration, affects butterfly species richness. We expect richness to increase with greater natural cover and larger natural patch size, and decrease with greater isolation (Kivinen et al., 2007; Öckinger et al., 2009; Tammaru et al., 2023). Responses to agricultural cover may be nonlinear since moderate agriculture can add resources and positively influence butterfly richness (Zingg et al., 2019), whereas very high cover tends to homogenize habitats and depress richness (Maes & Van Dyck, 2001).

H2 (traits—additive): functional traits add independent explanatory power to species richness beyond landscape predictors. After accounting for landscape, we expect that community trait composition (wingspan, host-plant specificity) should still explain variation in species richness, given repeated links to habitat amount, compositional heterogeneity and spatial configuration (Franzén et al., 2012; Habel et al., 2019; Kőrösi et al., 2022; Perović et al., 2015). We therefore predict higher richness in communities dominated by more mobile and/or broader-diet species, independent of composition and configuration.

H3 (traits and landscape—interactive): trait–landscape interactions shape species richness. Landscape sets the resource and movement framework, while traits determine how species perceive resources and space (Kőrösi et al., 2022; Schleuning et al., 2022). Consequently, the same change in composition or configuration can affect communities differently depending on trait composition. Here, we test two mechanistic expectations: resource filtering and movement filtering. Under resource filtering, treating composition as a resource filter, we expect synergy such that richness gains under increasing complex agricultural cover are larger in generalist-dominated communities. Under movement filtering, treating configuration as a movement filter, we also expect synergy such that as isolation increases, richness declines less (or increases) in large-winged communities, due to greater dispersal capacity (Kőrösi et al., 2022; Öckinger et al., 2009). We acknowledge that alternative outcomes, antagonism or sign reversals are possible along some gradients.

2 | MATERIALS AND METHODS

2.1 | Study sites and sampling design

Butterflies were surveyed at 50 sites in Serbia in 2022 (Figure 1) across spring (April–May), summer (June–August) and autumn (September), with each site visited three times, under standard weather (≥13°C sunny or ≥17°C overcast, 09:00–17:00). Data from all seasons were pooled for the analyses.

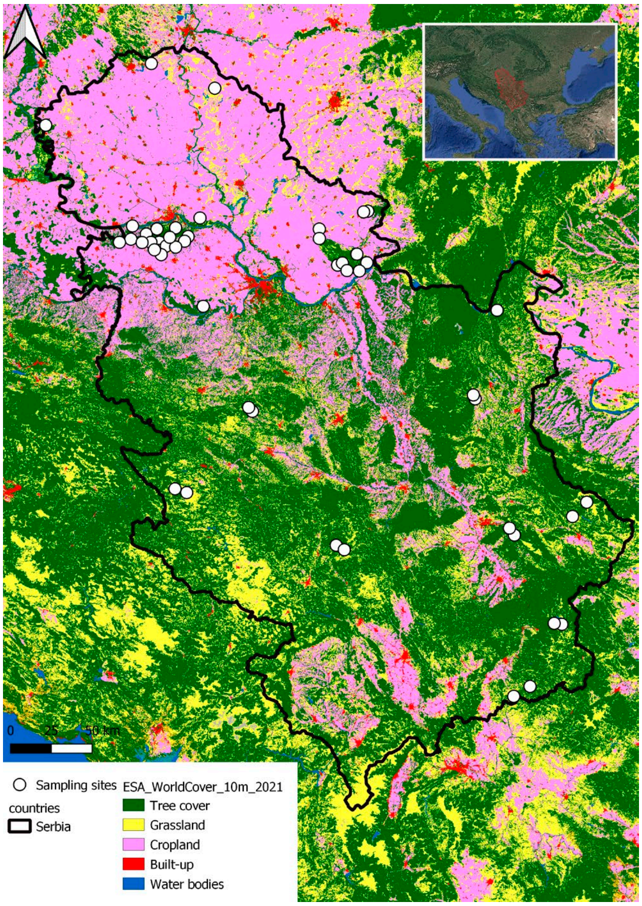

FIGURE 1 Map of the study area showing the location of the 50 butterfly survey sites (white circles).

Field data and functional traits data used in the analyses have been archived in Zenodo (Vujanović, 2025). Sites, all semi-natural grasslands, maintained by grazing, mowing or both, were selected at a distance of a minimum of 2 km to reduce spatial autocorrelation. We used 2 km landscape buffers to capture butterfly responses across both typical dispersal distances (1–2 km), making this scale ecologically relevant for landscape-level analyses (Brückmann et al., 2010; DiLeo et al., 2022).

We used the line–transect method by Pollard and Yates (1993) to record and count the butterflies. Each site was surveyed using a single 600-m-long transect, with observations recorded within a 5-m-wide belt (2.5 m on each side of the observer), which corresponds to a total surveyed area of 3000 m^2 per site. The transect was split into five 120 m segments, which were walked continuously at a constant pace of 20 m min^{-1}, taking 6 min per segment (total 30 min per transect). Butterflies within the 5 m belt were recorded continuously while walking, and the timer was reset at each segment boundary. Uncertain individuals were netted, identified and released. Specimens needing detailed examination were identified in the laboratory and deposited in the collection of FSUNS (Faculty of Sciences, University of Novi Sad, Serbia). No ethical approval was required for this study.

