Social cues and habitat structure influence the behavior of a non-social insect

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Lay summary

In Europe, the *L. sinapis* butterfly grapples with dwindling habitats. Our research dives deeper, revealing that while they are non-social, females heavily weigh social cues when selecting a place to stay. Sensing fellow butterflies signals them to stay put, a behavior that may be vital for population survival. Moreover, habitat structure influences their egg-laying success and movement patterns, underscoring the intricate balance between social signals and environmental factors.

Title: “Social cues and habitat structure influence the behaviour of a non-social insect”

Abstract

Habitat fragmentation and loss is a known threat to biodiversity. Their combined effect leaves organisms in small isolated patches of habitat, contributing to the current biodiversity crisis. The first response of animals to environmental change is typically behavioral. Beyond the physical elements of the environment, the "social landscape" shapes the spatial distribution of the habitats available to organisms. In this article, we test the hypothesis that social cues and habitat structure alter behaviors in a non-social insect. We tested 85 wild-caught *L. sinapis* females from landscapes with various habitat structures in outdoor cages reproducing habitats with or without social cues. We demonstrate that the presence of same-sex congeners is a social signal to remain within a suitable patch of habitat. We further show that habitat structure is associated with oviposition success and investment in navigation but not with emigration. Butterflies from small, fragmented habitat patches relied more in routine movement and had lower oviposition success. Like many other insects in Europe, *L. sinapis* is in decline. Our results suggest that this decline may be exacerbated in degraded habitats due to behavioral strategies selected by both physical and social landscape elements.

Keywords: Habitat fragmentation; Insect behavior; Land use changes; Insect conservation; Habitat structure; Social cues.

Introduction

Human activities cause habitat loss which contributes to the current biodiversity crisis (IPBES 2019). Europe underwent multiple cycles of habitats alteration over millennia, with alternation of exploitation and abandonment of land surfaces (Winkler et al. 2021). Following the industrial revolution, Western Europe experienced a phenomenon known as the "forest transition", characterized by a gradual increase in forest cover. However, this transition had limited positive effects on biodiversity conservation (Rudel et al. 2005; Kaplan et al. 2012). Despite the forest transition, a substantial 55.9% of Western Europe's land territory continues to be devoted to agriculture, with an additional 7.9% covered by urban areas, resulting in detrimental impacts on organisms (Benton et al. 2021; Laurance and Engert 2022).

Habitat loss causes habitat fragmentation and their combined effects leave organisms within patches of isolated habitats surrounded by a hostile maze of intensive agriculture, transport infrastructure, and urban environment (Franklin 2000; Püttker et al. 2020). The remnant patches of habitat are characterized by longer edges, smaller sizes, and reduced connectivity (van der Ree, Rodney et al. 2011; Benton et al. 2021). These conditions toll on biodiversity due to multiple synergetic effects. The increased edge density modifies habitat conditions even within the remaining habitat (Saunders et al. 1991; Püttker et al. 2020) and reduce even more resources in the small habitat patches (Martinson and Fagan 2014; Ziv and Davidowitz 2019). Lower habitat connectivity jeopardizes the extinction-colonization dynamics essential for the maintenance of meta-populations, reduce gene flow and therefore genetic diversity (Chesson 2001; Horváth et al. 2019; Püttker et al. 2020). To comprehend the long-term survival of populations amid environmental changes, it is essential to recognize and understand the core physical elements comprising the landscape, often referred as the "physical landscape." These elements and their intricate interactions play a pivotal role in shaping the outcomes of such changes.

The initial response of animals to changing environments typically manifests through behavioral adaptations (Wong and Candolin 2015). A pertinent illustration of this phenomenon is the observed range shifts in various species over recent decades, which can be attributed to the flexible allocation of resources to behavioral traits, driven by the impacts of climate change (Travis et al. 2013). To gain further insight into the impact of environmental changes on populations and ecosystems, it is crucial to recognize that behavior plays a central role. Butterflies, for example, have demonstrated significant adaptations in their flying patterns in response to altered landscapes. In fragmented areas, where suitable habitat elements are scarce, butterflies tend to favor more direct flight paths, likely as a strategy to mitigate the elevated risk of mortality (Schtickzelle et al. 2007). These behavioral adaptations are not without consequence. In habitats modified by human activities, such as urbanization or agriculture, butterflies may incur higher energy costs due to localized behavioral adjustments. These costs have been linked to reduced reproductive success, as evidenced by a decrease in the number of eggs laid (Leimar et al. 2003; Merckx et al. 2003; Gibbs and Van Dyck 2009). Thus, understanding how behavioral responses relate to environmental changes is central to predicting their impact on both populations and ecosystems (Couzin and Heins 2023).

In addition to the physical landscape, it has been proposed that the “social landscape”, defined as the set of individuals and their social relationships in a given environment, affects the movement of animals (Armansin et al. 2020). This dimension of the landscape demonstrates how social information can impact animal behaviors and movement patterns. For example, social information has been found to influence the dispersal behaviors of *Zootoca vivipara* lizards that interact with local congeners (informants). In situations where these informants exhibit traits associated with scarce resources in the current habitat, these lizards are more likely to disperse (Cote et al. 2008; Brevet et al. 2021). Likewise, movements of eusocial insects are known to be affected by their social landscape. *Apis millifera* bees inform each other in the colony about the direction and distance of food sources through the “waggle dance” (Frisch 2013). Eusocial insects showed also social processes that decrease the perceived habitat availability of some individuals (Guerrieri et al. 2009; Sheehan and Tibbetts 2011). Ants were able to discriminate between nest-mates from non nest-mates (Guerrieri et al. 2009), and to change their foraging performances (Hwang-Finkelman et al. 2021) or levels of aggressiveness (Yagound et al. 2017) depending on which conspecifics were present. Similarly, carpenter bees demonstrate increased aggression towards unfamiliar conspecifics, actively defending their nests against potential threats (Vickruck and Richards 2017). These examples illustrate how social interactions and information-sharing processes profoundly influence the spatial distribution of habitats and resources available to dispersing individuals, going beyond the mere physical characteristics of landscapes.

