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ORIGINAL ARTICLE

Insect Conservation and Diversity

Conservation implications of shifting habitat use in migrating insects: Selection patterns in a threatened damselfly show that season-specific actions are needed

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Abstract

1. Migratory insects use different habitats during their movements, exposing them to multiple threats, whose conservation implications are rarely considered.
2. This study explores the conservation consequences of short-range insect migration, focusing on the regionally threatened damselfly *Sympecma paedisca*. In Italy, its breeding and wintering grounds are tens of kilometres apart, and how the species moves between them is unclear.
3. To close this knowledge gap, we investigated the effects of multi-seasonal habitat composition on species' abundance at the landscape scale and its fine-scale habitat selection.
4. At the landscape scale, the abundance of *S. paedisca* increased with the cover of well-preserved heathland, regardless of season. In contrast, farmland cover had varying effects: positive in summer, strongly negative in autumn and winter and neutral in spring.
5. Habitat selection analysis showed that, in summer, the species uses all habitats according to availability. In autumn, heathlands were strongly positively selected, whereas farmland grassy margins were clearly negatively selected, and these differences are further strengthened in winter.
6. These findings support the hypothesis that the species migrates from breeding to overwintering grounds in late summer, following grassy margins throughout the agricultural matrix. Individuals that survive the winter return in spring, likely following the same corridors.
7. Conservation efforts should address the seasonally shifting species' needs, conserving well-preserved heathlands, crucial for overwintering, and grassy margins along crops to ensure the connectivity between breeding and wintering areas.
8. The conservation of migrant insects requires measures targeting the different phases of their life cycle, even for short-distance migratory species.

KEYWORDS
farmland, grassy margins, habitat connectivity, heathland, movement ecology, Odonata, *Sympecma paedisca*

INTRODUCTION

Animal migration is one of the largest and most stunning phenomena of the natural world, involving a multitude of taxa and billions of individuals moving on the planet every year (Cresswell et al., 2014; Dingle, 2014). Animal journeys can take place through land, water or air, covering from a few metres (e.g., in *Lygaeus equestris*) to pole-to-pole travels (e.g., in *Sterna paradisaea*) (Cooke et al., 2024; Dingle, 2014; Dingle & Drake, 2007). Animal migration has evolved several times independently as a response to spatio-temporal variation in resources, and migratory animals represent the majority of modern lineages (Cresswell et al., 2014; Dingle & Drake, 2007). Despite the incredible evolutionary success of this adaptation, migratory species are generally more threatened with extinction when compared to sedentary taxa (Hardesty-Moore et al., 2018). This is because migratory animals, unlike sedentary ones, use many habitats in the course of their life cycle and are therefore exposed to multiple threats, such as habitat loss or degradation, poaching and climate change (Cooke et al., 2024; Shuter et al., 2014). This is particularly true for long-distance migrants, whose migration routes often cross countries or continents (Assandri et al., 2024; Serratosa et al., 2024).

An increasing number of studies are targeting the identification of effective conservation strategies for mobile species (Cooke et al., 2024; Runge et al., 2014; Shuter et al., 2014). However, most research has focused on long-distance migrants, mostly mammals, birds and several insects (e.g., *Autographa gamma*, *Danaus plexippus*, *Pantala flavescens*) (Chapman et al., 2012, 2015; Chowdhury et al., 2021; Hsiung et al., 2018). This has led to a knowledge bias concerning the conservation of species that move over shorter distances, a large proportion of which are migratory insects (Gao et al., 2020; Satterfield et al., 2020). Insect migration is still a little-studied phenomenon, but one that has garnered increasing interest from ecologists in recent years (Chapman et al., 2015). Although less understood than vertebrate migration, mainly due to technological limitations that make it challenging to track individuals over large scales, the total biomass of migratory insects exceeds that of vertebrates, being an ecological phenomenon of primary interest (Holland et al., 2006). Indeed, the cyclical movement of such large numbers of insects has profound consequences on the functionality of ecosystems, human and livestock health and vertebrates' conservation (Satterfield et al., 2020). Migration routes, navigational mechanisms, energetic costs, and mortality rates are some of the aspects that are mostly inaccessible today due to the technological limitations imposed by the weight of tracking devices (May & Matthews, 2022). The vast majority of insect migrations occur as multi-generation events (i.e., *Anax junius*, *D. plexippus*, *Vanessa cardui*), that is, several generations are involved in completing an entire migration cycle, which is one of the major differences with vertebrates' migration (Holland et al., 2006).

Dragonflies (Odonata), among insects, are one of the orders with the most pronounced migratory behaviour, rivalling some vertebrates in terms of travel distance and large-scale biomass movement (May, 2013). In Odonates, migration is believed to have evolved in response to adverse seasonal weather events (i.e., cyclical droughts) and, in temperate regions, it is considered to be an opposed strategy to nymphal diapause (Samways, 2024). Because of their large size and relative ease of observation, they currently are the insect taxon with the largest number of studies on migration, focusing in particular on two model species: *Anax junius* and *P. flavescens*. These two species can travel thousands of kilometres, across continents in the case of *P. flavescens* (May & Matthews, 2022; Samways, 2024). Due to its body size, *A. junius* is to date the only dragonfly for which it has been possible to study certain aspects of its migration (e.g., migratory directions, daily distances travelled, influence of weather) using 0.3 g radio transmitters, which are still too heavy to be applied to most migratory insects (Knight et al., 2019).

While the dispersal ability of Anisopterans is well understood, Zygopterans, the other suborder of Odonata, are still considered mainly sedentary. However, some species (e.g., *Pseudagrion glaucescens* and damselflies of the genus *Ischnura*) can disperse over hundreds of kilometres, and colonise oceanic islands (e.g., *Ischnura hastata*) (Góral, 2024). The ability to move over relatively long distances has also been documented in species that were previously considered to be purely sedentary, such as *Nehalennia speciosa*, able to colonise restored habitats located tens of kilometres from the nearest populations (Bernard et al., 2011; Góral, 2024). However, among Zygopterans, it is the Lestidae family that presents the most pronounced migratory behaviour, with numerous species performing relatively long-range movements. *Lestes* adults have been found in areas without suitable habitats for nymphal development, suggesting that, in this family, post-emergence movements have evolved to find maturation sites, rather than new breeding habitats (Corbet, 1999; Góral, 2024). In some cases, maturation takes place in seasonal refuges reached after emergence, with the species of the genus *Sympecma* being the most obvious example of this behaviour.

