

Anthropogenic disturbance promotes the abundance of a newly introduced butterfly, the European common blue (*Polyommatus icarus*; Lepidoptera: Lycaenidae), in Canada

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Abstract: The frequency of introductions of non-native species is increasing worldwide, but only a few introduced species undergo rapid population growth and range expansion, and even fewer become invasive, leading to negative impacts on native communities. Predicting which non-native species are likely to become widespread and abundant can be difficult when there is a lack of species' information in the early stages of colonization. Here, we investigate the ecology of a newly introduced butterfly in Canada, the European common blue (*Polyommatus icarus* (Rottemberg, 1775)), by modelling its local- and landscape-scale habitat suitability in Montréal, Quebec, Canada, and the surrounding region, and by assessing its dispersal ability using a mark–release–recapture study. At a local scale, we found that *P. icarus* abundance was highest at sites with moderate levels of habitat disturbance (e.g., mowed every 2–3 years), the presence of their preferred larval host plant and low proportional cover of grasses. At a landscape scale, *P. icarus* abundance increased with an increasing proportion of urban area and decreasing proportion of forests. We also found that *P. icarus* is a low to moderate disperser relative to other butterflies. Our results suggest that *P. icarus* may become widespread in disturbed and urban areas across Canada, but that further investigation into additional potential range-constraining factors (e.g., microclimate), especially larval preferences, and modelling of the trajectory of *P. icarus* range expansion is needed.

Key words: non-native, anthropogenic disturbance, habitat suitability, dispersal, scale of effect, land cover, European common blue, *Polyommatus icarus*.

Résumé : Si la fréquence des introductions d'espèces non indigènes augmente partout sur terre, seules quelques espèces introduites connaissent une forte croissance de leur population et une forte expansion de leur aire de répartition et elles sont encore moins nombreuses à devenir envahissantes et ainsi entraîner des effets négatifs sur les communautés indigènes. Il peut être difficile de prédire quelles espèces non indigènes sont susceptibles de devenir répandues et abondantes en l'absence d'information sur les premières étapes de la colonisation. Nous examinons l'écologie d'un papillon nouvellement introduit au Canada, l'argus bleu (*Polyommatus icarus* (Rottemberg, 1775)), en modélisant la qualité des habitats aux échelles locale et du paysage à Montréal (Québec, Canada) et dans la région environnante et en évaluant sa capacité de dispersion par l'entremise d'une étude de marquage–lâcher–recapture. Nous constatons que, à l'échelle locale, l'abondance d'argus bleu est la plus grande dans des sites où la perturbation de l'habitat est modérée (p. ex., sites fauchés deux ou trois fois par année), où la plante hôte de prédilection de ses larves est présente et où le couvert de graminées est proportionnellement faible. À l'échelle du paysage, l'abondance d'argus bleus est directement proportionnelle à la superficie urbanisée et inversement proportionnelle à la couverture boisée. Nous constatons également que l'argus bleu présente une capacité de dispersion faible à moyenne comparativement à d'autres papillons. Nos résultats donnent à penser que l'argus bleu pourrait devenir répandu en zones perturbées et urbaines à la grandeur du Canada, mais qu'il est nécessaire d'effectuer des études plus poussées sur d'autres facteurs qui pourraient en limiter la répartition (p. ex., le microclimat), en particulier les préférences des larves, et de modéliser la trajectoire d'expansion de l'aire de répartition de l'espèce. [Traduit par la Rédaction]

Mots-clés : non indigène, perturbation anthropique, qualité de l'habitat, dispersion, échelle de l'effet, couverture terrestre, argus bleu, *Polyommatus icarus*.

Introduction

Since the late 20th century, growing global economies and trade networks combined with advancements in transport efficiency have led to unprecedented increases in the frequency of non-native species introductions worldwide (Meyerson and Mooney 2007; Hulme 2009). Upon introduction, most non-native species fail to establish or remain at sufficiently low population sizes such that their impacts are minimal (Williamson and Fitter 1996; Blackburn

et al. 2011). However, some non-native species undergo rapid population growth and range expansion (Sakai et al. 2001) that can have negative impacts on native biota (Wilcove et al. 1998; Simberloff 2000; Bradley et al. 2019) and ecosystem function (Vitousek et al. 1997; Guy-Haim et al. 2018). Consequently, one of the primary aims of invasion biology is to predict which non-native species are likely to become widespread, abundant, and potentially invasive in the future.

Received 9 January 2021. Accepted 10 April 2021.

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Knowledge of the geographical and ecological factors that constrain the distribution of non-native species is essential for predicting their range expansion. Anthropogenic disturbance has long been associated with the successful establishment and spread of non-native species (Elton 1958; Hobbs and Huenneke 1992). For non-native insects, disturbance can accelerate their spread into new sites by increasing propagule pressure along transport pathways (Pyšek et al. 2010; Gippet et al. 2019); increase the diversity and abundance of non-native plants (Jauni et al. 2015) that in turn increases the efficiency of non-native herbivorous insects which forage on non-native hosts (Jactel et al. 2005); and can lead to less diverse communities of enemies and competitors that occur in more natural habitats, resulting in fewer negative biotic interactions (i.e., lower biotic resistance) (Elton 1958). For example, non-native yellow crazy ants (*Anoplolepis gracilipes* (Smith, 1857)) are more likely to occur in managed agroforests than natural rainforests because of reduced competition with native ants that are largely excluded from the more disturbed sites (Bos et al. 2008).

Anthropogenic disturbance often facilitates the establishment and spread of non-native insects, but not all introduced species respond to disturbance in the same way. While studies generally report higher non-native insect species richness and (or) abundance in disturbed habitats (Petit et al. 2008; Roques et al. 2009; Pyšek et al. 2010), the shape of the relationship is not always linear. For instance, Estay et al. (2012) found that the disturbance–richness relationship for non-native forest insects becomes saturated at intermediate levels of disturbance. A study on non-native Argentine ants (*Linepithema humile* (Mayr, 1868)) showed that their abundance peaks at intermediate levels of disturbance due to higher resource availability than can be found in more natural habitats and reduced competitive interactions with other non-native ant species that are more dominant in highly disturbed habitats (Vonshak and Gordon 2015). Therefore, specifying how disturbance impacts non-native species is important to guide management efforts (e.g., by prioritizing the right areas for control).

In addition to human disturbance, the spread of non-native species depends on the dispersal ability of the species. Dispersal limitation is considered a significant barrier to range expansions by non-native species (Renault et al. 2018), and like native species, can prevent them from occupying suitable habitat beyond the edge of their ranges (Tilman 1997; Araújo and Pearson 2005). Given the importance of dispersal to range expansion, quantifying dispersal distance for non-native insects is an important step in understanding their potential for spread. This is particularly important for newly introduced insects whose dispersal ability is likely not known.