The role played by social interactions (i.e., the social landscape) in shaping animal exploration of physical landscapes, and the potential colonization of suitable new habitats, has remained virtually unexplored for most non-social invertebrates, including non-social insects (Nieberding et al. 2021). One reason is that non-social species live solitary and, as such, are often assumed to take no information about their social environment. However, emerging evidence challenges this assumption, suggesting that social information is not exclusive to social species but can also be utilized by non-social ones, particularly in the context of resource availability. Dispersive individuals of *Cornu aspersum* land snails were found to follow mucus trails left by earlier dispersers more frequently than chance, potentially facilitating habitat colonization (Vong et al. 2019). Conversely, the phenomenon of "social resistance" may also influence the behavior of certain Lepidoptera species, particularly in their decision-making processes regarding oviposition sites with varying risks of intraspecific competition (Williams and Gilbert 1981; Dempster 1992). Thus, while social interactions are more commonly associated with social species, their influence extends to non-social invertebrates as well, highlighting the interconnectedness of the social landscape with the exploration of physical landscapes and habitat dynamics.

Building upon the understanding of the interplay between social and physical landscapes, it is crucial to consider that insects, which comprise 98% of non-social species (Wilson 1985; Johnson and Carey 2014), are the cornerstone of all terrestrial ecosystems accounting for more than 60% of all species (Mora et al. 2011; Stork 2018). However, these invaluable insect populations have experienced alarming declines ranging from 50% to 80% in recent decades, placing the essential ecosystem services they provide, such as pollination and bio-degradation, in jeopardy (IPBES 2016; Lister and Garcia 2018). Among the major drivers of this decline, habitat loss has been particularly influential (Sánchez-Bayo and Wyckhuys 2019; Raven and

Wagner 2021; M. S. Warren et al. 2021; Rada et al. 2019; Delpon et al. 2019) and this loss is escalating at an alarming pace. In light of these challenges, it is imperative to delve deeper into how social cues can influence the ability of non-social insects, such as butterflies, to explore and select suitable habitats, beyond the physical structure of the landscape. Butterflies are important bioindicators for habitat quality and are flagship taxa for documenting the ongoing biodiversity crisis as their population trends and spatial distributions have been monitored particularly well in Europe for decades (van Swaay et al. 2011). Butterfly population dynamics depend on the abundance of host plants, and butterfly decline in Europe is most pronounced for habitat specialists or sedentary species that depend on host plants or habitats most susceptible to regression (Habel et al. 2016; Seibold et al. 2019). Furthermore, recent research has revealed that some butterfly behaviors depend on the presence of social cues (Nieberding et al. 2021; Webster 2023; but see Aikins, Altizer, and Sasaki 2023), for example during sexual interactions (Dion et al. 2019).

In this paper, we focus on the role that social cues and habitat structure play in shaping behavioral differences in a non-social insect, *Leptidea sinapis* butterflies. Oviposition-related behaviors are essential for fitness in most non-social insects, as the survival of the next generation depends largely on the selection of oviposition sites by the mother (Thomas et al. 2011). Our experiment, conducted with wild-caught individuals tested in outdoor cages, was designed to maximize the ecological relevance of the results. The aim was to bridge the gap between laboratory studies and real-world conditions, providing valuable insights into how these factors influence behavior in a natural setting. Our results reveal that the presence of same-sex congeners serves as a social cue for female *L. sinapis* butterflies, influencing their choice to remain within a suitable patch of habitat. Additionally, we explore how various aspects of habitat structure, including fragmentation, isolation, and coverage, in the butterflies' native environments are associated with distinct behavioral patterns. These findings contribute to a comprehensive understanding of the intricate interplay between social cues and habitat features in shaping the behavior of non-social insects.

Material and methods

Leptidea sinapis (Linnaus, 1758) [Pieridae] is a Palaearctic species distributed from southern Siberia to western Europe that rely on legumes such as *Lotus corniculatus* and *L. pedunculatus* as larval food plants (Hager and Fiedler 2002). *Leptidea sinapis* overwinters as a pupa, with the adults emerging in two successive generations in April and June, then flying until August. Adults are found in a variety of habitats that contain their host plants: from open, predominantly grassy habitats to undisturbed shady woodlands (Wiklund 1977; Warren 1984). *Leptidea sinapis* is considered as a relatively weak disperser, with a maximum dispersal distance less than 1 km (Kuussaari et al. 2014), but a good habitat colonizer, thanks to its wide range of host plants (Dennis and Shreeve 1996). The morphological species *L. sinapis* has recently been shown to be a complex of three cryptic species: *L. sinapis*, *L. juvernica* and *L. reali,* that cannot be distinguished by imago morphology (Dincă et al. 2011). Our sampling locations within Belgium were strategically chosen to optimist the probability of obtaining *L. sinapis* sensu stricto specimens.

Spatial and oviposition behavior of butterflies in outdoor flight arenas

We collected female butterflies from areas in Wallonia with different landscape structure in terms of habitat cover, isolation and fragmentation to quantify their oviposition and movement behaviors. Upon field collection, we recorded the geographical coordinates of each butterfly collection point by using the Android App LocusMap. Butterflies had access to 20% sugar solution ad libitum and were kept in 25x25x25 cm transparent plastic boxes placed inside incubators under constant temperature (day/night: 22°C/16°C), relative humidity (60%) and photo-period (light/dark: 2h/22h under solar light spectrum simulating lamps; Philips HPI-T Plus 400W/645). Butterflies were maintained in these conditions for at least 24 hours before behavioral trials.

We quantified the movement and oviposition behaviors of butterflies in 4 outdoor 20x20x4 m arenas, placed in a semi-natural grassland next to the UCLouvain university experimental forest “Bois de Lauzelle” (50.68 N, 4.6 E; Figure 1A). The flight arenas were covered with a thin green insect mesh (33% radiation shield). Four host plants of two different species, *Lotus corniculatus* and *L. pedunculatus,* were planted in 12 of the 25 sectors following a chequered pattern (Figure 1C). A temperature and humidity sensor (Onset HOBO U23-001A Pro v2) equipped with a solar radiation shield (Onset RS1) was placed at the center of each flight arena and recorded data every 10 minutes.