The three species in the genus *Sympecma* are the only Odonates adapted to survive at the adult stage in the harsh winters of the Eurasian temperate climate, hibernating on plant stems and reactivating on warmer days. This unique adaptation is believed to have originated in the steppes of central Asia as a response to a dry water regime (Harabiš et al., 2012). Moreover, due to the ephemeral characteristics of breeding habitats, nymphal development in the genus *Sympecma* is rapid, lasting 8–12 weeks (Jödicke, 1997). Emergence occurs in the second half of the summer, and the new generations rapidly move away from their emergence sites to reach overwintering quarters. Then, at the onset of the spring, they move back to breeding sites (Billqvist et al., 2022; Boudot & Kalkman, 2015). *Sympecma* represents a unique eco-evolutionary case among Odonata (Samways, 2024), and one of the few cases among insects in which a single generation performs a complete migration from breeding to wintering areas, and back (Chapman et al., 2015; Holland et al., 2006). A better understanding of this phenomenon can thus have important consequences also for conservation, considering that insects which are obligate migrants are not only subjected to human threats in their breeding sites (as for non-migrant insects), but they experience multiple (and often very different) threats in the various phases of their cycle (Gao et al., 2020; Runge et al., 2014). This further challenges conservation efforts and calls for solid ecological knowledge in every phase of the life cycle of these animals.

Aiming at understanding the conservation consequences of short-range migratory movements in insects, we selected as a case study the damselfly *Sympecma paedisca*. In Italy, where this species reaches its southernmost latitudinal limit in Europe, it is considered critically endangered, being confined to a small range in the north-western part of the Country. Recent evidence suggests that the rice fields of the Po floodplain are their main breeding ground, whereas remnants of subalpine lowland heathlands and dry grassland of north-western Italy represent the main overwintering habitat (Siddi, Battisti, et al., 2025). These two geographical areas are separated by approximately 20 km, and to date, there are no data on the timing, modality or geographical extent of the movements that allow the species to commute between these two areas. To close this knowledge gap and shed new light on the consequences of migration in this regionally endangered damselfly, we first investigated how the abundance of the species outside the breeding period varied according to phenological phases, accounting for the landscape composition. We predicted that abundance starts to increase in heathlands in late summer when the species leaves its breeding sites, peaks in autumn/at the beginning of winter and then decreases towards spring, when the wintering grounds are abandoned. Additionally, during the movements between breeding grounds and wintering grounds, the species is forced to cross an intensive farmland matrix; thus, we predicted a peak of abundance in agroecosystems in late summer and the beginning of spring.

Secondly, we conducted a local-scale habitat selection analysis, again differentiating the phenological phases of the non-breeding cycle of the species, aiming at disentangling the environmental drivers that influence the occurrence of the species and thus provide evidence-based and seasonally tuned support to the conservation of this evolutionarily unique species.

METHODS

Target species

S. paedisca is a medium-sized damselfly (body length: 36–39 mm; wingspan: 18–22 mm; Dijkstra et al., 2020) with a cryptic pale brown colouration promoting camouflaging in grassy and shrubby wintering habitats (Figure 1). Its range extends across the temperate belt of the

FIGURE 1 Wintering *Sympecma paedisca* perched on *Calluna vulgaris* in the heatlands of northwestern Italy (a; artwork by Martina Cadin) and examples of the three different habitats used by the species outside the breeding season in this area: (b) grassy margin bordering cultivated fields (Salussola, Biella province, Piedmont); (c) well-preserved heathland (Baraggia di Candelo, Biella province, Piedmont); (d) degraded heathland (Brughiera del Gaggio, Varese province, Lombardy). Photos by Leonardo Siddi.