When identifying associations between non-native species occurrence and (or) abundance and different habitat factors (i.e., habitat suitability modelling), spatial scale is an essential consideration. This is because the influence of abiotic controls (e.g., temperature) and biotic interactions (e.g., competition) on non-native species are known to vary with spatial scale (Brown et al. 2008). For both native and non-native species, the scale at which habitat factors are measured greatly influences the magnitude and direction of their effects (Levin 1992; Brennan et al. 2002; Martin and Fahrig 2012). For example, a study on native dryad butterflies (*Minois dryas* (Scopoli, 1763)) showed that the availability of nectar plants was most important for determining butterfly abundance at local scales, but plant community composition was more important at landscape scales (Kalarus and Nowicki 2017). Like native species, meaningful determination of associations of non-native species with habitat factors requires a multi-scale approach; yet most habitat studies are still conducted at a single scale (Brown et al. 2008; McGarigal et al. 2016).

Here, we investigate the ecology of a newly introduced butterfly in Canada: the European common blue (*Polyommatus icarus* (Rottemberg, 1775)). Introduced to Montréal, Quebec, Canada,

from Europe as early as 2005 (Hall 2007), initial observations of this species suggest that it can reach extremely high local densities compared with native butterflies and that it is rapidly expanding its distribution (J. Newman, unpublished data; M. Larrivé, personal communication, 2016). However, the factors that are likely to influence the range expansion of *P. icarus* in its range in North America are unknown. The recent introduction of *P. icarus* provides a rare opportunity to study a non-native insect during the early stages of its colonization (e.g., Rosati and VanLaerhoven 2007; Haavik et al. 2015), allowing us to gain further insights into the progression of an invasion.

In this study, our first objective is to identify the key habitat characteristics that best predict *P. icarus* abundance and provide other descriptors of its ecology and relative abundance in the butterfly community. To do so, we use standard butterfly survey techniques and model *P. icarus* habitat suitability at a local and a landscape scale. Specifically, we consider the role of plant community characteristics and disturbance at a local scale, and land-cover types at a landscape scale, on adult abundance. Following only a small number of studies, we use a type of scale optimization approach (i.e., testing multiple scales to determine which produces the strongest species–habitat relationship) (Martin and Fahrig 2012; McGarigal et al. 2016) that is critical for increasing the predictive power and interpretability of results (McGarigal et al. 2016). Our second objective is to determine the dispersal ability of *P. icarus* adults in its introduced range using a mark–release–recapture study.

Materials and methods

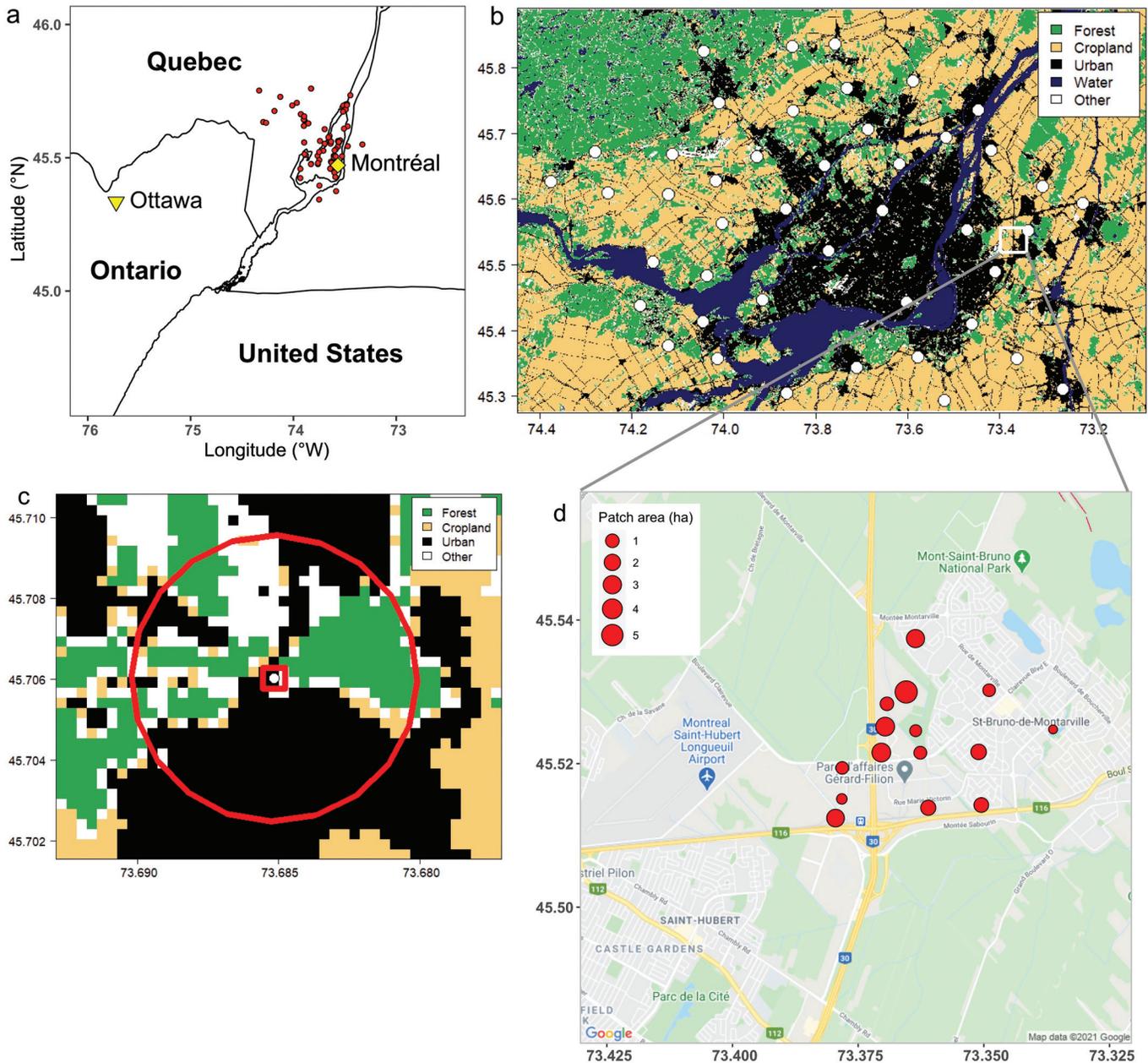
Study system

Polyommatus icarus is a small, non-migratory butterfly native to temperate Europe and Asia that occurs in discrete closed colonies (i.e., individuals rarely leave natal breeding grounds, especially females) (Thomas 1984; Emmet and Heath 1989; Thomas and Lewington 1991). In its native range, *P. icarus* is tolerant of a range in climatic conditions with a large distribution extending from northern Africa to Norway and Finland (Thomas and Lewington 1991; Tolman and Lewington 2008). In Europe, *P. icarus* is considered extremely common (i.e., widespread and abundant), occurring in a variety of habitats (e.g., pastures, dunes, heaths, grasslands, roadsides, and waste places; Emmet and Heath 1989).