2.2 | Landscape structure variables

Using a 2-km buffer around each transect midpoint, we computed three composition metrics: percent cover (%) of grassland (Grass; CLC 321), forest (For; CLC 311) and complex agricultural land (CAGR; CLC 243), with CAGR representing mosaics of small parcels with varied cultivation types and semi-natural patches. These variables capture habitat availability and human land use (Han et al., 2021; Öckinger & Smith, 2006; Tammaru et al., 2023; Vujanović et al., 2025).

Within the same buffer, we quantified configuration using edge density (ED; km km^{-2}), calculated as the total length of edges of natural patches per buffer area; nearest natural patch size (NAT_Size; km^2), defined as the mean area of the single nearest natural patch within 2 km, and distance to the nearest natural patch (DNAT; m), the Euclidean distance from the transect midpoint to the boundary of the nearest natural patch.

We defined natural patches as contiguous areas of semi-natural grassland (CLC 321), shrubland (CLC 324), and forest (CLC 311). These metrics capture aspects of spatial connectivity and fragmentation (Öckinger et al., 2010; Polus et al., 2007; Steffan-Dewenter & Tscharntke, 2002; Uhl et al., 2021).

We used Corine Land Cover (CLC) 2018 (V2020) and processed data in ArcGIS Pro 3.0.

2.3 | Functional traits

We used two functional traits: (1) wingspan (WS) and (2) larval diet breadth, expressed as host-plant specificity (HPS). WS was used as a dispersal proxy and compiled at the species level from Middleton-Welling et al. (2020), using tip-to-tip wingspans on spread specimens averaged across sexes for each species (Table S1).

Host-plant specificity (HPS) was derived from Popović and Đurić (2011), and Brückmann et al. (2010) and coded as an ordered three-level factor: 1 = monophagous (one host), 2 = oligophagous (two hosts) and 3 = polyphagous (≥3 hosts).

2.4 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Butterfly community	2 km landscape buffers around transects	50 independent butterfly communities (sites)
Functional traits, wingspan and larval diet breadth	Site-level community-weighted means and landscape metrics	50 site-level combinations of functional traits and landscape data

2.5 | Data analysis

2.5.1 | Species-level trait pool and community-level trait composition

At the species level, the regional pool was described using wingspan distribution (WS; continuous) and the class frequencies of host-plant specificity (HPS; ordinal: 1 = one host, 2 = two hosts, 3 = ≥3 hosts). WS is shown as a histogram (25 equal-width bins, with median), and HPS as percent of species per class.

At the community level, abundance-weighted community-weighted means (CWMs) of WS and HPS were calculated after matching species between the community and trait matrices. For visualization, WS was binned into tertiles (low/mid/high), and HPS kept its original classes. Stacked bar charts show class proportions per site (summing to 100%).

Treating HPS as ordinal, we use CWM(HPS) as an abundance-weighted index (bounded 1–3), do not assume equal spacing between categories (i.e. 1 → 2 need not equal 2 → 3) and interpret effects as trends along the specialization–generalization gradient rather than per-unit changes, while WS was analysed as a continuous CWM.

2.5.2 | Landscape and trait effects on butterfly richness

Before modelling we checked pairwise correlations among community-weighted traits (WS, HPS) using Spearman, and among landscape variables using variance inflation factor ($\text{VIF} < 2$).

We analysed species richness (SR) using generalized additive models (GAMs; Poisson, log link) with all predictors included as smooth terms (s) to allow for potentially nonlinear relationships. Models were fitted separately for landscape composition (Grass, For, CAGR) and configuration (DNAT, NAT_Size, ED) predictor sets. Functional traits were incorporated as abundance weighted community-means and were mean-centred so that landscape smooths represent effects at average trait values.

We used continuous CWMs over categorical groupings (e.g. 'small' vs. 'large') to preserve ecological gradients and avoid arbitrary thresholds. All smooths used thin-plate regression splines with shrinkage (bs = 'ts', $k = 4$, select = TRUE) to control effective degrees of freedom with $n = 50$.

To test H1 (landscape structure alone explains SR) we fit two models with landscape covariates only: SR ~ s(Grass) + s(CAGR) + s(For), and SR ~ s(DNAT) + s(NAT_Size) + s(ED).

To test H2 (functional traits add predictive power beyond landscape) we fit two additive models: Add s(WSc) + s(HPSc) to each H1 model.

To test H3 (trait–landscape interactions significantly shape species richness) we pre-specified one interaction per set using tensor-product smooths ti() beyond the main effects: SR ~ H2_composition terms + ti(HPSc, CAGR) (diet breadth moderating agriculture) and SR ~ H2_configuration terms + ti(WSc, DNAT) (mobility moderating isolation).

We compared models using maximum likelihood (ML)–based likelihood ratio tests (LRTs) and differences in Akaike's information criterion (ΔAIC), while final model summaries were reported from restricted maximum likelihood (REML) fits. We checked basis adequacy with gam.check (*k*-index, residual patterns), residual diagnostics with DHARMa (uniformity, overdispersion, zero-inflation), evaluated concurvity (nonlinear collinearity) and tested spatial autocorrelation of residuals using Moran's *I* and empirical semivariograms (Moran, 1950).