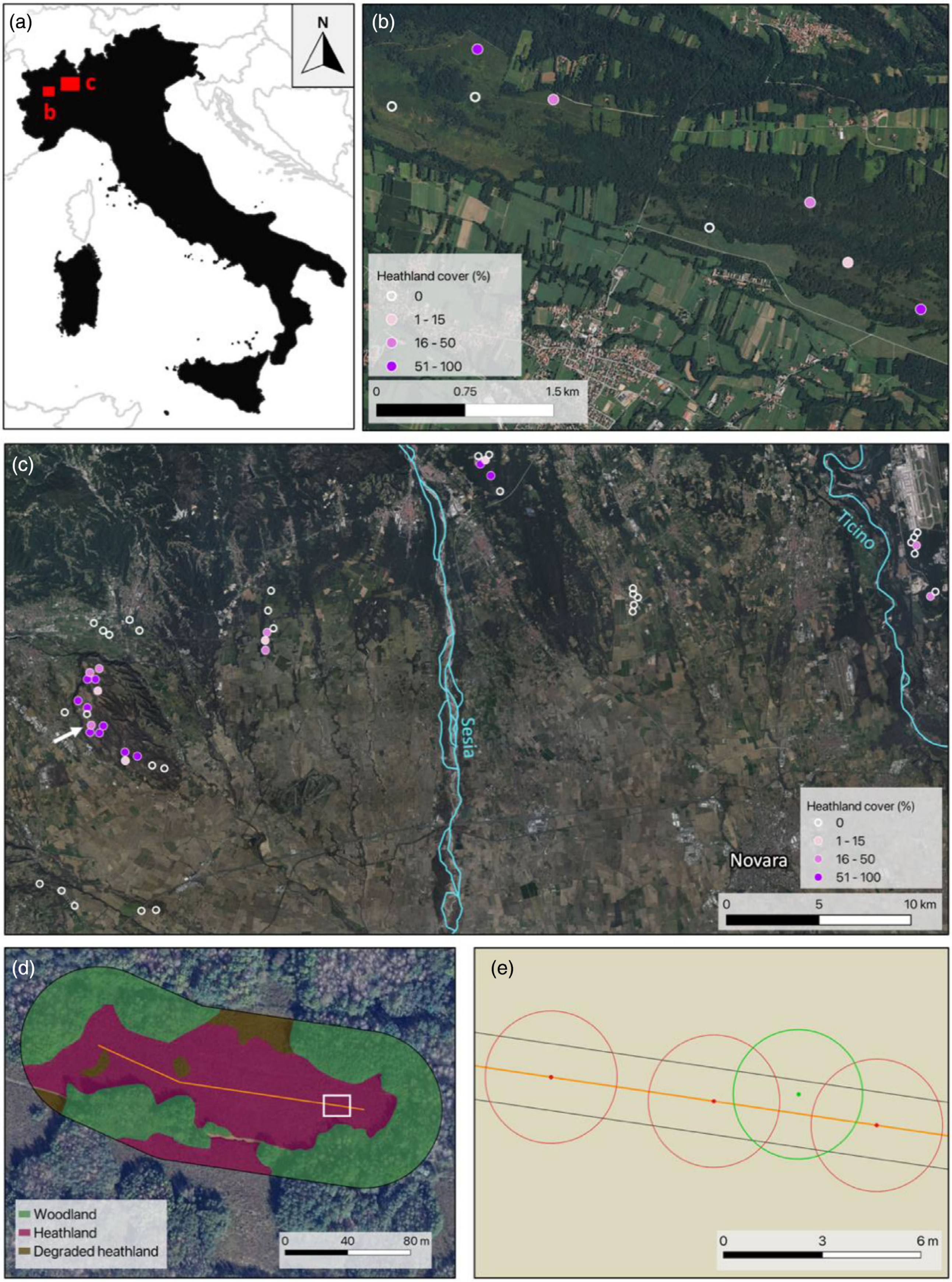

FIGURE 2 Legend on next page.

Eurasian continent, from central and southern Europe to Japan. It breeds in a wide range of standing or slow-flowing waters surrounded by abundant bank vegetation, in both natural (e.g., marshes, lakes, bogs, fens, ponds, dead oxbows) and anthropogenic (e.g., quarry/post-mining ponds, rice field ditches and restored wetlands) habitats (Billqvist et al., 2022; Keil et al., 2024; Siddi, Battisti, et al., 2025). The European population of *S. paedisca* suffered a significant decline during the second half of the 20th century, mainly driven by the loss of breeding habitat caused by human activities (Billqvist et al., 2022; Boudot & Kalkman, 2015). For this reason, *S. paedisca* is listed in Annex IV of the 'Habitat' Directive (92/43/EEC) as a species of community interest in need of strict protection. After this decline, the species has recovered in most of its range, and the population trend is now generally positive, but it is still threatened at the southern margin of its range, for example, in Italy, where it is considered critically endangered (Riservato et al., 2014).

Study area and sampling design

The study area is located in northwestern Italy, in the upper part of the Po Valley, between Piedmont and Lombardy (approximately 1090 km^2; coordinates 45.5°N–8.2°E, Figure 2). The area encompasses most of the current known range of *S. paedisca* in Italy (Siddi, Battisti, et al., 2025). Lowland heathlands (habitat 4030 under the 'Habitat' Directive 92/43/EEC) are among the most distinctive habitats of the study area, where they occur heavily fragmented (Gheza et al., 2020). In this area, heathlands are transitional vegetations resulting from human activities: The natural succession leads to the reforestation of these environments through the progressive invasion of open heathlands (dominated by *Calluna vulgaris* and *Molinia caerulea*) by ecotonal shrub species (e.g., *Populus tremula*, *Betula pendula*, *Rosa canina*), and the climax stage is represented by the lowland oak-hornbeam forest (Ascoli et al., 2013; Borghesio, 2009). In Italy, lowland heathlands are maintained by traditional management including mowing and livestock grazing, which suppresses the succession towards forest, and are now threatened by the abandonment of such traditional practices (Olmeda et al., 2020). Another relevant threat to the conservation of these delicate ecosystems is the conversion to agricultural habitats, and particularly rice fields, which have also expanded on land previously occupied by heathlands (Bonelli et al., 2010).

To address the objectives of the study, we selected 60 study sites within the area described above (Figure 2; Siddi, Battisti, et al., 2025). A stratified design was conceived to best sample the successional gradient found in heathlands, the main known wintering habitat of *S. paedisca* in the study area. Of the 60 sampling sites, 40 were thus located in heathlands and 20 in ecotonal herbaceous environments (e.g., grassy field margins, road/trail borders and fallow land) in agricultural landscapes surrounding the main heathland sites surveyed. At each sampling site, we defined a linear transect, which was placed as much as possible in a uniform habitat following the sampling design. Habitat recognition and transect placement were done using updated orthophotos and field inspections. The final transect length was variable (mean ± SD: 142 ± 39.9 m) to optimise the efficiency/effort trade-off. Transects were spaced at least 200 m apart to keep them independent as much as possible and grouped into geographically homogeneous clusters of a minimum of five transects each.

S. paedisca survey and collection of environmental variables

S. paedisca survey

The target species was surveyed at each transect walking at a constant slow pace on days with favourable weather, avoiding strong wind and precipitation. Individuals were counted within 1 m from each side of the transect (Figure 2e). The species is almost impossible to see when resting in the thick vegetation, thus the contact occurs when the operator causes flight. Particular attention was given to the starting point of each individual and the direction when taking off, to assess the resting habitat and avoid double counts. We surveyed 5–11 transects per day, belonging to 1–2 clusters. Five repetitions for each transect were carried out, from late August to April, to encompass the entire non-breeding season of the species (Siddi, Battisti, et al., 2025; Siddi, Cadin, et al., 2025). Specifically, we surveyed the species in summer (24 August–5 September 2023), autumn (9 October–22 October 2023), early winter (27 November–15 December 2023), late winter (31 January–18 February 2024) and at the beginning of spring (2 April–13 April 2024). Surveys were always performed during the peak activity of the species, which is late morning in the hot summer days and the central hours of the day from autumn to the beginning of spring. Due to a fire that affected one of our clusters, we removed four transects from the last survey (spring). We surveyed 296 transects for a total of 42,095 m.