Polyommatus icarus larvae can forage on several leguminous plants (Fabaceae), but they have a preference for bird's foot trefoil (*Lotus corniculatus* L.) (Thomas and Lewington 1991; Tolman and Lewington 2008). *Lotus corniculatus* was introduced to North America in the mid-1700s and is now extremely widespread and abundant, occurring in every Canadian province (Zandstra and Grant 1968). In Canada, *L. corniculatus* is considered an agricultural escapee. Originally, it was imported as a common hay crop and impurity of seed mixtures, but can now be found growing in pastures, meadows, lawns, roadsides, and waste places in every Canadian province (Turkington and Franko 1980). Adult *P. icarus* feed on nectar from a wide variety of plant species from several families (Emmet and Heath 1989), including *L. corniculatus* (Janz et al. 2005).

In Canada, *P. icarus* is in the early phases of its colonization. As of 2017, when this study began, the area inhabited by this butterfly was estimated to be 6000 km² and centralized in the largely urban and agricultural region of Montréal, Quebec (Fig. 1a). It is one of the most densely farmed and populated areas of Canada (Statistics Canada 2014). Aside from urban and agricultural areas, the region is composed of remnant patches of mixed wood forest (most forests in the region are deciduous (57%) or mixed deciduous and coniferous (40.5%)) and an extensive system of waterways including the St. Lawrence River (Wiken 1986). The range of *P. icarus* continues to expand in Montréal with more observations being added each year (e.g., 47 records added in 2019 compared with

Fig. 1. Maps of the study region. (a) Occurrence records ($n = 204$ sightings) of European common blue (*Polyommatus icarus*) butterflies, shown by red dots, in eastern Ontario and western Quebec, Canada, from eButterfly (eButterfly 2020) as of 2017 when this study began. The cities of Ottawa, Ontario (yellow triangle), and Montréal, Quebec (yellow diamond), are also shown. (b) Location of sites ($n = 44$ sites), shown by white dots, used for the local- and landscape-scale habitat suitability modelling centred in Montréal, Quebec, overlaid on a 30 m resolution 2015 land-cover map (Canada Centre for Remote Sensing 2015). (c) Close-up view of one focal site showing the two sampling areas used in our local-scale (inner red square, radius 30 m) and landscape-scale (outer red ring, radius 400 m) analyses. (d) Location of sites ($n = 15$ sites), shown by red dots, used for the mark–release–recapture study conducted in St. Bruno-de-Montarville, Quebec, and an indication of their area (size of red dot). Maps were created using R version 3.5.3 and Google Maps (Map Data ©2021). Colour version online.



only 8 records in 2011; eButterfly 2020) and to locations outside the Montréal region (e.g., records in Toronto, Ontario, added in 2019 over 400 km away from our study region in Montréal; eButterfly 2020).

Butterfly and local habitat surveys

To assess habitat suitability, we conducted field surveys of adult butterflies and their habitat at 44 sites that spanned the introduced range of *P. icarus* as of 2017 (Fig. 1b). We chose sites along a gradient of anthropogenic disturbance by visually assessing

surrounding land cover using Google maps, and local site features (e.g., evidence of human presence) upon an initial visit. This was a purely qualitative exercise to approximate differences between sites. To ensure our sampling locations were independent, we chose sites that were at least 7 km apart, a distance which we were confident far exceeded the dispersal abilities of *P. icarus* adults based on European estimates (mean distance 165 to 191 m) (Gutiérrez et al. 2001; Kuussaari et al. 2014). It also took into account the patchiness of the landscape and the total extent of the study region (sites >7 km apart would likely have exceeded

Table 1. Criteria for assigning a qualitative index of local-scale habitat disturbance to each site that combined observations about approximate time since disturbance and severity of disturbance.

	Disturbance index			
	Level 1 (low)	Level 2 (low to mid)	Level 3 (mid to high)	Level 4 (high)
Approximate time since last disturbance	>15 years	5–15 years	1–5 years	<1 year
Type and age of vegetation	Numerous large, tall trees; high vegetation height	Numerous trees with a mix of large and tall and small and short; high vegetation height	Some trees that are mostly small, short; mid-length vegetation height	Few to no trees that are mostly small, short; short vegetation height
Evidence of human traffic	No evidence	Trampled vegetation, dirt paths, remnants of buildings, or stone fencing	Dirt or gravel paths, litter, construction materials, hydro towers	Paved paths, litter, parking lots, buildings, hydro towers, benches, playgrounds
Examples	Natural meadow, forest clearing	Semi-natural meadow, abandoned farmstead, low-traffic nature trail	Abandoned commercial lot, unmowed hydro field, high-traffic nature trail	City park, roadside, residential lawn, mowed areas

the distribution of *P. icarus* based on eButterfly records as of 2017). We visited sites 3–4 times from May to August, with 39 sites surveyed in 2017 and an additional 5 sites in 2018. Beyond the surveys, we checked for the presence of *P. icarus* every 3–4 days in 2017 until 4 November.

We estimated butterfly abundance using the transect walk method, which is a standardized protocol used in many butterfly monitoring schemes around the world (Thomas 2005; Van Swaay et al. 2008). To compare the abundance of *P. icarus* to other butterfly species, we estimated the abundance of all butterfly species. Total site area varied, so we kept our survey area and search time constant. To do so, we walked a spatially fixed 300 m long route, divided into five separate transects of 60 m each that were arranged side by side and 15 m apart (i.e., approximate square 60 m × 60 m; Fig. 1d). Two observers identified and counted all butterflies that flew within 5 m in front of them or on either side of the transect (Pollard and Yates 1993). We walked transects at a consistent speed of 10 m/min. Although this method has been criticized for its poor ability to detect cryptic species (Pellet et al. 2012), low detection is unlikely to be an issue for *P. icarus* because it is a highly conspicuous butterfly, an active flyer, and has bright blue colouration. We only walked transects when conditions were suitable so that butterflies would be fully active: 10 am to 4 pm, temperatures of 13–40 °C or >17 °C when cloud cover exceeded 75%, wind below 30 km/h, and no rain.