Behavioral trials were set up by placing a cage containing the butterfly in the center the arena; the cage was connected to a pulley system which allowed it to be opened by an operator from a distance. A behavioral trial started when the butterfly left the cage: every change in section and/or behavior of the butterfly was voice-recorded by an observer placed at a distance greater than 2 m so as not to interfere with the movements of the butterflies (see Figure 1B for a conceptual scheme). Recorded behaviors were oviposition, navigation or departing flight, resting and feeding (Table 1). The maximum duration of a behavioral trial was set to 20 minutes, since *L. sinapis* has been observed to lay an egg every 13.8 minutes on average in the wild (Warren 1984); in case of oviposition, the trial would be immediately stopped.

Butterflies were divided in two separate experimental cohorts to test spatial and oviposition behaviors either with or without social cues (hereafter referred to as “non-social” and “social” trials, respectively; Figure 1C). Social trials included *L. sinapis* female dummies (double-faced high-resolution cardboard print-outs) fixed with transparent nylon attached at the top of the arenas, and left fluctuating above or in close proximity of four of the twelve sectors with host plants. Sectors with a social cue were held constant for all subsequent trials (maximum 7) of the same individual, but were changed between individuals (Figure 1B). Each voice-recorded file logged during behavioral trials was converted in a comma-separated value text file which contained a second-by-second account of location (sector) and behavior of each tested individual.

Quantification of habitat spatial structure

Landscape analysis

We characterized the landscape structure of areas where butterflies were collected by using standard land use datasets to derive indexes pinpointing habitat cover, fragmentation and isolation. First, we defined what was habitat and what was matrix for *L. sinapis* by using a detailed land use/land cover (LULC) map for Wallonia, LifeWatch Ecotope 2018 (http://maps.elie.ucl.ac.be/lifewatch/ecotopes.html) together with a citizen-science dataset of *L. sinapis* observations (source: "Observations.be, Stitching Observation International and local partners"). This latter dataset consisted in 1,805 observations from 2010 to 2021 with high coordinate accuracy (<= 100 m) and validated by an expert. Next, we extracted the land use category for the coordinates of each observation and calculated the relative proportion of observations falling in each land use category. We then compared the proportion of *L. sinapis* observations in each category with the respective proportions of the land use categories of the whole of Wallonia. We considered habitats for *L. sinapis* land cover categories that were over-represented for *L. sinapis* relatively to Wallonia: "Diversified grasslands" (44.1% for *L. sinapis*, compared to 4.3% in Wallonia) and Broad-leaved forests (35.6% *L. sinapis*, 20.5 % Wallonia), that were thus considered as constituting *L. sinapis* core functional habitat (Wiklund 1977; Dennis, Shreeve, and Van Dyck 2006). The Ecotope 2018 map was transformed in a binary map where 1 represented *L. sinapis* functional habitat (e.g., the two LULC categories described above), whereas 0 represented all the other LULC categories (hereafter "matrix"). We then built a 5 km radius circular buffer (Bergman et al. 2004) around each *L. sinapis* collection point to derive four landscape indexes (with the R package "*landscapemetrics"*; Hesselbarth et al. 2019) that quantified complementary aspects of the habitat deemed important for butterfly's life cycle:

- **Size**: the average patch area (AREA, in hectares) describes the average extent (in hectares) of connected (i.e., Queen's case) habitat in a landscape. Patch size is an important characteristic of butterfly habitat (e.g., linked to available resources) that impacts population dynamics. For example, smaller habitat patches may not provide enough resources for a population compared to bigger patches with similar characteristics (Dover and Settele 2009). In a landscape where AREA is small, butterflies may express specific behaviors such as complementation of resources in adjacent patches and, more in general, species communities show a less stable dynamics due to a higher susceptibility to stochastic events (Ouin et al. 2004; Wissel, Stephan, and Zaschke 1994).

- **Shape:** the shape area index (SAI) quantifies the proportion of core respect to edge habitat and ranges between 1 (in the case of a habitat patch shaped as a perfect circle that maximizes the proportion of core habitat) and infinite (McGarigal and Marks 1995). Core habitat provides key resources (i.e., host plants, overwintering sites for juveniles and low disturbance) for the persistence of butterfly populations (Clausen et al. 2001).
- **Isolation**: the Euclidean nearest neighbor (ENN, in meters) quantifies the average connectedness between habitat patches and thus their potential availability to dispersive butterflies. An increased isolation of habitat patches is consequence of habitat loss; there are indications that isolation may contribute to a higher extinction rates in butterfly populations due to inbreeding depression or lower resilience to catastrophic events (Nieminen et al. 2001; Cassel-Lundhagen and Sjögren-Gulve 2007).

- **Fragmentation**: the “clumpiness” index (CLUMPY) measures how interspersed habitat is, by comparing the observed proportion of like cell adjacencies with the proportion expected under a spatially random distribution (Neel et al. 2004). CLUMPY is largely independent from habitat abundance and ranges theoretically between 1 (maximum aggregation) to -1 (maximum fragmentation; Wang, Blanchet, and Koper 2014). Habitat fragmentation separates resources in spaces and suppresses gene flow with devastating consequences on species extinction risk (Ramírez-Delgado et al. 2022).