Landscape-scale variables

To understand how the landscape composition influences the abundance of the species, we mapped the land cover in a 50-m buffer

FIGURE 2 Study area and sampling design. (a) Location of the study area in Italy (represented by 'b' and 'c' red insets). (b. c) Location of the 60 surveyed sites within the study area. The dot colour represents the percentage of heathland cover within the 50-m buffer of the transects. The white arrow shows the transect represented in 'd'. (d) Example of a linear transect (orange line) and characterisation of the landscape composition within a 50-m buffer. The white rectangle represents the inset zoomed-in 'e'. (e) Local-scale habitat sampling design. A transect section (orange line) is shown, with the 1-m-per-side buffer within which damselflies were counted (black lines). Red dots represent control points used in the habitat selection analysis (available), while the green point represents a *Sympecma paedisca* occurrence point (used); both occurrence and control points have a 2-m buffer in which habitat assessment was performed.

around each transect (Figure 2d). Given the absence of quantitative data on the local movements performed by the species during the overwintering period, the 50-m distance was set based on our experience with the species and considered appropriate to our aim. Indeed, in the only capture-mark-recapture study conducted during the entire overwintering season, all recaptured individuals ($N = 22$) were found in the same locality as the first capture, suggesting that in the colder months, the species is almost completely sedentary (Manger & Dingemanse, 2009). Digitalisation of habitat patches was carried out by photointerpretation of orthophotos, followed by field validation. We measured the cover of the following six habitats: (1) heathland (best-preserved stages of lowland heathland, with the predominance of *C. vulgaris* and *M. caerulea*); (2) degraded heathland (heathlands that are being reforested or overgrazed, which are invaded by ecotonal species); (3) woodland (oak-hornbeam woods, *Robinia pseudoacacia* thickets and other wooded habitats); (4) farmland (cultivated areas); (5) grassy margins (uncultivated patches with a predominance of herbaceous species); (6) shrubland (areas dominated by shrub species). *Molinia* grasslands were included with heathlands, as in the study area, the distinction between these two habitats is not easy, as they occur largely interspersed. Details on the relative surfaces of these habitats are provided in Table S1. Other land cover classes with unrepresentative extents (altogether 3.74%) were excluded from the analysis.

Local-scale variables

We investigated the local-scale habitat selection of the species by assessing the prevailing habitat typology in a circle of a 2 m radius around each location at which an individual *Sympecma* was recorded (see "*S. paedisca* survey" section; 'used locations', $N = 741$) and at 1741 random control circles ('available locations'). These latter were located based on a regular sampling, positioning their centre every 5 m along the transect (Figure 2e). Habitat classification was carried out using the same criteria as for the landscape scale (50 m, see "Landscape-scale variables" section), with the only difference being that, at the 2-m scale, no occurrence/control points were located in farmland habitats. In addition, we noted which plant species each individual was resting on before taking flight. In cases when plant identification was difficult in the field due to the occurrence of morphologically similar species (e.g., Poaceae), we noted a higher taxonomic rank (e.g., genus, family).

Statistical analysis

Landscape scale

We investigated how the landscape composition (at a 50-m spatial scale) affected the linear density of *S. paedisca*, calculated as the number of individuals divided by the length of the transect, through generalised linear mixed models (GLMMs) while accounting for the season. Initially, we fit a Poisson GLMM with the number of individuals counted at each transect as the dependent variable, the log of the length of each transect as an offset to account for the different lengths of the transects, and the six habitat covariates (see "Landscape-scale variables" section), which were preventively standardised, as predictors. An interaction term with season (five levels: summer, autumn, early winter, late winter and spring) was included for heathland cover and farmland cover, the habitats in which, given our predictions, we expected differential abundance according to season. The transect identification code nested into the cluster identification code was included as a random intercept to account for non-independence potentially determined by repeating counts in the same transects and selecting groups of transects in different areas. This model (and any corrections on error distribution/zero inflation) resulted in poor fits and a strong underestimation of the observed density. Model validation suggested this happened due to a strong right-skewness of the data. We thus opted to directly model the linear density of the species with a Gaussian GLMM in which we applied an inverse hyperbolic sine transformation of the response variable. This transformation is akin to a log transformation except for the fact that it manages the zeros and the right-skewness in a more efficient way (Bellemare & Wichman, 2020). This model outperformed any others (i.e., better predictions/observed values accordance, successful model validation, no spatial autocorrelation). Degraded heatland was removed from the final model due to its correlation with farmland ($r = -0.45$, $p < 0.001$; Figure S1) and because it caused an increase (>2.5) in multicollinearity (measured with the aGVIF; R package *misty*; Yanagida, 2025). Model validation was performed with the *DHARMa* package (Hartig, 2024). Models were built based on ecological hypotheses, and non-significant interactions were removed, but no model selection on the fixed effects was performed. All the analyses were performed with R 4.2.1 (R Core Team, 2024).

Local scale

To assess the local-scale (2 m) habitat selection of *S. paedisca*, and how it changes according to season, we fitted a standard resource selection function (RSF) using a generalised linear model (GLM) in which the response variable assumed the value 1 for used locations and 0 for available locations and a binomial distribution for errors. Given the very low number of used locations in woodland ($N = 4$) and shrubland ($N = 13$), we excluded these two habitats and two transects dominated by these typologies at the local scale from the analysis, to prevent model convergence issues. The used available location ratio in the season with the highest number of recordings (autumn) was 1:5. We kept this ratio also for the other seasons by subsampling the available locations within transects, keeping constant the relative proportions of habitat as in the original sample. As predictor variables, we included an interaction habitat × season (habitat:categorical variable with three levels; season:categorical variable with five levels). Following Chamaillé-Jammes (2019) and Fradin and Chamaillé-Jammes (2023), RSF scores were converted into selection ratios for interpretability. Model validation was conducted through the *DHARMa* package (Hartig, 2024). We repeated the same analysis with a binomial GLMM with transect ID nested into cluster ID as random intercepts, to account for spatial independence induced by our sampling design. However, the residuals of this model showed spatial autocorrelation, which was not present in the GLM, which was thus selected as the final model. All the analyses were performed with R 4.2.1 (R Core Team, 2024).