To test for dominance artefacts, we recomputed CWMs after zeroing the top-1 and top-2 most abundant species at each site, refit the same GAMs and compared against originals via ML LRTs and ΔAIC. Effects that persisted were interpreted as community-level rather than dominance-driven.

As a complementary, mechanism-oriented response, we examined functional divergence (FDiv; 0–1; Villéger et al., 2008), which quantifies the spread of trait values within a community and highlights trait-mediated responses to landscape gradients. We modelled FDiv using beta regression (logit link; Smithson-Verkuilen adjustment for 0/1) with the same composition and configuration predictors (*z*-scored; $k = 4$, bs = 'ts'). Guided by detected interactions, we tested whether the same landscape gradients influenced FDiv. To ensure FDiv patterns were not merely richness artefacts, we added a smooth of richness s(SR, $k = 4$) and assessed whether CAGR and DNAT remained significant conditional on SR. Model adequacy followed the same diagnostic (gam.check, concurvity, DHARMa).

All analyses were performed in R 4.4.1 (R Core Team, 2024), using *tidyverse* for data import/manipulation and plotting (Wickham et al., 2019), *car* for multicollinearity (VIF; Fox & Weisberg, 2019), *mgcv* for GAMs (Wood, 2017), DHARMa for residual diagnostics and Moran's *I* spatial tests (Hartig, 2024), *gratia* for GAM visualization and diagnostics (Simpson, 2021), *sf* for spatial data handling (Pebesma, 2018) and *gstat* for semivariograms (Pebesma & Wesseling, 1998).

3 | RESULTS

3.1 | Functional trait distribution and community patterns

We recorded 110 species and 7569 individuals across 50 sites (Table S2). WS ranged from 22.5 to 73.5 mm (median 36.38 mm; IQR 30.0–46.9 mm), with 50.9% of species 30–45 mm in length, whereas 8.2% exceeded 60 mm, indicating a right skew with relatively few large-bodied species (Figure 2a). Host-plant breadth was dominated by two-host species (64.5%), with one-host species rare (6.4%) and ≥3-host species accounting for 29.1% (Figure 2b).

Site-level trait composition of wingspan (WS) showed that most communities are mixed, with some strongly skewed to one class (Figure 2c). Communities were mostly dominated by smaller-winged taxa, with 78% of sites in the low or mid WS classes and only 22% dominated by large-winged species.

Across sites, oligophagous species (2-host) formed the main component of communities, species with ≥3 hosts contributed a secondary share, whereas 1-host species were generally minor (commonly near 0%–10%; Figure 2d).

3.2 | Landscape and trait effects on butterfly richness

Checking trait–trait correlation, we found no monotonic association between site-level CWMs (Spearman $\rho=0.107$, $p=0.458$), indicating non-redundant trait axes suitable as distinct predictors. Landscape-only GAM for composition predictors (Grass, For, CAGR) explained little variation in butterfly richness (adj.$R^2=0.04$; deviance explained = 5.4%, Table S3a). Only CAGR was significant ($p=0.026$; Table S4a; Figure 3a).

Adding trait CWMs (HPS, WS) substantially improved fit (ML LRT $\chi^2=18.9$, $p<0.001$; ΔAIC = −13.6; Table S3a), with adj.R^2 rising to 0.22 and deviance explained 27% (Figure 4a,b). The HPS smooth was strongly significant ($p<0.001$; Figure 3b), whereas WS showed no main effect (Table S4a).

Pre-specified HPS × CAGR interaction was borderline by term test ($p=0.050$; Table S4a), produced only small descriptive gains (adj.$R^2=0.26$; deviance explained = 34.1%) and did not improve fit in ML comparison (LRT $p=0.15$; ΔAIC = −0.7 relative to additive), so we treat this interaction as unsupported (Figure S1).