Host plant survey

We estimated the abundance of *L. sinapis* host plants (e.g., *Lotus corniculatus*, *L. penduncculatus* and *Vicia cracca*) in the butterfly collection areas using constrained random sampling and a standard plant survey protocol. After the butterfly collection season, we grouped the butterfly collection locations that were less than 10 km apart in “collection macro-areas” (Figure 1A), to account for the potential genetic heterogeneity of butterfly populations between collection sites at increasing distance. Each macro-area was further expanded by using a 1 km buffer to avoid unwanted edge effects (i.e., low probability of sampling plants at the edge of the macro-areas), and used to draw 500 random points that were further constrained inside *L. sinapis* habitat patches (e.g., category 1 in the binary map described above). Afterwards, we selected at random from each area 15 points closer than 2 km from any butterfly collection point and with a minimum pairwise separation of 200 m. For practical reason, the geographical coordinates of at least 5 of such points were used as central coordinates to build 20x20 m vegetation plot surveys; inside each plot, we recorded the total number of host plant stems (limiting the count to a maximum of 100 stems per species and per plot due to time constraints). Generalized Linear Mixed Models (GLMMs) were used to test whether the landscape indexes (obtained as described in the previous section) were associated with abundance of host plants.

Statistical analyses

First, we employed a Markov Chain (MC) approach to contrast the rate of behavioral transitions between social and non-social trials while accounting for temperature variability (R package *msm*; Jackson 2011). We initially quantified the transition rates between “idling” and “movement” behaviors, the former combining resting and feeding behaviors, whereas the latter navigation, departure, walking and pre-oviposition behaviors (Table 1). Afterwards, we quantified the transitions between “departing”, “navigation” and “idling” in social and non-social trials. For all MC analysis, we concatenated the sequence of trials of each individual in the original dataset to obtain a continuous time series of behaviors per individual. Thus, each individual was considered as an independent statistical unit in the Markov Chains. The probability of pairwise transition between all considered behaviors were *a priori* equal (with the exceptions detailed in SM.02).

Second, we tested how the structure of the landscape in the areas of origin of the butterflies was associated to behaviors during trials. We filtered and aggregated the original dataset to derive response variables that summarized the following behaviors per trial: 1) the binary outcome of oviposition success, 2) the time in seconds elapsed between the start of the trial and oviposition (oviposition readiness), 3) the time spent in departing and navigation flight and 4) the time spent idling (Table 1). Generalized linear mixed models (GLMMs) with error family matching the corresponding type of response variables (see Table 1) were employed to analyze the variation in such behaviors associated with the four landscape indexes in areas of origin as well as temperature, humidity and the presence of social cues during trials. The identity of butterflies was included as models random factor. The full model for each response variable was "dredged" to select the best reduced model by using the *MuMIn* R package and AICc (Bartoń 2023).

Results

We collected 126 female *L. sinapis* from 9 macro-areas covering all of Wallonia except for the Northwest, where we were not able to locate *L. sinapis* (Figure 1A). Our samples were representative of the whole range of landscapes with habitat characteristics still suitable for this species in Wallonia (SM.03). The selected landscape indexes represented complementary information about *L. sinapis* habitat in the study region, since pairwise comparisons reported low correlations among them (SM.04). Moreover, landscape indexes reported a strong historical stability, with only small changes in few collection sites in the 1990-2000 time period (SM.05).

We found *L. sinapis* host plants in 17 over 95 plant surveys and their abundance (average 40.35; range 4 and 100 plants per survey) was negatively associated with AREA (GLMM NBinomial $\beta=-0.014$, p-value<0.001), ENN (GLMM NB; $\beta=-0.04$, p-value<0.01) and SAI

(GLMM NB; β=-8.65; p-value<0.001) landscape indexes. In contrast, HP abundance did not show any significant association with CLUMPY (SM.05).

We were able to test 85 (Non-social=41, Social=44) out of the 126 collected *L. sinapis* in 254 (Non-social=115, Social=139) behavioral trials, for a total of 74 hours and 50 minutes of behavioral data recorded between the 2nd of May and the 9th of August 2022. Overall, butterflies spent 84.2% of the total trial duration idling, 9.0% departing and 6.8% navigating. Oviposition was recorded in 36 trials (14.8% of total number of trials) by 27 different individuals (31.8% of all tested individuals). Temperature and relative humidity varied between 10.2-35.0 °C (average 21.6 °C) and 27.7-100% (average 62.9%), respectively, during trials.

Dummies of female congeners adjacent to host plants reduce emigration from habitat patch

The Markov chain analysis showed that butterflies were less likely to transition from idling to movement in the presence of congener female dummies adjacent to host plants than when tested alone (non-social trials; Figure 2A). The probability to move in social trials was 43% (hazard ratio (HR): 0.57 [95% CI 0.29-0.88]) lower than in trials without social cues. Temperature had a positive effect on the probability to move that increased by 2.7% (HR: 1.027 [1.013-1.042]) with every 1°C increase in temperature (Figure 2C).

In a second step, we repeated the MC analysis discriminating between departing and navigation flights. We found that butterflies had a 69% lower probability (HR: 0.31 [0.15-0.64]) to transition from idling to departing flight in social than in non-social trials (Figure

2B). By contrast, we did not find a statistically significant difference for transitions to navigation flight (HR: 0.75 [0.31-1.77]; not shown in the figure). In addition, the transition probability from idling to departing flight in all trials increased with temperature (HR: 1.04 [1.02-1.06]; Figure 2D), which likewise reduced the transition probability from navigating to idling (HR: 0.93 [0.95-0.97]).

Habitat fragmentation and size affect oviposition and movements

Temperature explained most of the variation in *L. sinapis* behaviors, and overall intensified the butterfly movements (Table 2). The time spent departing increased by 6.2%, whereas time spent idling decreased by 2.0% for each 1°C increase in temperature. Furthermore, some behaviors were associated with the spatial structure of the butterflies' habitat of origin. The time spent navigating decreased with average size (AREA) and aggregation (CLUMPY) of patches in the habitat of origin. The latter pattern was reversed at the higher temperatures (Figure 3A). By contrast, time spent departing and idling did not vary with the structure of the landscape of origin. Interestingly, the presence of social cues negatively affected the time spent departing, which decreased by 30% in social versus non-social trials, consistent with the observed reduction in transitions from idling to departing movements shown by the MC analysis.