During each site visit, we characterized habitat at a local scale (i.e., within the area surveyed for butterflies; Fig. 1d) by placing five 1 m² quadrats along the same five 60 m transects used to survey butterflies. For each visit to a site, we selected the locations of our quadrats before we arrived at the site using an algorithm that randomized the distance from the start (0 to 300 m) and which side of the transect the quadrat would be placed. Once at the site, we ensured the placements of the quadrats adequately covered the site and any larger site features present (e.g., large patch of a single plant species, rock cover).

Within each quadrat, we visually estimated the proportional cover of shrubs, forbs, grasses, bare ground, *L. corniculatus* flowers, and all flowers. We also recorded *L. corniculatus* occurrence (presence and absence) in these quadrats. If we happened to notice *L. corniculatus* on our butterfly surveys, the we included this observation as evidence of its occurrence at the site, but this only occurred 4 times over the survey period. As the aim of our study was to describe habitat suitability for *P. icarus* adults, we

chose variables most likely to be important for adults. However, some variables (e.g., *L. corniculatus* flower cover) could indicate suitable habitat for both larva and adults based on oviposition preference of females (Janz et al. 2005). We note here that forb cover included the cover of *L. corniculatus* flowers, all other flowers, and plants not flowering at the time of observation. The proportional cover of all quadrats from all seasonal replicates were averaged to produce a site-level estimate. We estimated canopy cover once for each site, during a mid-season visit, using a densiometer at five randomized locations along the 300 m butterfly transect.

At the end of the season, we assigned an index of disturbance to each site. This represented a qualitative measure of local-scale habitat disturbance (four levels) that combined observations about approximate time since disturbance and severity of disturbance. Specifically, we considered the type and age of vegetation (e.g., presence and size of trees, plant height (shorter = younger)), evidence of human traffic, and whether human-made objects were present (e.g., paths, buildings, construction materials) (Table 1).

Landscape habitat surveys

To quantify the landscape surrounding our sites, we used a 30 m resolution 2015 land-cover map (Canada Centre for Remote Sensing 2015). For the purposes of this analysis, we aggregated land-cover classes to represent seven major types: forest (three classes: needleleaf, broadleaf, and mixed), cropland, wetland, grassland, shrubland, water (i.e., lakes and rivers), and urban land (Fig. 1b). We aggregated the three classes of forest because we had no a priori reasons to expect that different forest types would impact *P. icarus* abundance differently. We calculated the proportional cover of each land-cover type within circular buffers of varying sizes surrounding our sites.

Statistical analysis: habitat suitability modelling

We divided the analysis into two sections: local scale (i.e., within site) and landscape scale (i.e., within 400 m; Fig. 1d). For both scales, we analyzed the total number of *P. icarus* observed across the season. As *P. icarus* abundance was an overdispersed count (mean:variance = 1:66), we used generalized linear models from the MASS package (Venables and Ripley 2002). We used the negative binomial probability distribution, which has been shown to be the best approach for overdispersed data (Welsh et al. 2000). We combined the 2 years of surveys, as there was no effect of year on the results (Supplementary section 1.1 and Table S1).¹ We included the number of visits to sites in all models

¹Supplementary analyses, tables, and figures are available with the article at <https://doi.org/10.1139/cjz-2021-0009>.

to account for variation in the number of times that a site was surveyed. We assessed non-linear effects by visually checking plots and comparing model fit.

We explored potential relationships among our predictor variables in several ways. For continuous variables, we explored collinearity using variance inflation factors (i.e., correlated if $VIF > 5$; Zuur et al. 2007) from the car package (Fox and Weisberg 2011). To determine overall independence for categorical variables, we used Fisher's exact tests due to our smaller sample sizes in some contingency categories (Bower 2003; McCrum-Gardner 2008) and corrected these for multiple comparisons when conducting post hoc analyses (Shan and Gerstenberger 2017). For the relationships between disturbance index (i.e., categorical) and our continuous variables, we fit beta regression models (Supplementary section 1.2 and Figs. S1a–S1d)¹ (Ferrari and Cribari-Neto 2004; Cribari-Neto and Zeileis 2010; Douma and Weedon 2019).

Model selection followed a forward stepwise approach based on Akaike's information criterion (i.e., $\Delta AIC > 2$) (Burnham and Anderson 1998) with the final models being those that were the most parsimonious (i.e., lowest AIC). Using the package DHARMA in R, we validated final models by visually assessing scaled residual plots and evaluated spatial autocorrelation with a Moran's I test ($p > 0.05$ for all models) (Hartig 2018). DHARMA uses a simulation-based approach to produce scaled residuals (between 0 and 1) that are readily interpretable for generalized models (Hartig 2018). We used likelihood ratio tests (type II ANOVA) to assess model fit and Nagelkerke pseudo- R^2 values (Nagelkerke 1991), a coefficient of determination for logistic regression, to determine model goodness of fit. Post hoc comparisons between levels of categorical variables were conducted using a modified Tukey's test from the multcomp package (Hothorn et al. 2008). To account for unequal variances and sample sizes between factor levels (Herberich et al. 2010), this modified test uses a heteroscedastic consistent covariance estimation technique from the sandwich package (Zeileis 2004). All statistical analyses were performed using R version 3.5.3 (R Core Team 2019).

Local-scale analysis

To identify the local-scale characteristics that best predict the abundance of *P. icarus*, we began with nine predictors: disturbance index (factor with four levels), canopy cover, the occurrence of *L. corniculatus* (two levels: presence and absence), and the mean proportional cover of shrubs, forbs, grasses, bare ground, *L. corniculatus* flowers, and total flowers. Proportional cover of shrubs and *L. corniculatus* flowers had insufficient data and were therefore excluded. Preliminary analyses exploring the relationships between our predictor variables showed a high degree of non-independence. Specifically, disturbance index was correlated with all of our other variables (i.e., those describing the plant community structure; Supplementary Figs. S1a–S1d)¹. We therefore chose to model the effects of disturbance (i.e., disturbance model) separately from the effects of plant community structure on *P. icarus* abundance (i.e., plant model). For the plant model, from the remaining six predictor variables, grass and forb were collinear ($VIF > 5$). Therefore, we excluded forb due to its weaker influence on *P. icarus* abundance as determined by model AIC and pseudo- R^2 .