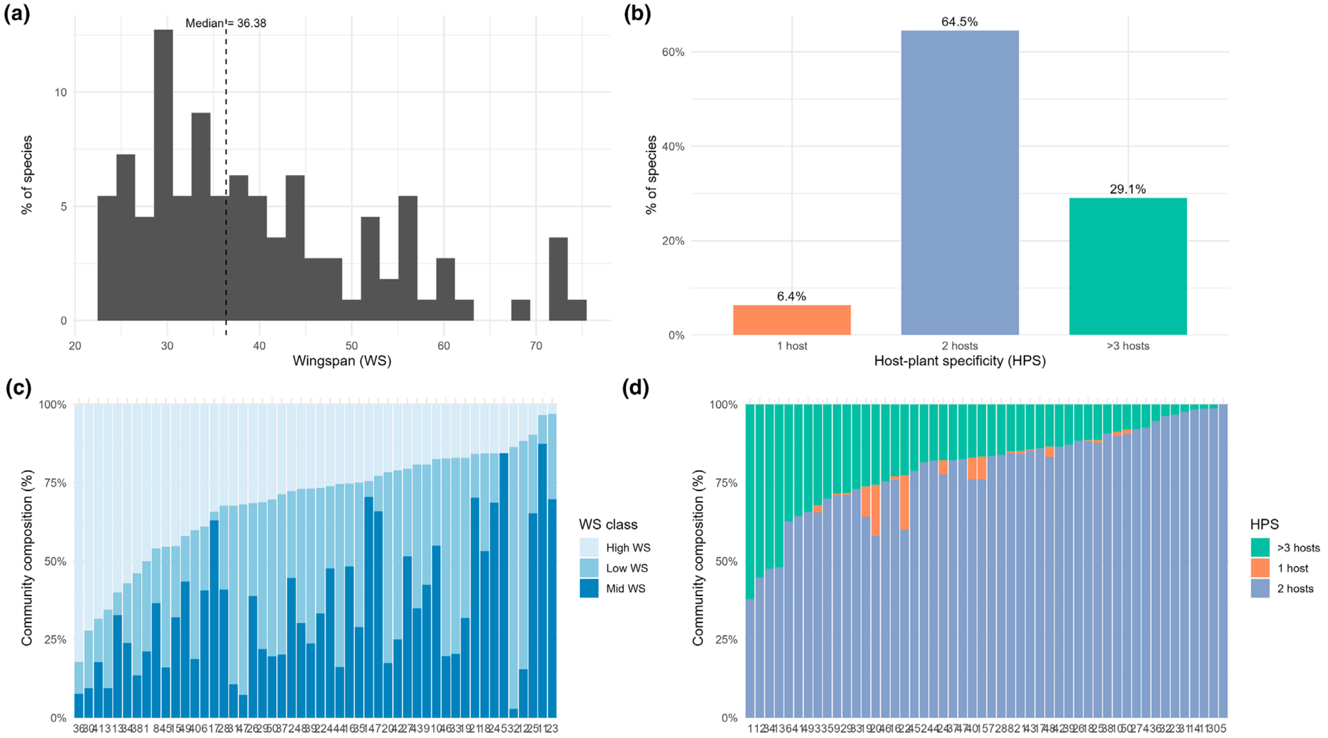

FIGURE 2 Regional trait pool at the species level (a, b) and community trait structure (c, d). (a) Species-level WS histogram, % of species per bin; the median WS is drawn as a dashed line; (b) species-level HPS: Bar chart of % of species in each HPS class; (c) site-level WS composition: Stacked percentages of low/mid/high WS (abundance-weighted) for each site; (d) site-level HPS composition with stacked percentages of 1/2/≥3 hosts (abundance-weighted) for each site.

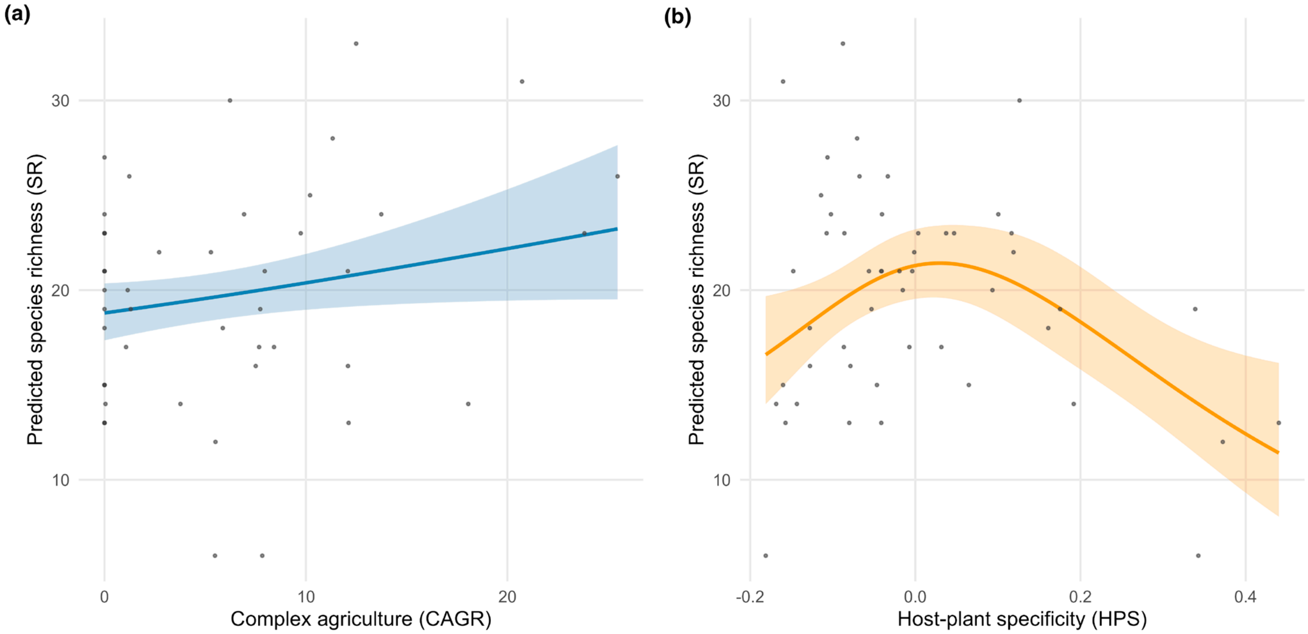

FIGURE 3 Predicted butterfly species richness (SR) from landscape composition (GAMs). (a) Landscape-only model: Partial response of SR to complex agriculture (CAGR) across its observed range. Solid line shows fitted values on the response (count) scale, shaded ribbons are 95% and points are observed SR per site. (b) Additive trait model: Partial response of SR to host-plant specificity (HPS; centered community-weighted mean), holding the landscape covariates at their medians. Solid line and CI as in (a).