We then modeled the probability to oviposit and the time elapsed until oviposition (i.e., oviposition readiness), and found that oviposition probability increased by 2.5% on average for each 1°C increase in temperature, which brought about a maximum 26.3% increase between trials carried out at the lowest (16 °C) and highest (34 °C) temperatures. Importantly, temperatures also affected oviposition probability in interaction with average distance between habitat patches (ENN). At lower temperatures (<21 °C), oviposition probability remained low despite variations in ENN in butterflies' habitat of origin, whereas it increased with ENN at higher temperatures (>21 °C; red line in Figure 3B). In addition, the time elapsed until oviposition decreased by 5.7% with each unit increase (e., 1 hectare) in AREA.

Discussion

The interplay between the physical and social aspects of landscapes, alongside their spatial configuration, imposes constraints on animal movements and shapes their behaviors. However, despite the profound impact of landscape alterations on animal behavior or population dynamics, empirical evidence on these connections, especially in ecologically relevant contexts, is scarce. This scarcity is even more pronounced for non-social insects. To bridge this knowledge gap, we conducted a manipulation study in semi-field conditions using wild-caught butterflies. Our approach integrated spatial analysis and host plant surveys, revealing intricate relationships between landscape elements and non-social insect behavior.

In our experiments, we observed a consistent association between temperature and increased likelihood of movement and oviposition in *L. sinapis*. Given that butterflies are ectothermic insects, their behavior is notably influenced by ambient temperature. They tend to capitalize on favorable weather conditions for activities such as feeding, egg-laying, or dispersal (Gossard and Jones 1977). In addition to the expected positive role of temperature, we found more interesting associations Beyond the temperature effect, we made interesting findings regarding the connection between habitat of origin and behaviors. Specifically, landscapes characterized by smaller, more fragmented, less clumped, and less isolated habitat patches were associated with extended periods of navigation flight and reduced readiness and success in oviposition. *Leptidea sinapis* are weak dispersers (Dennis and Shreeve 1996) that, as such, pay significant energetic cost to cross an unsuitable landscape matrix and thus to access fragmented habitat patches. Our findings may be attributed to the selection for increased local explorative behaviors in butterfly populations living in more fragmented and smaller habitats, as suggested in previous studies (Vandyck and Baguette 2005; Braem et al. 2021). Our host plant surveys reported that these smaller and isolated patches of habitat harbored a lower abundance of host plants. Locating resources scattered in space requires higher investment in navigation flight which could reduce investment in egg production and reduce oviposition success. An increase in the time invested in routine movement (e.g., opposed to dispersal), for example to search for suitable oviposition sites, was linked to reductions in the number of eggs produced in *Pararge aegeria* butterflies (Gibbs and Van Dyck 2009). Considering that *Leptidea sinapis* is an egg-limited insect with a average lifetime fecundity of just 30-40 eggs (Hager and Fiedler 2002), any negative impact on egg development would severely reduce its success in oviposition. Consequently, the lower success and readiness of oviposition observed in our study could be due to reduced egg availability in butterflies from more fragmented and smaller habitat patches (see Gibbs and Van Dyck 2009).

In addition to our findings, there is other evidence that routine movements (e.g., navigation flight) are affected by landscape features in animals, however, that dispersal is also influenced remains an assumption (Vandyck and Baguette 2005). Nor do our results support this assumption, since *L. sinapis* showed no significant association between time spent in departing flight and habitat of origin. This finding may support the hypothesis that selection on explorative movements can be decoupled from selection on dispersal movements (Vandyck and Baguette 2005). Indeed, there can be significant variation among individuals with respect to dispersal that is not necessarily reflected in their routine, explorative movements (Bowler and Benton 2005). An alternative explanation for the lack of support for the connection between habitat and dispersal in our study may be related to the experimental setups which allowed us to detect only the first phase of dispersal, i.e. moving away from the habitat boundary. Dispersal is in fact a much more complex process involving transience or traversing through a landscape (e.g., movements in non-habitat, resource-poor matrix) and settlement (immigration or colonization), after departure from current habitat (Ims and Yoccoz 1997; Clobert et al. 2004). The partial detection of dispersal movements in our experiments may therefore underpin the lack of association between this type of movements and habitat of origin.

Besides the physical elements of the landscape, we found that the presence of dummy adult female conspecifics in the experimental arenas decreased the overall flight probability of *L. sinapis*. This decrease was underpinned by a lower probability of transitioning from idling to departing flight in the presence of social cues (e.g., from the Markov chains) and further confirmed by their negative association with time spent departing (e.g., GLMM). Overall, these findings suggest that *L. sinapis* is able of perceiving and reacting to visual social cues that may contribute to the likelihood of settling in a specific patch. The presence of conspecifics is in fact considered a widespread cue among taxa to evaluate habitat quality (e.g., Danchin et al 2004) and over 80% of insect studies on this topic have found that social cues have an attractive effect (Buxton et al. 2020). However, to the best of our knowledge, this is the first time that same-sex congener social cues are connected to such a specific attractive role in Lepidoptera. Social information is used by some insects also to select oviposition sites (Nieberding et al. 2021) and an increase in oviposition success in the presence of social cues, such as conspecific eggs or juveniles, is documented in several species such as the vinegar fly *Drosophila suzukii* (Elsensohn et al. 2021), the mosquito *Aedes aegypti* (Wong et al. 2011), the butterfly *Pieris rapae* (Raitanen et al. 2014) or the diamondback moth *Plutella xylostella* (Shiojiri and Takabayashi 2003). Despite this evidence, we did not observe a significant effect of conspecific social cues on *L. sinapis* oviposition success or readiness. Our findings suggest that *L. sinapis* females utilize conspecific social cues primarily to assess general habitat suitability but rely more on individual, private information when making specific oviposition-related decisions, such as host-plant selection. This aligns with a recent study on Monarch butterflies, which demonstrated that they assess host plant quality subjectively to determine whether or not to lay eggs on them, effectively disregarding the presence of social cues, such as the presence of existing eggs, in their oviposition decisions (Aikins et al. 2023). Conspecific attraction related to oviposition can lead to major costs, such as increased risk for infectious disease and intraspecific competition for larval food sources (Buxton 2020). For example, female *Anthocharis cardamines* butterflies deploy oviposition-deterrant pheromones upon oviposition to “protect” the seed-bearing stems of their host plants from other egg-laying congener females (Dempster 1992). Similarly, *Heliconius* butterflies use visual social cues to avoid ovipositing on plants already with eggs. Their host plants are in fact capable of developing leaves with egg-mimicking structure, which have been shown to decrease egg laying (Gilbert 1975 Dec 31; Williams and Gilbert 1981). *Pieris brassicae* butterflies are able to assess the egg load of host plants and prefer to lay eggs on unused leaves, even of a less suitable host plant, to avoid overloaded leaves (Rothschild and Schoonhoven 1977). The potential fitness costs associated with social cues playing an exclusively attractive role in butterfly oviposition decisions may shed light on the prevalence of the single-egg oviposition strategy, which is observed in 93% of butterfly species worldwide (Stamp 1980) underscoring its significance in the evolutionary ecology of butterflies.