RESULTS

Landscape scale

The analysis of the effect of the landscape composition (on a 50-m scale) on the linear density of *S. paedisca* showed a positive effect of heathland cover, whereas the interaction heathland × season was not supported (and was thus removed from the models), suggesting that the direction of the effect is consistent among seasons (Table 1, Figure 3a). However, a relevant increase in the number of individuals is evident in autumn, reaching high densities of 400 individuals per linear km (Figure 3a). The interaction farmland × season was supported (Table 1, Figure 3b), meaning that the abundance of *S. paedisca* in response to farmland cover varied according to the seasons. Specifically, in summer, the abundance increased with the cover of farmland, while in all the other seasons, it decreased (Figure 3b). In early winter, late winter and spring, the highest abundance of *S. paedisca* is observed with very low (virtually zero) farmland cover (Table 1, Figure 3b).

The cover of grassy margins, shrubland and woodland did not affect the linear density of *S. paedisca* (Table 1).

Local scale

At the local scale (2 m), habitat selection in *S. paedisca* varied seasonally in the three habitats considered (heathland, degraded heathland and grassy margins; $\chi^2 = 59.47$, df = 8, $p < 0.001$; Figure 4). Indeed, in summer, all the confidence intervals encompassed one, suggesting that all habitats are used according to availability. In autumn, heathlands were strongly positively selected, whereas degraded heathlands were used according to availability. Contrarily, grassy margins were clearly negatively selected. Heathland selection remained positive at the beginning of winter and further strengthened in late winter and spring. On the contrary, grassy margins were strongly negatively selected in winter, with a limited increase in spring (but still negative). After autumn, degraded heathlands showed a different trend in selection compared to well-conserved heathlands; they were used according to availability, with a negative selection emerging in spring.

Overall, 62.5% of *S. paedisca* observations occurred on a single plant species, *M. caerulea* (Poaceae), and a further 17.9% on *C. vulgaris* (Ericaceae; Figure 5a). Restricting the analysis to grassy margins in this habitat, 50.9% of the occurrences of *S. paedisca* occurred on grass species (Poaceae family), and most of the remaining on a wide range of ruderal species, including several non-native ones (e.g., *Bidens frondosa* and *R. pseudoacacia*). These species are used mostly in summer and, to a lesser extent, in autumn and spring (Figure 5b).

DISCUSSION

In this study, by providing new data on the non-breeding ecology of the damselfly *S. paedisca*, we shed new light on the conservation

TABLE 1 Results of a Gaussian GLMM testing the effect of landscape (50 m) composition on the linear density (individuals/km) of *Sympecma paedisca*.

Variable		β	CI	χ^2	df	p
Intercept		**3.07**	**(2.55 to 3.59)**	**134.98**	**1**	**<0.001**
Heathland cover (%)		**0.48**	**(0.14 to 0.82)**	**7.78**	**1**	**0.005**
Grassy margins cover (%)		0.025	(−0.30 to 0.35)	0.023	1	0.879
Shrubland cover (%)		−0.18	(−0.44 to 0.076)	1.92	1	0.166
Woodland cover (%)		−0.30	(−0.63 to 0.028)	3.22	1	0.073
Farmland cover * Season	**Summer**	**0.28**	**(−0.21 to 0.76)**	**24.58**	**4**	**<0.001**
	Autumn	**−0.75**	**(−1.24 to −0.26)**			
	Early winter	**−0.58**	**(−1.07 to −0.096)**			
	Late winter	**−0.78**	**(−1.27 to −0.29)**			
	Spring	**−0.21**	**(−0.70 to 0.28)**			
$\sigma_{\text{transect}} = 0.59$						
$\sigma_{\text{cluster}} = 0.52$						

Note: An inverse hyperbolic sine transformation was applied to the response variable. Overall variables and interaction significance were obtained by Wald χ^2 tests (R *car* package; Fox et al., 2026). Statistically significant effects are reported in bold. The standard deviation of the random intercept terms is also given (σ_{transect}, σ_{cluster}). $N = 296$.