Landscape-scale analysis

To identify the landscape-scale characteristics that best predict the abundance of *P. icarus*, we began with seven predictor variables: the proportional cover of forest, cropland, wetland, grassland, shrubland, water, and urban land surrounding the sites. Wetland, grassland, and shrubland had insufficient data in the study region and were excluded. Cropland and urban land were collinear ($VIF > 5$) at almost all spatial scales assessed (see further discussion below), so we excluded cropland due to its weaker influence on *P. icarus* abundance as determined by model AIC and

pseudo- R^2 (400 m scale: $\beta \pm SE = -1.17 \pm 0.85$, $\chi^2_{[1]} = 1.43$, $p = 0.232$, pseudo- $R^2 = 0.022$). Therefore, final models included the proportional cover of forest, water, and urban land surrounding the sites.

As spatial scale is central to determining habitat associations of species (Levin 1992; Brennan et al. 2002; Martin and Fahrig 2012), we used a scale optimization approach to determine the scale at which the species–landscape relationship was strongest (Martin and Fahrig 2012; McGarigal et al. 2016). As recommended by Jackson and Fahrig (2012), we tested multiple scales that ranged over more than one order of magnitude with the largest scale exceeding 9 times the mean dispersal distance (i.e., 75 m; see Results) of the focal organism. This meant that we fit generalized linear models at scales between 100 and 2500 m at intervals of 100 m. Models consisted of all predictors together or each predictor individually. We then evaluated model fit based on AIC. We found that the relationship between *P. icarus* abundance and the three land-cover types was strongest at a spatial scale of 400 m (Supplementary Fig. S2).¹ This scale was consistent even when we modelled the land-cover types separately. Therefore, all landscape-scale analyses were conducted at a 400 m scale.

Mark–release–recapture

To assess the dispersal ability of *P. icarus* adults, we conducted a mark–release–recapture (MRR) study in 2018 at 15 semi-disturbed sites in St. Bruno-de-Montarville, Quebec (Fig. 1c), which is located approximately 15 km from metropolitan Montréal. We chose sites based on their likelihood to contain *P. icarus* (i.e., close proximity to human developments, floral resources), as our goal was to capture as many individuals as possible. Because measurements of dispersal are directly proportional to total study area (Shreeve 1992; Schneider 2003), we chose sites to maximize the total study area (5.7 km²) while keeping the study design feasible (larger areas require more sites and sampling effort). This is much larger than other MRR studies looking at adult butterfly movement patterns (e.g., 3 km²: Dover et al. 1992; 0.11 km²: Kuussaari et al. 2014). Smaller study areas can underestimate dispersal by restricting the distance of possible movements (Schneider 2003).

We visited sites in rotation (one visit/week) for 6 weeks in July and August of 2018. During each visit, two observers actively searched for and captured *P. icarus* for 1–2 h, depending on the number of butterflies present. For all captured individuals, we noted their sex, condition of their wings (e.g., fresh, worn, tattered), time and location of capture, and gave both hind wings a unique mark using a waterproof permanent marker (Sakura Micropen). Butterflies were handled for no more than 2 min each and were released at the location of capture. After release, butterflies typically flew a <5 m away before landing on vegetation or bare ground to bask in the sun.

To test for differences in dispersal between male and female *P. icarus*, we conducted a Welch's two-sample t test in R. To determine the sensitivity of our dispersal measurements to an aspect of the study design, we also report results based only on observations of dispersal >20 m. We chose this threshold because 20 m was the approximate distance that observers would walk in between bouts of capturing and marking individuals. Other MRR studies have made similar methodological choices, but in different ways, e.g., by releasing all marked butterflies from a central point at the end of the survey day (Ricketts 2001) or only recapturing individuals a minimum distance away from a given release area (25 m × 25 m area; Kuussaari et al. 2014).

Results

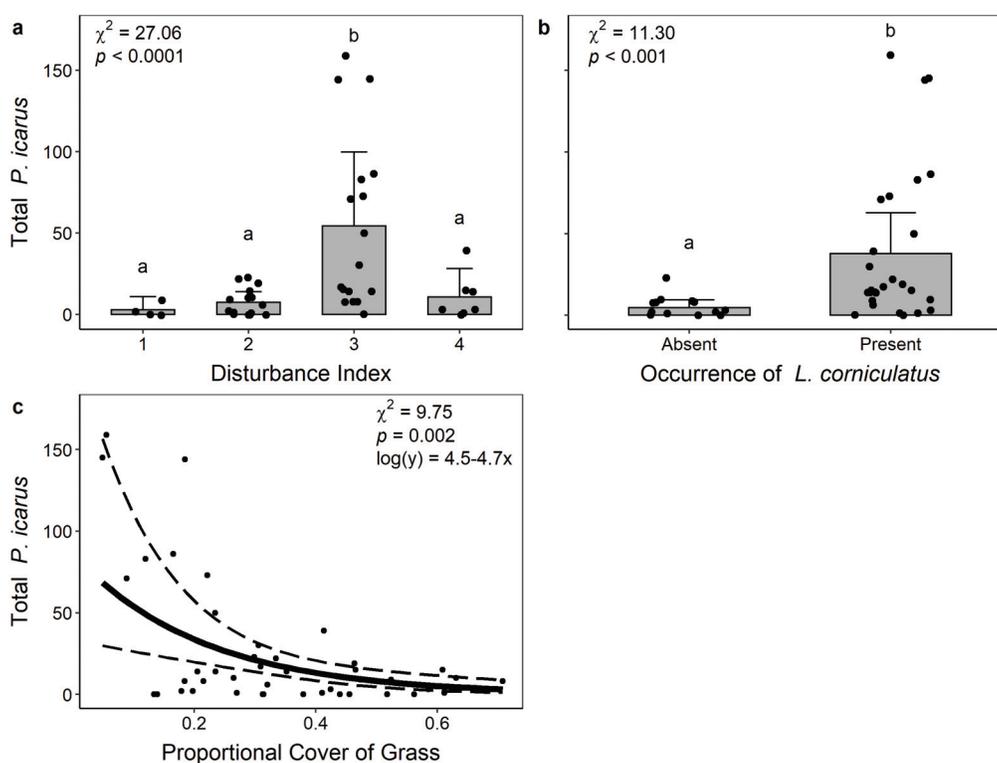
We counted 1128 *P. icarus* adults at 35 (80%) of our 44 sites. We observed two generations of *P. icarus* during our survey period in 2017 (first sighting: 4 June) (Supplementary Fig. S3).¹ However, we continued to make anecdotal observations of *P. icarus* adults until 28 October 2017, suggesting that the flight period of *P. icarus* can

Table 2. Results of local- and landscape-scale habitat suitability models for European common blue (*Polyommatus icarus*) butterflies using generalized linear models with a negative binomial distribution ($n = 44$ sites).