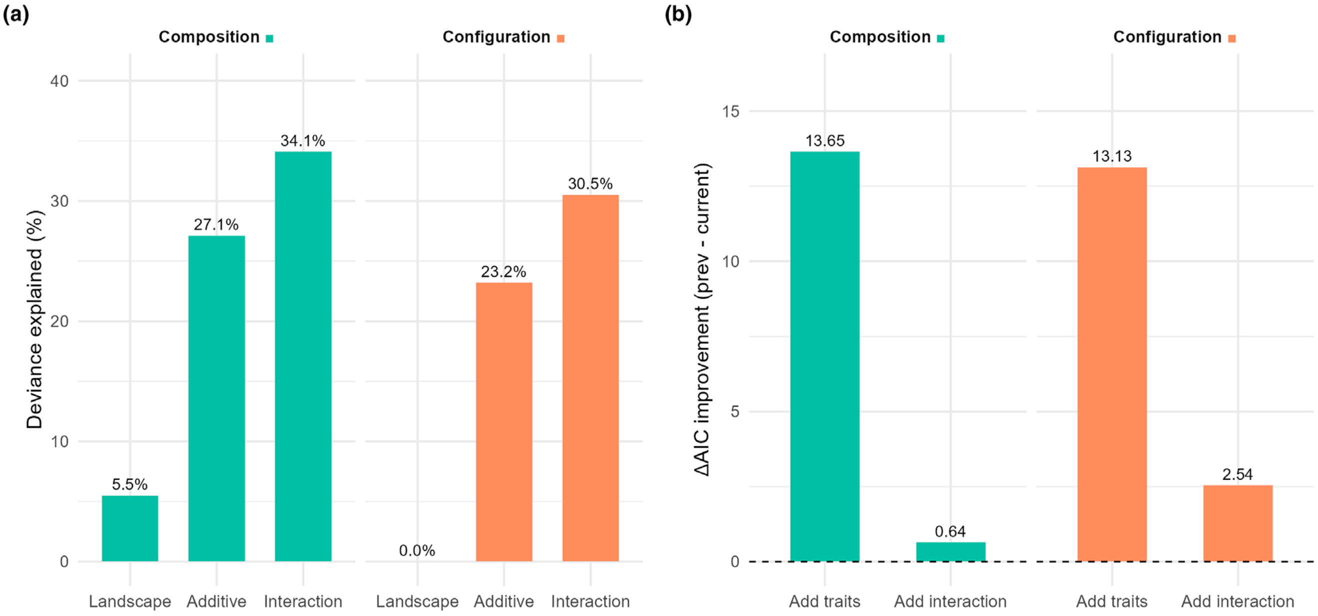

FIGURE 4 Performance comparison of the three GAM models. (a) Deviance explained (%) for three models: Landscape-only, additive and interaction, shown separately for the composition and configuration predictor sets; (b) ΔAIC improvement relative to the previous tier (higher bars indicate better fit), computed from ML-fit models to ensure AIC comparability. Traits are community-weighted means (wingspan, host-plant specificity).

Landscape-only GAM for configuration predictors (DNAT, ED, NAT_Size), explained virtually no variation in richness (adj.$R^2 = 0.00$; deviance explained = <1; Table S3a). Adding trait CWMs (HPS, WS), again improved fit (ML LRT: $\chi^2 = 20.2$, $p < 0.001$; ΔAIC = −13.1; Table S3a), raising adj.R^2 to 0.18 and deviance explained to 23% (Figure 4a,b), HPS remained strongly associated with richness ($p < 0.001$; Table S4b; Figure 5a). Pre-specified WS × DNAT interaction provided further improvement (ΔAIC = −5.9; LRT: $p = 0.037$) with adj.$R^2 = 0.24$ and deviance explained = 30.4% (Table S3a) and the interaction term was highly significant ($p = 0.003$; Table S4b; Figure 5b).