Conclusion

In this study, we show that the presence of congeners in the same habitat patch is an attractive social cue for *L. sinapis* female butterflies. While this role of social cues is well established for social insects, to our knowledge this is the first time it has been reported for non-social insects. We further show that butterflies from small habitat fragments invest more resources in routine movements but less in oviposition. This balance of investments could be due to reduced egg production which selects for behaviors optimized to locate the best oviposition sites.

Physical and social landscapes thus emerge as complementary in determining the movements of individuals even in a non-social species. We are aware that the social landscape has historically been neglected in studies of non-social insects and the time has come to complement our knowledge by including it in future experiments. This step will help us also unravel the interactions with other abiotic factors, such as habitat structure and its alteration due to global changes.

Like many other insects in Europe, *L. sinapis* is in decline, and our results suggest that this decline may be exacerbated in degraded habitats due to behavioral strategies influenced by both the physical and social elements of the landscape. Recognizing the intricate interplay between these landscape factors provides valuable insights for the conservation of not only *L. sinapis* but also numerous other non-social insects facing similar challenges. By integrating all landscape elements, we can gain a more comprehensive understanding of population dynamics, which is crucial for developing effective conservation strategies aimed at preserving biodiversity and ecosystem health in a rapidly changing world.

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Figure captions

Figure 1: Overview of the study that shows butterfly collection sites, experimental arenas, and the protocol followed during behavioral trials. **A)** A map of the study area (Wallonia). Each triangle represents a collection point of *L. sinapis* while triangles of the same color are part of the same collection macro-area (9 in total). The white circles are additional sites visited during butterfly collection but where we were unable to locate female *L. sinapis*. The two small square inset at the top and bottom of the map show exemplary landscapes with habitat structures (habitat in green, matrix in white) corresponding to the minimum (top right) and maximum (bottom left) values of the 4 habitat indices considered in this work, clockwise: AREA, SAI, CLUMPY and ENN. The larger inset on the left shows a satellite imagery of the meadow where the four 20x20 m experimental arenas, divided into 25, 4x4 meters, sectors (in green), were located. Background map data from OpenStreetMap Standard. **B)** Flowchart outlining the experimental protocol for behavioral trials. **C)** Representation of the experimental arena divided into 25 sectors, during non-social (left) and social trials (right). In these depictions, the butterfly in the center represents the individual being tested, while the other four butterflies represent the dummies of *L. sinapis* placed next to the host plants (*Lotus corniculatus* and *L. pedunculatus*) during the social trials (butterfly and plant photos by Didier Descouens - Own work, CC BY-SA 4.0).

Figure 2: Markov chain hazard plot displaying the estimated average effects of social cues (left, in green) and temperature (right, in orange) on behavioral transitions. **A** and **C**

correspond to the simplified two-step model, while **B** and **D** are from the full model considering departing, navigation, and idling behaviors.

Figure 3: Model interaction effect plots showing how: **A)** the average distance to the nearest habitat patch (in meters) in the area of origin had a positive effect on the probability that *L. sinapis* oviposited during a behavioral trial at higher temperatures (low= blue, medium=yellow, high=red lines), but a negative effect at medium and lower temperatures; **B**) the average size of habitat patches in the habitat of origin had a positive effect on the time (in seconds) that *L. sinapis* spent navigating the habitat during behavioral trials at higher temperatures, whereas it had a negative effect at lower temperatures.

Tables

Table 1*: Description of the behavioral categories recorded during trials, of the behavioral datasets derived for data analysis and the specification of the models used to analyze each of the behavioral category.*

Behavior		**Description**	**Derived dataset**	**Model specification**
Oviposition		Punctual event recorded when a butterfly was observed depositing an egg on the host plant.	**Success**: Binary outcome for oviposition success or failure.	Binomial GLM.
			Readiness: Time (seconds) elapsed before oviposition.	Negative binomial GLM with offset.
Movement	***Navigation***	Active exploration of the environment inside the arena. This category included flight, walking and pre-oviposition behaviors (e.g., leaf inspection and drumming, which represented a very small portion of the total displayed behaviors).	Total time (seconds) spent in “navigation behaviors”	Gaussian GLMM; butterfly ID and AREA as random effects.
	Departing	All types of flight employed when	Total time	Negative binomial

	attempting to leave the arena (i.e., emigration), such as flying straight or bumping into the covering net.	(seconds) spent in “dispersal-type flight”.	GLMM with butterfly ID and AREA as random effects.
Idling	All periods that did not result in a spatial displacement of the butterflies, i.e. resting or feeding behaviors.	Total time (seconds) spent idling.	Negative binomial GLMM with offset; butterfly ID and AREA as random effects.