Scale	Model	Model R^2	Term	Coefficient	SE	χ^2	df	p
Local	Disturbance	0.37	Disturbance index	NA	NA	27.06	3	<0.0001
	Plant	0.41	Bird's foot trefoil, <i>Lotus corniculatus</i>	1.58	0.40	11.30	1	<0.001
			Grass	-3.50	1.17	9.75	1	0.002
Landscape	NA	0.45	Urban	2.81	0.72	11.05	1	<0.001
			Forest	-2.56	0.90	6.97	1	0.008

Note: Shown are pseudo- R^2 values for all models and results from likelihood ratio tests (type II ANOVA) including χ^2 statistics, degrees of freedom (df), and p values. Model coefficients and standard errors (SE) are also shown where applicable. NA is not applicable.

Fig. 2. Effects of local-scale habitat factors on the abundance of European common blue (*Polyommatus icarus*) butterflies using generalized linear models with a negative binomial distribution ($n = 44$ sites). The relationship between *P. icarus* abundance and local-scale (a) disturbance index, (b) bird's foot trefoil (*Lotus corniculatus*) occurrence, and (c) proportional cover of grasses. Shown are the mean predicted values (grey bars; a, b) or predicted line of best fit (black solid line; c) and 95% confidence intervals (error bars (a, b) and broken lines (c)). Raw data (solid circles) have been jittered in panels a and b to increase visibility. Lowercase letters in panels a and b represent significant ($p < 0.05$) pairwise comparisons. For details on the meaning of disturbance indices refer to Table 1.



be up to 5 months long (June–October) and that there are likely more than two generations. We observed *P. icarus* adults foraging for nectar on multiple plant species from at least four plant families (Fabaceae, Asteraceae, Orobanchaceae, Lythraceae).

Relative to other butterfly species that we observed, *P. icarus* was the most abundant (mean (\pm SE) abundance = 6 ± 1.05 individuals) and reached extremely high densities (maximum abundance in one site visit = 83 individuals; Supplementary Fig. S4a).¹ The second most abundant species was the non-native European skipper (*Thymelicus lineola* (Ochsenheimer, 1808)) (mean (\pm SE) abundance = 2 ± 1.05 individuals); maximum abundance in one site visit = 79 individuals; Supplementary Fig. S4b).¹ In comparison, native butterfly species never exceeded a mean abundance of 2 individuals or a maximum abundance of 29 individuals in one site visit (Supplementary Figs. S4a and 4b).¹ Interestingly, we observed no individuals of the more recently introduced European peacock (*Aglais io* (Linnaeus, 1758)) butterfly.

Habitat suitability modelling

At a local scale, the variables that best predicted *P. icarus* abundance were disturbance index (pseudo- $R^2 = 0.37$), the presence of *L. corniculatus*, and the proportional cover of grasses (Table 2). *Polyommatus icarus* was most abundant at intermediate levels of disturbance (level 3: every 1–5 years (Table 1); $\chi^2_{[3]} = 27.06$, $p < 0.0001$; Fig. 2a). *Polyommatus icarus* is predicted to be 20 times more abundant in sites with intermediate levels of disturbance (i.e., level 3) compared with low levels (i.e., level 1).

Polyommatus icarus was also more abundant where *L. corniculatus* was present ($\beta \pm$ SE = 1.58 ± 0.40 , $\chi^2_{[1]} = 11.3$, $p < 0.001$; Fig. 2b) and where grass cover was lower ($\beta \pm$ SE = -3.50 ± 1.17 , $\chi^2_{[1]} = 9.75$, $p = 0.002$; Fig. 2c). Combined, the two plant variables explained 41% (pseudo- R^2) of the variation in *P. icarus* abundance. *Polyommatus icarus* is predicted to be 5 times more abundant where *L. corniculatus* is present compared with where it is absent (Fig. 2b). In addition, *P. icarus* abundance is predicted to increase by a factor of 6 if grass

Fig. 3. Effects of landscape-scale habitat factors on the abundance of European common blue (*Polyommatus icarus*) butterflies using generalized linear models with a negative binomial distribution ($n = 44$ sites). The relationship between *P. icarus* abundance and (a) proportional cover of urban land and (b) proportional cover of forest. Shown are the predicted lines of best fit (solid line), 95% confidence intervals (broken lines), and raw data (solid circles).

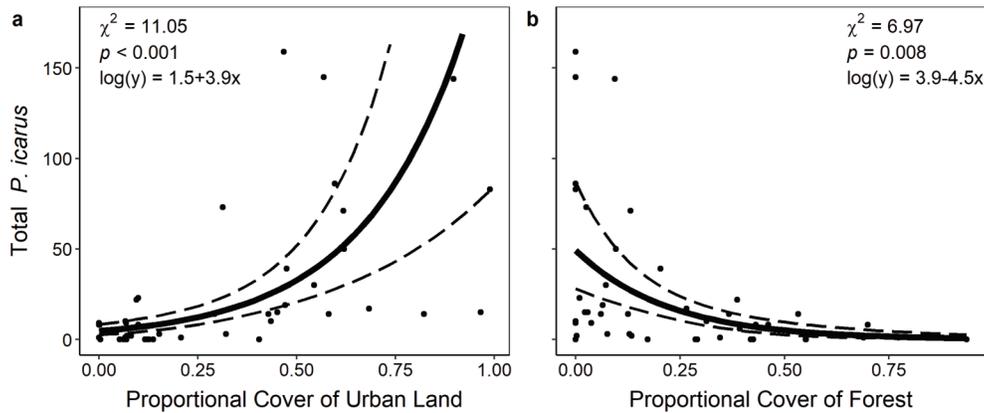


Table 3. Results of the mark–release–recapture study conducted on adult European common blue (*Polyommatus icarus*) butterflies at 15 semi-disturbed sites in St. Bruno-de-Montarville, Quebec.