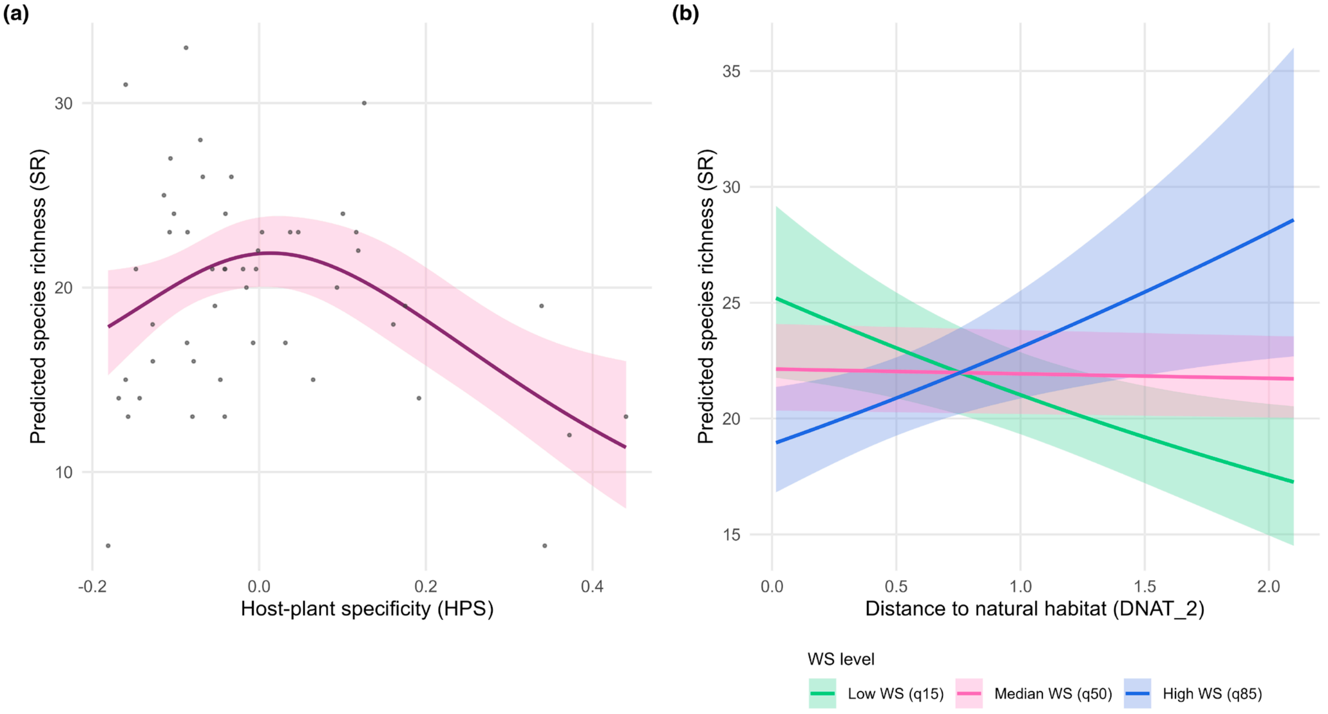

FIGURE 5 Predicted butterfly species richness (SR) from landscape-configuration GAMs. (a) Additive trait model: Partial response of SR to host-plant specificity (HPS; centred community-weighted mean). Solid line shows fitted mean on the response (count) scale with 95% pointwise CI; points are observed SR per site. (b) Interaction model: Slice plot for the interaction between wingspan (WS) and distance to the nearest natural patch (DNAT). Lines are predicted SR across the observed range of DNAT at low (15th percentile), median (50th) and high (85th) levels of WS; centred CWM. Shaded ribbons are 95% CIs.

Sensitivity analyses reinforced these conclusions (Table S3b). In the composition models, HPS remained a strong positive predictor when removing both top-1 and top-2 species. The HPS × CAGR interaction was borderline under top-1 (LRT: $p=0.068$, ΔAIC $=-2.5$) and not supported when removing top-2 species (LRT: $p=0.23$; ΔAIC $=+0.6$). Notably, WS gained a positive main effect under top-2 ($p=0.003$), suggesting that dominance can mask a WS signal.

In the configuration set, WS × DNAT interaction remained significant when removing both top-1 (LRT: $p=0.030$; ΔAIC $=-4.0$) and top-2 (LRT: $p=0.05$; ΔAIC $=-2.5$).

While checking diagnostics, landscape-only models showed overdispersion (DHARMa dispersion test $p=0.02$ and 0.004), but this was resolved after adding traits and then also interactions (all dispersion tests were non-significant), meaning that the extra-Poisson variation was structural (missing covariates) rather than distributional.

Moran's *I* tests indicated no significant spatial autocorrelation in any model (all $p>0.05$; closest $p=0.06$ in top-2 configuration fits; Table S3b). Empirical semivariograms of DHARMa residuals rose slightly at very shortest distances and then plateaued, both for main models and after dominance removal, indicating minimal spatial autocorrelation (Figures S2: main, S3: removal of top-1 and S4: removal of top-2).

Two landscape variables showed clear associations with functional divergence (FDiv), CAGR ($\chi^2=13.13$, $p<0.001$; Figure 6a) and DNAT$_2$ ($\chi^2=12.62$, $p<0.001$; Figure 6b), while other predictors showed no detectable relationships. The models explained 26.6% (composition) and 26.0% (configuration) of the deviance, with good diagnostics.

After controlling for SR, CAGR remained negatively associated with FDiv ($\chi^2=8.25$, $p=0.006$) and DNAT remained positively associated ($\chi^2=10.67$, $p=0.002$).

4 | DISCUSSION

4.1 | Functional trait distribution and community structure

At the regional scale, the species pool is biased towards larval diet generalists and against strict specialists, consistent with theory and cross-taxonomic evidence from European agricultural mosaics (Börschig et al., 2013; Brückmann et al., 2010; Clavel et al., 2011; Winfree et al., 2015). Habitat loss, fragmentation and agricultural intensification tend to filter out species with narrow host requirements, whereas dietary generalists cope better with spatiotemporal variability and exploit matrix resources.