***Table 2**: Summary table which reports coefficients, p-values and R^2 of models addressing the association between five butterfly behavioral categories (rows) with the spatial structure of their habitat of origin, temperature and presence of social cues as well as their interactions (columns).*

Covariate ***Response***	*Intercept*	*Temperature*	*CLUMPY*	*ENN*	*AREA*	*Temp: ENN*	*Temp: CLUMPY*	*Social cues*	*R^2*
Oviposition success	-2.14 ***	0.44 *		-0.35		0.70 *			0.21^1
Oviposition readiness	-1.59 ***				-0.31 $^{\cdot}$				0.13^2
Time navigating	3.52 ***	0.05	-0.24 *		-0.17 $^{\cdot}$		0.23 ***		0.36^2
Time departing	4.22 ***	0.25 ***						-0.36 *	0.37^2
Time idling	-1.12 ***	-0.08 $^{\cdot}$							0.01^2

$^1R^2$=*Theoretical;* $^2R^2$=*log-normal;* *** *p<0.001;* ** *p<0.01;* * *<p<0.05;* $^{\cdot}$ *p<0.1*

Figure 1

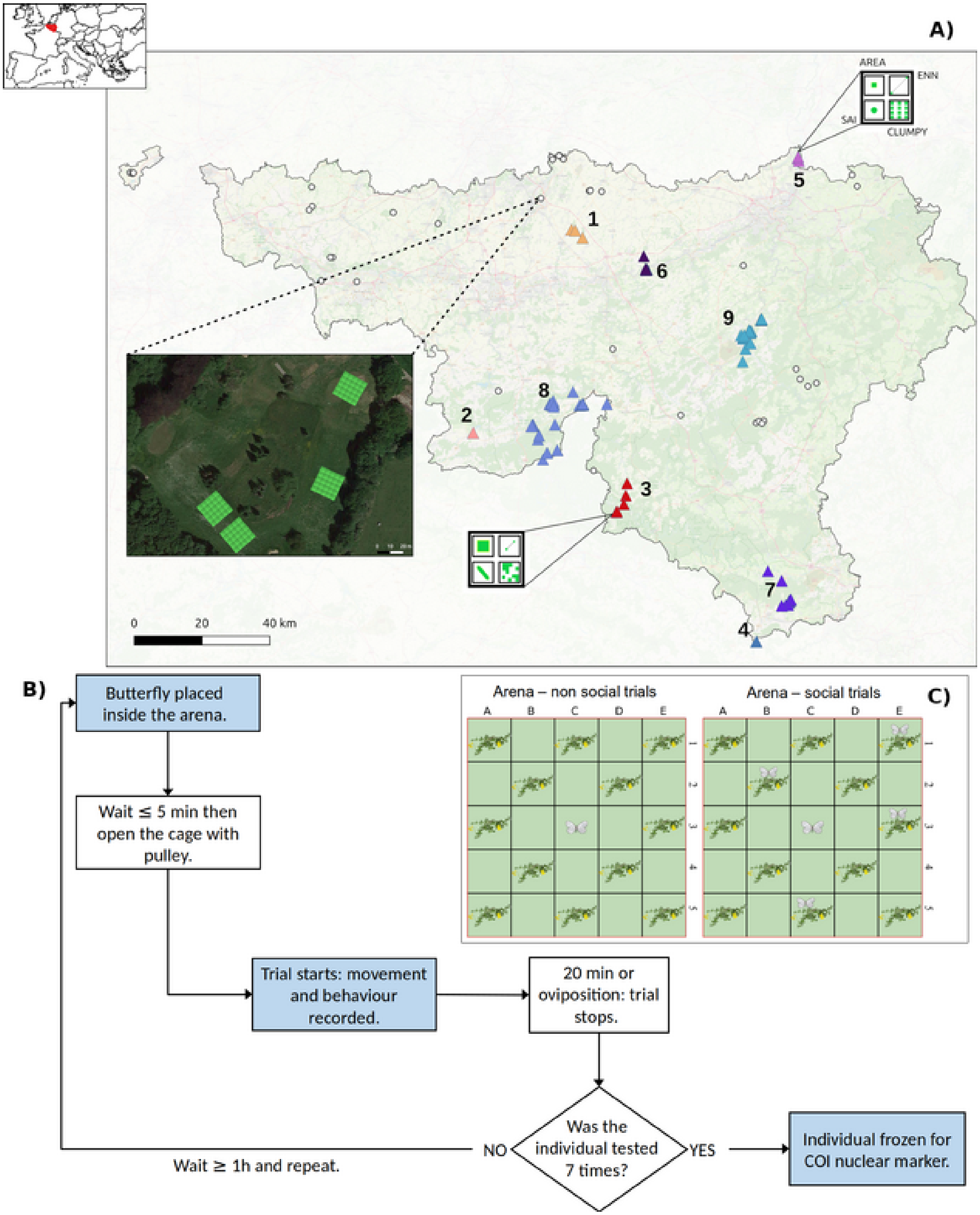
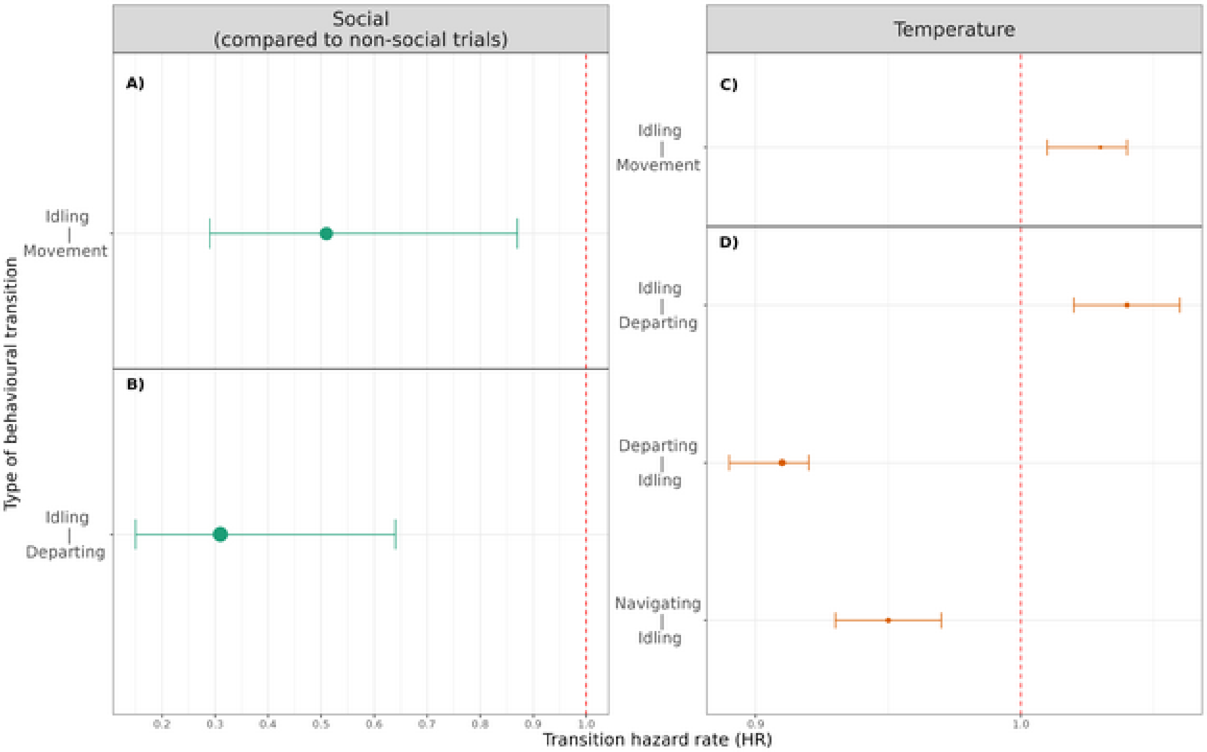
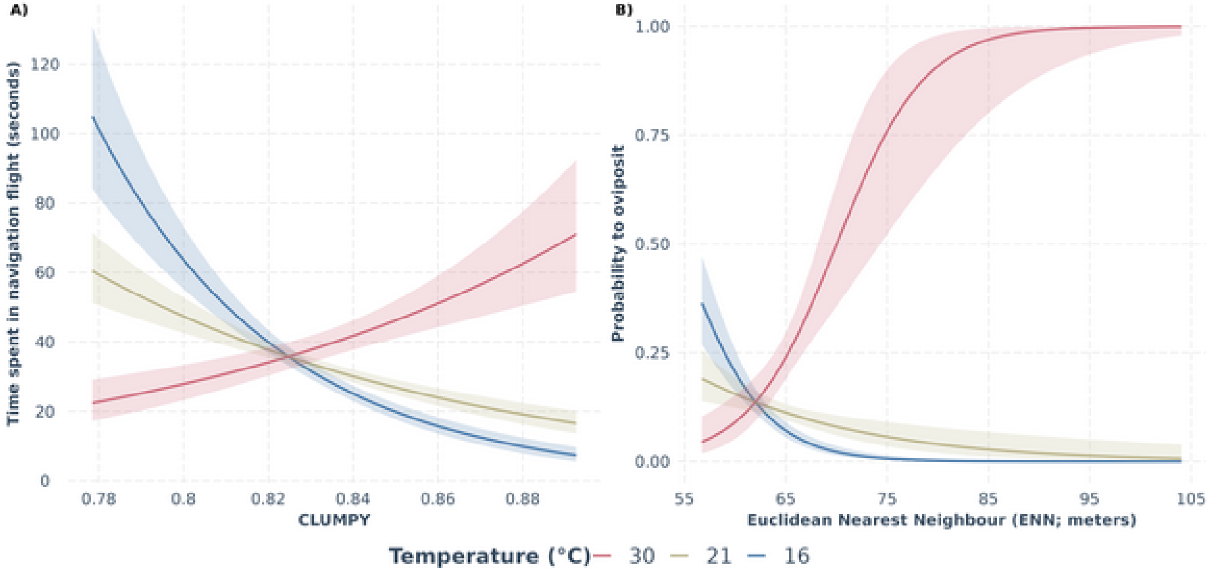