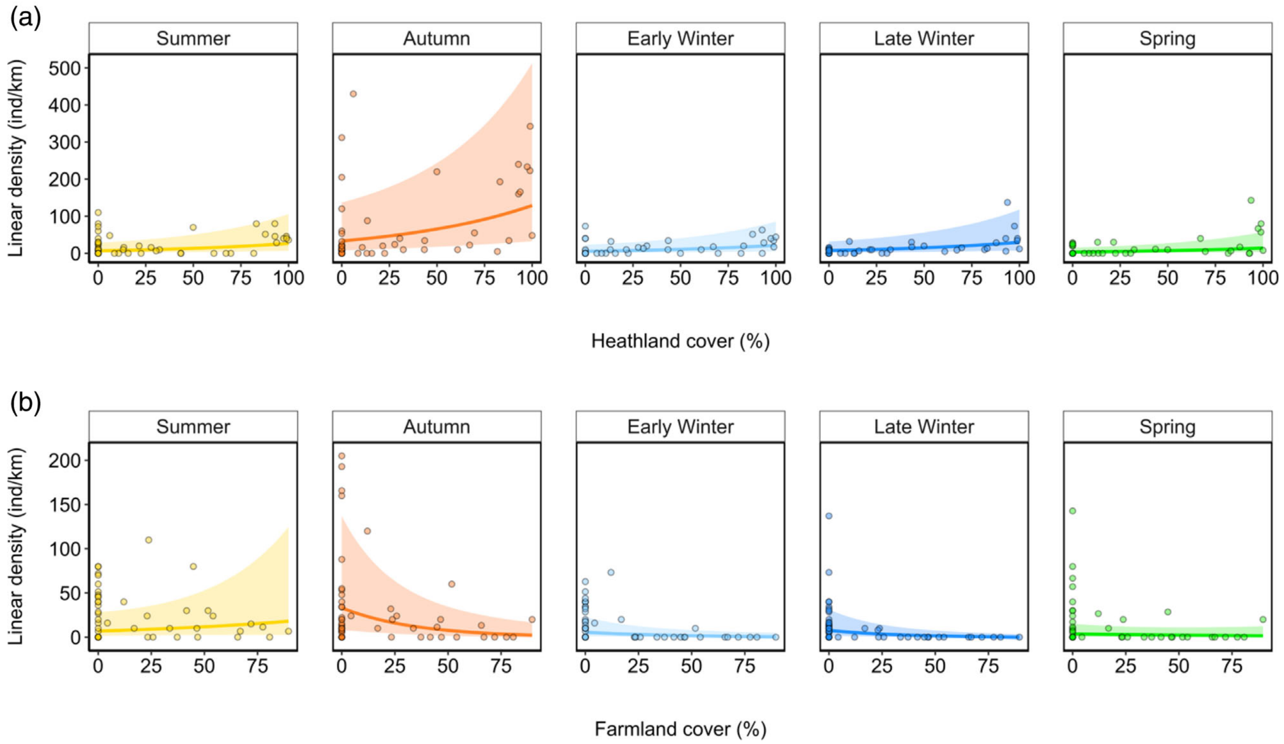

FIGURE 3 Model-predicted (with 95% confidence intervals) variation of the linear density (individuals/km) of *Sympecma paedisca* in response to the landscape cover of heathland (a), and farmland (b) (within 50 m). To improve figure readability, the word 'individuals' on the *y*-axis is abbreviated as 'ind'. The results are presented separately for each season. Predictions were derived from a Gaussian GLMM via the *visreg* R package (Breheny & Burchett, 2025). Other predictors included in the model are kept constant at their mean values. Dots represent observed values. $N = 296$.

consequences of short-range migratory movements in insects, a topic poorly explored but of potentially high interest for practical conservation. In brief, we showed how the abundance of the species outside the breeding season changed seasonally (from late summer to early spring) in the different habitats characterising the small Italian range of the species (Siddi, Battisti, et al., 2025). In addition, our fine-scale habitat selection analysis showed how the species selects habitats differently depending on the season. Taken as a whole, these results provide an indirect confirmation that the species can migrate twice a year from its aquatic breeding grounds to the overwintering heathlands and back, covering tens of kilometres and likely following the network of grassy margins found in the agricultural matrix. This seasonal-specific use of different habitats further challenges the conservation of this regionally endangered and eco-evolutionary unique damselfly.

The linear density of the species at the landscape scale increased with the increasing cover of well-conserved heathland. Even if this relation was consistent among seasons, overall higher density values were observed in autumn. Furthermore, the habitat selection analysis at the local scale showed a strong increase in heathland selection in autumn compared to summer, which was followed by a further increase in selection values in the winter and spring months. The preference of the species for heathland as an overwintering habitat has already been known (Ketelaar, Ruiter, Uilhoorn, & de Boer, 2007; Siddi, Battisti, et al., 2025); however, our results showed how, at the local scale, *S. paedisca* favoured more open stages of this vegetation, dominated by *C. vulgaris* and, above all, *M. caerulea*, which was the most used plant by wintering individuals. Degraded heathlands were used by the species according to availability at the beginning of the non-breeding season and winter, then were progressively avoided in late winter and spring, suggesting this habitat is mostly ecologically unsuitable for the species. This is likely to be due to a marked presence of small trees and shrubs (e.g., *P. tremula*, *Rubus* spp., *R. canina*), which were mostly avoided by the species. This can also suggest that the overwintering adults are subject to a higher mortality in this habitat, and that the low selection at the end of the overwintering season can depend on this, but this hypothesis needs further investigation.

A relevant result of this work is that at the end of summer, after reproduction, newly emerged imagoes of *S. paedisca* occurred in agricultural landscapes. In detail, the effect of farmland cover was positive in summer, strongly negative in autumn and winter, and substantially neutral in spring. The reason for this season-dependent relationship between the abundance of *S. paedisca* and the cover of farmland is best explained by the habitat selection of grassy margins, which were the habitat effectively used by the species in the agricultural matrix. Indeed, in late summer *S. paedisca* occurred in grassy margins bordering cultivated fields. Due to the huge expanse of this kind of habitat between the breeding and wintering ground of the species, and the relatively low number of *Sympecma* crossing it, we obtained from