Within communities, the prevalence of smaller-winged species likely reflects either limits of the regional pool or local filters that disfavour large-winged species (e.g. cluttered, edge-rich mosaics McCoy, 2018). Taken together, these patterns indicate mild functional homogenization towards smaller wing size and intermediate

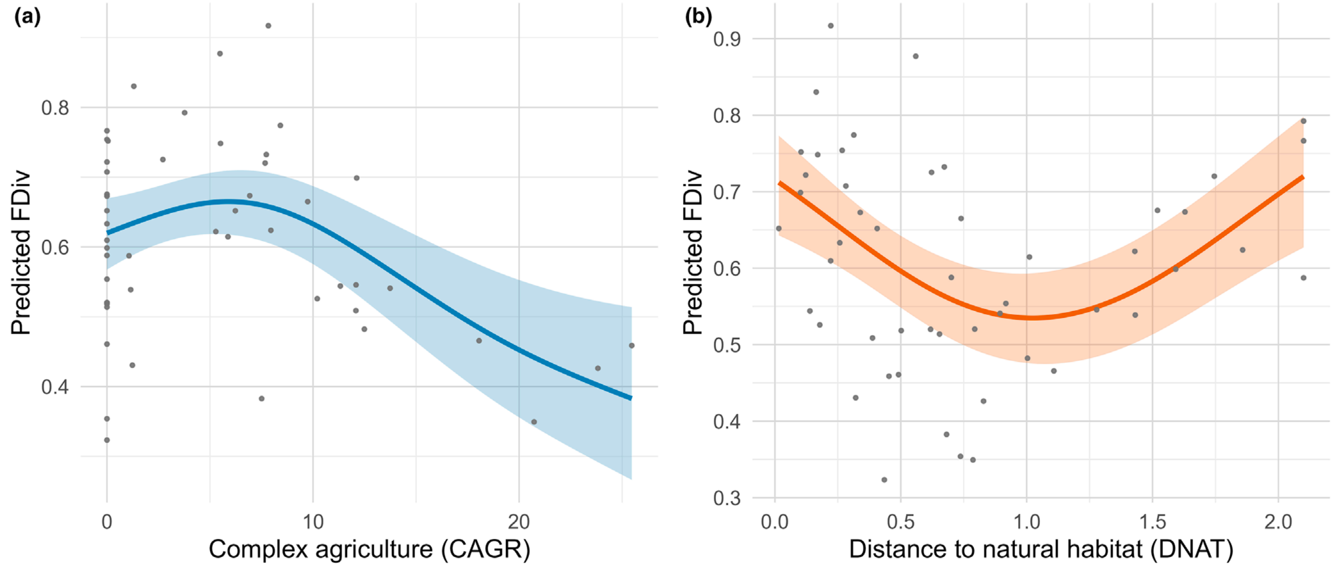

FIGURE 6 Predicted functional divergence (FDiv) of butterfly communities from GAMs. FDiv in relation to (a) the proportion of surrounding complex agriculture (CAGR) and (b) the distance to the nearest natural patch (DNAT). Solid lines show fitted responses from beta regression GAMs ($k = 4$), with shaded areas indicating 95% confidence intervals. Grey points represent observed site-level values of FDiv.

diet breadth (oligophagy), suggesting that local filtering reduces the range of functional strategies. Such homogenization may also have broader ecological and evolutionary consequences, potentially lowering community resilience and, where filtered traits are phylogenetically conserved, promoting phylogenetic clustering over longer timescales (Cadotte et al., 2011).

4.2 | Landscape and trait effects on butterfly richness

Landscape metrics alone explained little to no species richness (contrary to H1), whereas adding traits, specifically host-plant specificity (HPS), markedly improved fit (supporting H2). This indicates that HPS main effect (capturing resource use) provides substantive predictive power relative to landscape configuration and composition metrics. Although some systems do find richness primarily driven by landscape structure (Guderjan et al., 2023; Tammaru et al., 2023), such context dependence underscores the value of testing trait contributions alongside landscape predictors.

Within composition set, complex agriculture (CAGR) was positively associated with richness, likely via structural heterogeneity (variety in vegetation structure and features) and diverse foraging opportunities (Öckinger & Smith, 2007). Mechanistically, diverse agricultural mosaic (mixed vegetation and crop mosaic) can support more nectar and larval niches at the landscape scale. However, FDiv declined with higher CAGR, indicating that these gains arise from trait-similar species, consistent with functional homogenization in agriculturally rich regions (Jonason et al., 2017). This pattern is conceptually analogous to the intermediate disturbance hypothesis (IDH; Connell, 1978), underscoring the broader ecological principle that intermediate states, whether in environment or strategy, may maximize diversity.

Adding HPS had a significant additive main effect, substantially increasing explanatory power in both composition and configuration models, indicating that richness is closely tied to the trophic structure of communities that is, availability and partitioning of larval host plants, beyond what coarse landscape metrics capture (Gordon & Kerr, 2022).