	Marked individuals	Recaptured individuals	Recapture ratio (%)	Dispersal distance (m)	
				Maximum	Mean
Female	1060	16	1.5	227	60
Male	3569	87	2.4	862	78
Total	4629	103	2.2	862	75

Note: Values shown include number of marked individuals, numbers of recaptured individuals, recapture ratio (%), maximum dispersal distance (m), and mean dispersal distance (m) for males and females.

cover is reduced from 50% to 0% (Fig. 2c). Canopy cover and the mean proportional cover of bare ground and total flowers did not predict *P. icarus* counts (Supplementary Table S2).¹

At a landscape scale, the proportion of urban land and forest surrounding sites (pseudo- $R^2 = 0.45$) best predicted *P. icarus* abundance (Table 2). Specifically, *P. icarus* was more abundant where the proportion of urban land cover was higher ($\beta \pm \text{SE} = 2.81 \pm 0.72$, $\chi^2_{[1]} = 11.05$, $p < 0.001$; Fig. 3a) and proportion of forest cover was lower ($\beta \pm \text{SE} = -2.56 \pm 0.90$, $\chi^2_{[1]} = 6.97$, $p = 0.008$; Fig. 3b). The proportion of water in the surrounding landscape did not predict *P. icarus* abundance (Supplementary Table S2).¹

Dispersal ability

Over the 6 weeks of our MRR study, 4629 *P. icarus* adults were captured and 103 were recaptured (2.2% recapture rate; Table 3). Females were observed less often than males; 23% of initial captures and 16% of recaptures were female (Table 3). There was no significant difference between males and females in terms of the mean distance dispersed (78 m (males), 60 m (females); $t_{[49]} = 0.82$, $p = 0.4$). Only male *P. icarus* butterflies were detected to have flown longer distances (>350 m, $n = 4$). Almost all observations of *P. icarus* dispersal (97%) were of distances less than 400 m, confirming the results of our scale optimization approach (Supplementary Fig. S2).¹

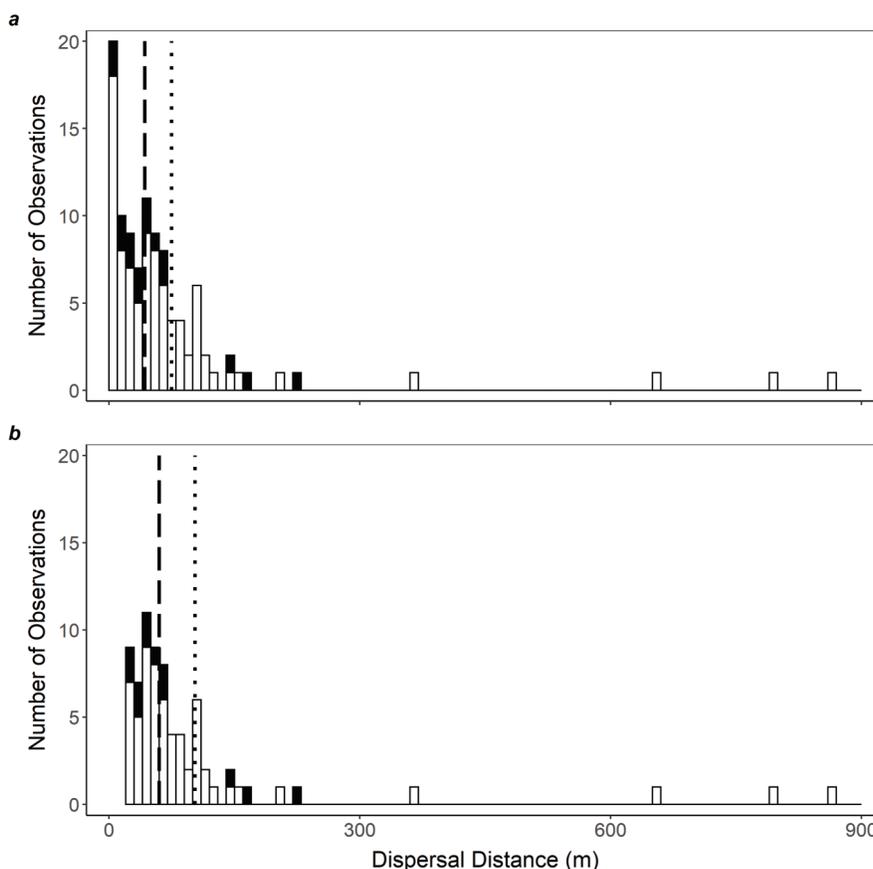
Based on all observations, the mean, median, and maximum distances dispersed were 75, 43, and 862 m, respectively ($n = 103$; Fig. 4a). When we only included observations that were >20 m, the mean and median distances dispersed increased to 103 and 60 m, respectively ($n = 73$; Fig. 4b).

Discussion

Here we report the findings of the first investigation of the ecology of *P. icarus*, a newly introduced butterfly in Canada. We found that the level of local-scale habitat disturbance and landscape-scale urban cover were important in shaping the abundance of *P. icarus*. We also found that plant community characteristics, such as local-scale grass cover and landscape-scale forest cover, influenced its abundance. Finally, the presence of the preferred larval host plant of *P. icarus*, *L. corniculatus*, promoted its abundance.

Polyommatus icarus was most abundant at sites that were moderately disturbed. These sites had mostly small and young trees with mid-height vegetation (e.g., shrubs, grasses, forbs), as well as evidence of human traffic such as dirt or gravel paths, litter, construction materials, and hydro towers. This result suggests that sites with greater disturbance — either more recent (e.g., <1 year, any form of land clearing (e.g., buildings, construction)) and (or) more frequent (e.g., annual or monthly mowing) — as well as sites with lower disturbance are less suitable for *P. icarus*. This hump-shaped pattern with the disturbance index has been observed for another non-native insect, the Argentine ant (Vonshak and Gordon 2015). Our finding that highly disturbed sites are less suitable for *P. icarus* is consistent with studies from its native range that report its occurrence is reduced where habitat management regimes are high in frequency (e.g., mowing, livestock grazing; Gutiérrez et al. 2001). However, we found that sites with low disturbance are less suitable for *P. icarus*, which is not supported in the native range where its occurrence was found to be high in unmanaged lands (Gutiérrez et al. 2001). This discrepancy in the type of habitat that is suitable between the native range

Fig. 4. The distribution of dispersal distances (m) for European common blue (*Polyommatus icarus*) butterflies (total: $n = 103$; female: $n = 16$; male: $n = 87$) based on a mark–release–recapture study conducted in 2018 at 15 sites in St. Bruno-de-Montarville, Quebec, for (a) all observations or (b) only observations >20 m. The median (broken vertical line) and mean (dotted vertical line) dispersals are also shown.



and the introduced range is most likely related to the presence of *L. corniculatus*, a non-native plant species in Canada, which tends to occur at disturbed sites in its introduced range (see further discussion below). However, this difference could also be related to the type, frequency, or severity of disturbance. Given that our measure of local-scale disturbance represented a combination of multiple aspects of disturbance, we are unable to tease apart their effects. As such, future work should consider the relative importance of different components of disturbance on *P. icarus* in its introduced range.