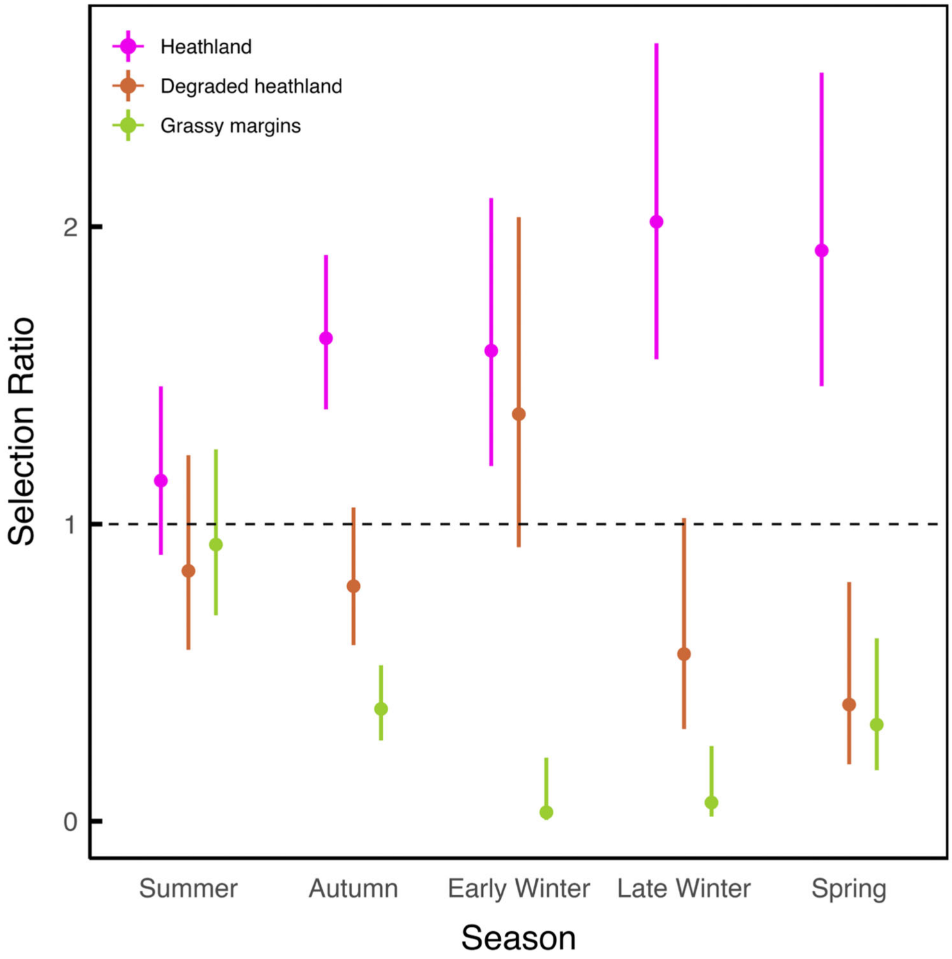

FIGURE 4 Model-predicted (with 95% confidence intervals) habitat selection ratios of *Sympecma paedisca* on the local scale (2-m) obtained from a standard resource selection function fitted through a binomial GLM. The results are presented separately for each season. Selection ratios (SRs) > 1 (with confidence intervals not encompassing one, represented by the dashed line) denote positive selection, SRs < 1 (with confidence intervals not encompassing one) denote avoidance, SRs ≈ 1 (with confidence intervals encompassing one) indicate habitat use according to availability. Number of used locations: 726; number of available locations (control points) = 3848.

the habitat selection model a use according to availability result, which is, however, much stronger than in the other seasons, from autumn onwards, when this habitat is strongly counter-selected. This is complementary to what occurred in heathlands in autumn, where an overall increase was observed, as described above. These results could suggest that the uncultivated ruderal vegetation—especially if dominated by grasses (Poaceae family)—found in the mostly unsuitable agricultural matrix was likely used by the species as preferential migration routes (i.e., corridors) from the breeding areas towards the wintering sites in heathlands and thus was not an overwintering habitat. The use of ecotones by species of the genus *Sympecma* during specific phases of their life cycle has already been demonstrated in *S. fusca* by Harabiš (2016), who suggested that for this species, ecotones are valuable sources of shelter and prey. However, the author only investigated ecotones surrounding a single breeding site and did not analyse actual habitat selection throughout the entire non-breeding season; thus, he cannot evaluate the possible use of ecotones as migratory corridors by the species.

Our predictions of different habitat use among seasons are thus supported by these results, although the predicted spring increase only partially emerges from the analyses. This could be mainly explained by the high mortality the species experiences during the winter months, which is estimated to be over 50% (Manger & Dingemanse, 2009). Return migration to breeding quarters was therefore likely carried out by a much smaller number of individuals, making it challenging to intercept these movements.

To summarise, our analysis, which is built on previous knowledge obtained in the same area on this species (Siddi, Battisti, et al., 2025), seems to (indirectly) demonstrate that, likely after emergence, the new generation left breeding sites—in our study area, mainly represented by rice fields—to reach wintering sites in subalpine heathlands, which are separated by several (even tens) of kilometres. In addition, our work suggests that the individuals surviving the winter returned to the breeding grounds at the beginning of spring. Studies conducted in the Netherlands have already reported the species' behaviour to move away from its breeding sites to reach its overwintering quarters