A)
AREA
ENN
SAI
CLUMPY
1
2
3
4
5
6
7
8
9
0
20
40 km
B)
Butterfly placed inside the arena.
Wait ≤ 5 min then open the cage with pulley.
Trial starts: movement and behaviour recorded.
20 min or oviposition: trial stops.
Was the individual tested 7 times?
NO
Wait ≥ 1h and repeat.
YES
Individual frozen for COI nuclear marker.
C)
Arena – non social trials
Arena – social trials
A
B
C
D
E
1
2
3
4
5

Figure 2


Social
(compared to non-social trials)
Temperature
A)
B)
C)
D)
Idling | Movement
Idling | Departing
Idling | Movement
Idling | Departing
Departing | Idling
Navigating | Idling
Type of behavioural transition
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
0.9
1.0
Transition hazard rate (HR)

474 **Figure 3**



A)
Time spent in navigation flight (seconds)
0
20
40
60
80
100
120
0.78
0.8
0.82
0.84
0.86
0.88
CLUMPY
B)
Probability to oviposit
0.00
0.25
0.50
0.75
1.00
55
65
75
85
95
105
Euclidean Nearest Neighbour (ENN; meters)
Temperature (°C)
30
21
16

Funding

This work was supported by UCLouvain, the Fédération Wallonie-Bruxelles, and by the Fonds National de Recherche Scientifique (F.R.S.-FNRS). M.M. was supported by the F.R.S.-FNRS grant number T.0169.21 of C.N.; S.M. was supported by the “Action de Recherche concertée” grant number 17/22-086 of C.N.

Acknowledgment

We are grateful to the ADPI and GPEX services at UCLouvain, particularly the dedicated teams led by Arnauld Morize and Thibaut Thyrion, for their technical assistance in establishing the flight arenas. Special thanks are owed to Mathias Blondet, Martin Coulon, Baptise Gangneux and Dr. Raluca Voda for their contributions, either in the initial setup of the experiments or in the data collection process. Additionally, we thank Dr. Caroline Nieberding, Dr. Bertanne Visser and Dr. Mathilde Scheifler for providing useful comments on the manuscript.

Data Availability Statement

All data essential for replicating the results presented in this manuscript will be deposited in the DRYAD repository upon publication. For any further data or related inquiries, please contact the corresponding author.