Contrary to expectation and simple specialist-loss scenario, sites skewed towards dietary specialists had higher richness, after controlling for landscape variables, whereas richness declined at both extremes of diet breadth, consistent with the concurrent drop in FDiv at those extremes. This suggests that landscapes can maintain richness while filtering out extreme diet strategies, resulting in communities dominated by intermediate strategies, in line with IDH-like patterns. Potential mechanisms driving this pattern include competitive overlap among extreme generalists in resource-poor settings, host- and habitat-specific constraints on larval survivorship (Wiklund & Friberg, 2009), reduced predation for specialists (Dyer, 1995) and mobility advantages allowing some monophages to remain abundant when host plants are ubiquitous. At the opposite end, loss of strict specialists can arise from poor patch connectivity affecting both specialist plants and butterflies (Brückmann et al., 2010; Öckinger et al., 2010). Land-use intensity and non-native plants may further disrupt the generalist–specialist balance (Burghardt et al., 2010; Kasiske et al., 2023). Importantly, the HPS effect persisted after removing the 1–2 most abundant species per site, indicating a community-wide pattern rather than dominance artefacts.

Among configuration metrics, distance to the nearest natural patch (DNAT) was most informative for richness through its interaction with WS, supporting H3 that dispersal capacity buffers isolation. This interaction took the form of a sign-reversal (crossover) pattern, rather than a synergistic or antagonistic effect. Richness declined with increasing DNAT in communities dominated by small-winged taxa, but increased with DNAT in communities composed of large-winged taxa (higher CWM-WS). Thus, the effect of isolation changes direction depending on community-level dispersal capacity, emphasizing context-dependent, trait-mediated responses to landscape configuration. In parallel, FDiv rose with DNAT, indicating greater representation of trait extremes along isolation gradients, consistent with movement-mediated filtering. Similar advantages for high-mobility species in fragmented landscapes (i.e. smaller, more isolated natural patches) are reported elsewhere (Kőrösi et al., 2022; Kuussaari et al., 2021; Rochat et al., 2017). It is important to note that elevated richness of large-winged species in isolated patches can include transient individuals rather than stable breeders (MacDonald et al., 2018), so we interpret this as an upper bound on dispersal filtering without breeding evidence.

Crucially, after conditioning FDiv on SR, landscape effects persisted, CAGR remained negatively associated and DNAT remained positively associated with FDiv. Thus, even at equal species richness, CAGR compresses trait space producing functionally similar communities, whereas isolation expands it, supporting more extreme strategies. This reflects trait sorting along resource (composition/HPS) and movement (configuration/WS) axes that is, representing genuine functional filters rather than richness-mediated artefacts. From a conservation perspective, this suggests that maintaining connectivity is important not only for species richness but also for preserving functional resilience ensuring that communities retain unique trait combinations even under landscape fragmentation. These mechanisms are likely relevant to similar temperate landscapes, though effect sizes may vary with species pools, matrix permeability, management and spatial scale (e.g. weaker filtering in landscapes where management maintains extensive semi-natural vegetation cover).

5 | CONCLUSIONS

Resource and movement filters, not landscape structure alone, shape butterfly communities. Agricultural complexity can add species while compressing trait breadth, whereas isolation elevates functional divergence and benefits large-winged communities. Because richness and functional structure decouple along real-world landscape gradients, biodiversity monitoring and management should track traits besides taxonomic lists, while paying attention to pairing diverse larval host resources with stepping-stone connectivity to sustain both species numbers and the functional breadth that underpins resilience.

AUTHOR CONTRIBUTIONS

Dušanka Vujanović conceived the ideas and designed methodology; Maja Knežević, Aleksandra Đorđević, Andrijana Andrić, Milica Ranković Perišić, Marina Janković Milosavljević, Sanja Veselić, Ante Vujiće and Snežana Radenković collected the data; Dušanka Vujanović analysed the data; Dušanka Vujanović, Gianalberto Losapio and Maarten de Groot led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. This study was conducted entirely by researchers based in the country where the research took place, with all co-authors (except two collaborators) affiliated with local institutions. All authors were engaged early on with the research and study design to ensure that the diverse sets of perspectives they represent were considered from the onset. Whenever relevant, literature published by scientists from the region was cited; efforts were made to consider relevant work published in the local language.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The datasets supporting this study are publicly available through the Zenodo repository at: https://doi.org/10.5281/zenodo.15855369 (Vujanović, 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Species functional traits.

Table S2. Recorded species abundances across 50 sites.

Table S3. GAM performance for butterfly species richness across two predictor sets, composition and configuration, and three model specifications per set: landscape-only, additive (+trait main effects) and interaction (+trait×landscape). (a) Main models; (b) robustness after removing the most abundant species at each site (top-1 and top-2). AIC and LRT are from ML fits; adjusted R^2 and % deviance explained from REML. ΔAIC is relative to the simpler model within each predictor set (negative = improvement).

Table S4. Term-level summaries for Poisson GAMs across composition (a) and configuration (b) predictor sets under three specifications (landscape-only, additive, interaction). Values are REML estimates.

Figure S1. Slice plot for the interaction between host-plant specificity (HPS) and complex agricultural cover (CAGR).

Figure S2. Empirical semivariograms of DHARMa residuals for the main GAMs.

Figure S3. Semivariograms of DHARMa residuals after removing top-1 (the most abundant species at each site set to zero before recomputing CWMs and refitting GAMs).

Figure S4. Semivariograms of DHARMa residuals after removing top-2 (top two most abundant species removed per site, CWMs recomputed).

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