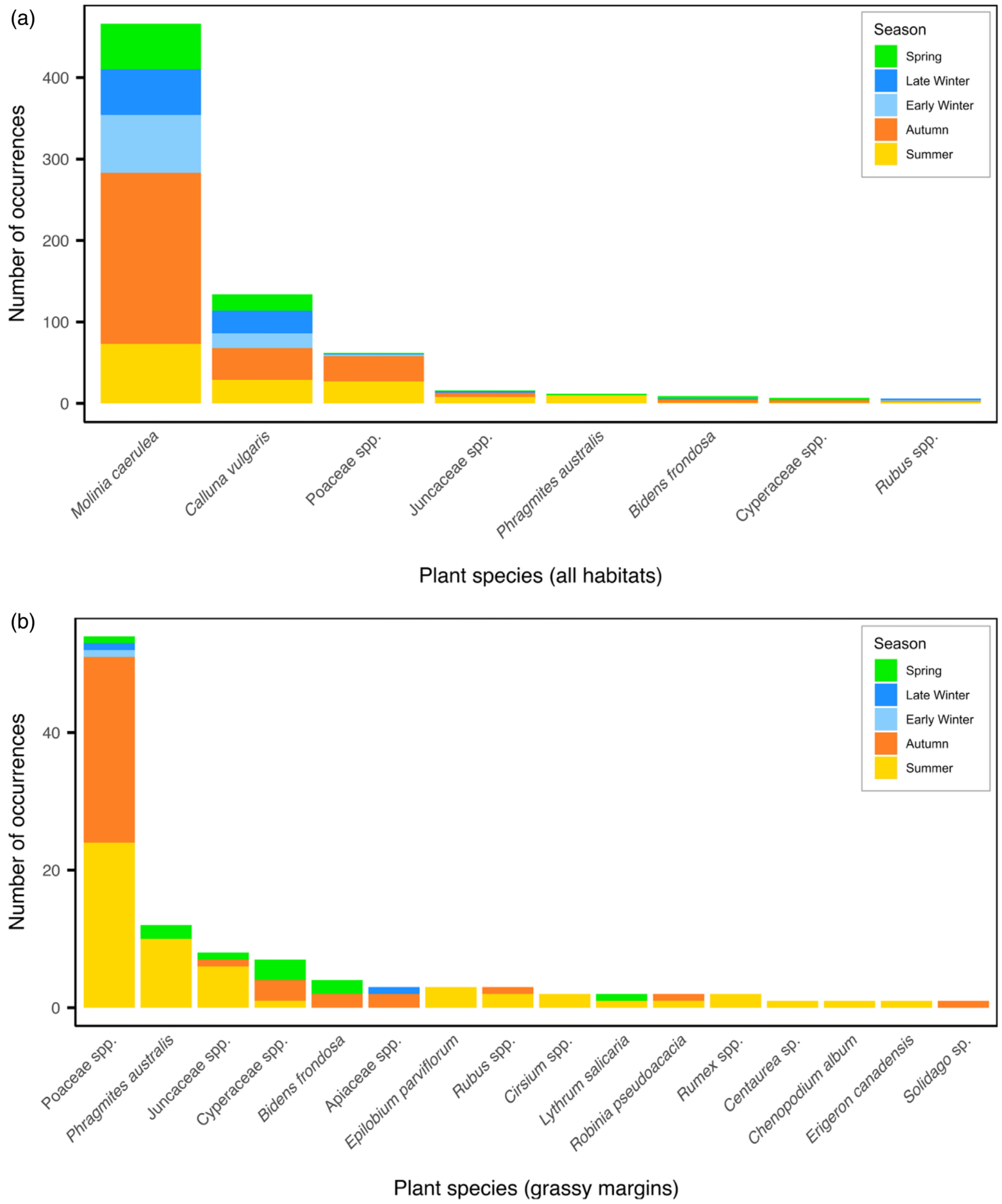

FIGURE 5 Plant species used by *Sympecma paedisca* as perching sites divided by season. (a) Overall sample. Only plants used more than five times are shown. $N = 712$. (b) Occurrence in grassy margin habitat only. $N = 106$.

(Ketelaar, Ruiter, Uilhoorn, Manger, & de Boer, 2007; Ruiter et al., 2007); however, our results suggest that these movements are both onwards and backwards and can thus be considered as migration in the strict sense, making *S. paedisca* one of the few known migratory insects in which a single generation undertakes a cyclical migration journey (Chapman et al., 2015; Dingle & Drake, 2007).

Conservation implication

European dry heaths (habitat 4030, according to the EU Directive 43/92/EEC) are severely threatened in Europe, now occupying a small portion of their original extent, with an estimated 80%–90% surface loss at the European scale since the 1950s, with the process still ongoing (European Environment Agency, 2016). The conservation status of this habitat in Italy is currently considered unfavourable or inadequate, with the main threat represented by forest encroachment, driven by the decline/cessation of traditional agro-pastoral practices such as sheep grazing and mowing (Ascoli et al., 2013; Borghesio, 2009; Olmeda et al., 2020). These threats, combined, are determining the disappearance of the main overwintering habitat of *S. paedisca*, potentially compromising the conservation of the species at the national scale. The preservation of the main overwintering habitat of this regionally threatened species will thus strictly depend on active management practices aimed at suppressing the ecological succession. Research conducted in the same study area has demonstrated that periodic fires help maintain the habitat. However, fire alone is insufficient to delay natural reforestation, making it necessary to integrate additional strategies such as grazing and mowing (Ascoli et al., 2013; Borghesio, 2009), all guided by regular assessments of forestation levels (Brüggeshemke et al., 2025). Additionally, the results of our work also imply that those kinds of interventions should be performed outside the main overwintering phase of the species, that is, at the end of the summer (August) when they are also less impactful on other ecosystem components (e.g., birds, pollinators, plants; Assandri et al., 2017; Gonthier et al., 2014; Sutter et al., 2017).

The second habitat typology, which emerged as relevant for the conservation of the species, grassy field margins within the agricultural matrix, are severely impacted by agricultural management activities, which directly affect this habitat through mowing, weeding and herbicide use (Assandri et al., 2018; De Snoo, 1999). Often neglected by the conservation literature (Magyar et al., 2025), also considering the high percentage of alien plant species with which they are composed, we showed how they can support a delicate phase of the life cycle of a species of conservation concern, that of migration. For the conservation of *S. paedisca* in Italy, preserving these habitats would be crucial, in particular during the species' migration in late summer (August) and early spring (April), as mowing the vegetation during these periods would limit the ability of individuals to reach wintering and breeding areas, further deteriorating the conservation status of the species in the country. However, late summer is often the recommended grassy margin mowing period in conservation plans to reduce the impact on farmland-dwelling biodiversity (Van Klink et al., 2019). Thus, in the areas affected by the migration of the species, it should be advisable to postpone summer grassy margin mowing to late autumn, to maintain suitable areas for the species' migration to overwintering sites.

Habitat loss negatively affects migratory species in all phases of their life cycle. During migration, it acts on corridors, preventing individual movement between breeding and wintering ranges and reducing connectivity (Runge et al., 2014). Conservation plans for migratory species cannot be limited to individual, regionally confined habitats, but must necessarily involve the network of corridors that support animal migration (Bond et al., 2017; Shuter et al., 2014). While this has been well established for vertebrates, similar evidence for invertebrates remains limited (Gao et al., 2020; Satterfield et al., 2020). Our results suggest that the conservation of the migrant damselfly species *S. paedisca* in Italy—where it is critically endangered—requires a comprehensive approach to the non-breeding ecology of the species, which must necessarily consider both the overwintering period and the migratory one. This implies that conservation measures need to be seasonally tuned and habitat-specific and that conservation efforts need to be extended outside the protected areas, and possibly cover the entire range of migratory species (Allen & Singh, 2016; Horns & Şekercioğlu, 2018).

AUTHOR CONTRIBUTIONS

Leonardo Siddi: Conceptualization; investigation; methodology; validation; formal analysis; project administration; data curation; writing – review and editing; writing – original draft; visualization; supervision. **Martina Cadin:** Investigation; writing – review and editing; formal analysis; writing – original draft. **Mattia Brambilla:** Conceptualization; methodology; supervision; writing – review and editing; writing – original draft; formal analysis. **Giacomo Assandri:** Writing – original draft; writing – review and editing; investigation; conceptualization; methodology; supervision; formal analysis; validation; visualization; project administration.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data used in this manuscript are available via the Figshare repository: https://doi.org/10.6084/M9.FIGSHARE.30245977 (Siddi, Cadin, et al., 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. Table of landscape (50-m scale) variables used in the statistical analysis. For each class, the average percentage cover with minimum and maximum values is reported. $N = 60$ transects.

Figure S1. Correlation matrix of landscape (50-m scale) transect habitat cover variables based on Pearson's correlation coefficient (r). Colours show whether the correlation is positive (red) or negative (purple). The colour intensity is proportional to the value of r. Values of the coefficient that are not significant ($p > 0.05$) are crossed out.

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