In our study, moderate local-scale disturbance likely benefited *P. icarus* by balancing the availability of its main food resource, *L. corniculatus*, and the amount of grass cover. First, *P. icarus* was more abundant where *L. corniculatus* was present. Consistent with other studies (Turkington and Franko 1980), the occurrence of this plant was dependent on disturbance index ($p = 0.048$; Supplementary Fig. S1a¹): *L. corniculatus* occurred most often in moderately disturbed sites. In fact, this plant was completely absent in our least disturbed sites (Supplementary Fig. S1a).¹ Our results are consistent with the native range where *P. icarus* larvae strongly prefer *L. corniculatus* (Thomas and Lewington 1991; Tolman and Lewington 2008) and adults occur more frequently where this plant occurs or is more abundant (León-Cortés et al. 1999; Gutiérrez et al. 2001). As our study did not include larval surveys, more work is needed on *P. icarus* larvae to confirm whether disturbance promotes abundance via an increase in larval food resources or if a different mechanism is at play.

Second, *P. icarus* was most abundant where the proportional cover of grass was lower. Grass cover was lower in our least to

moderately disturbed sites than in the most disturbed sites ($\chi^2_{[5]} = 14.19$, $p = 0.003$; Supplementary Fig. S1b¹). Because the proportional cover of grass and forb were negatively correlated in our study (Pearson $r = -0.81$), lower grass cover meant a higher cover of forbs, likely increasing the availability of herbaceous plants that *P. icarus* requires for both larval and adult feeding. However, we did not find an effect of forb cover or the number of total flowers on the abundance of *P. icarus*. It could be that more direct measurements of host plant availability (e.g., plant species identity or diversity, number of individuals, number of open flowers) may have increased our ability to detect an effect of herbaceous plants on *P. icarus* abundance. Alternatively, increased grass cover may reduce the amount of bare ground available, which could create cooler microclimates. Previous work has shown that a cooler microclimate reduces *P. icarus* flight activity in the native range due to its microhabitat use and behaviour (Howe et al. 2007); which could reduce the overall suitability of those sites. Nevertheless, our results suggest that sites with moderate disturbance, the presence of *L. corniculatus*, and low grass cover are most suitable for *P. icarus* and that other vegetation types (e.g., herbaceous host plants, nectar sources) may be required. Future studies should consider the role of microclimate in determining habitat suitability of *P. icarus* in the introduced range.

Anthropogenic disturbance in the surrounding landscape was also important in shaping *P. icarus* abundance. Specifically, *P. icarus* abundance increased with increasing proportional cover of urban land (e.g., cities, buildings, roads). This is inconsistent with studies from its native range that have found negative (Mersey Valley, U.K.; Hardy and Dennis 1999) and hump-shaped (Prague, Czech

Republic; Konvicka and Kadlec 2011) relationships with the amount of urban land cover. As stated previously, discrepancies between native and introduced ranges could be related to the presence of *L. corniculatus*, which tends to occur in disturbed areas in Canada. However, it could also reflect greater tolerance of *P. icarus* in the introduced range to conditions in urban landscapes, differences in how studies define urban land cover (e.g., residential vs. industrial), or the spatial scale of the study, as the relative importance of factors can change with scale (Brown et al. 2008). Studies from the native range were conducted at a smaller spatial scale than ours and only at a single scale (Hardy and Dennis 1999; Konvicka and Kadlec 2011).

Urbanization could positively influence *P. icarus* in its introduced range through several mechanisms. Urban areas can have higher diversity of non-native plant species than natural areas (e.g., González-Moreno et al. 2013), which could benefit *P. icarus* whose primary host plant is non-native in Canada. Urban areas can also alter microclimates by raising ambient temperatures (i.e., “urban heat island” effect; Oke 1973), which could favour insects like *P. icarus* by increasing their developmental and reproductive rates (Raupp et al. 2010). Overall, urban areas may provide habitat that is conducive to the establishment and proliferation of *P. icarus* in Canada, but more work is needed to elucidate the specific mechanisms.

In contrast to urban land cover, the proportion of forest cover had a negative effect on *P. icarus* abundance, suggesting that forests represent unsuitable habitat (i.e., matrix; Ricketts 2001). This pattern is consistent with observations in its native range where it is considered a grassland species and is most commonly found in dunes, calcareous grasslands, roadsides, and waste places (Emmet and Heath 1989; Van Sway 2002), not in woodlands. Forests in the surrounding landscape likely act as a barrier and could hamper the ability of *P. icarus* to travel between patches of suitable open habitat. Future studies could determine the effective isolation of habitat surrounded by forest cover by measuring dispersal distances of *P. icarus* adults in heavily forested landscapes.

Dispersal ability

Based on our MRR study (mean and median distances dispersed were 75 and 43 m, respectively), *P. icarus* is a low to moderate disperser relative to other butterfly species. In a review of 46 MRR studies of non-migratory butterflies of various sizes, the majority of species (57%) had a mean dispersal distance of less than 200 m, but estimates varied from just 23 m in the tailed copper (*Lycaena arota* (Boisduval, 1852)) butterfly to 600 m in the common alpine (*Erebia epipsodea* Butler, 1868) butterfly (Sekar 2012). Using less precise methods than MRR (i.e., tracking eggs), Jones et al. (1980) measured the dispersal range of non-native cabbage white (*Pieris rapae* (Linnaeus, 1758)) butterflies to be 250–600 m. Overall, our results suggest that *P. icarus* has a low ability for dispersal relative to other butterfly species.

Our estimates of the dispersal ability of *P. icarus* in its introduced range show both similarities and differences to estimates from its native range. Qualitative studies in the native range have described *P. icarus* as forming closed populations where individuals, especially females, tend to remain in natal breeding grounds (Thomas 1984; Emmet and Heath 1989; Thomas and Lewington 1991). These behavioural descriptions are similar to our findings that *P. icarus* tends to disperse short distances (82% of observations <100 m). However, we did not find differences between sexes. As our estimate of female dispersal was less precise than of males, a larger sample size is needed to determine if females disperse shorter distances than males in the introduced range. Our estimates for mean (75 m) and maximum (862 m) dispersal are lower and higher, respectively, than estimates obtained in the native range (Supplementary Table S3;¹ Gutiérrez et al. 2001; Kuussaari et al. 2014). It is unclear whether there are actual differences in the dispersal ability

between native and introduced ranges, or whether it is because there are methodological differences across studies (Supplementary Table S3).¹ Dispersal measurements can be sensitive to study design (Shreeve 1992; Schneider 2003) as evidenced by our sensitivity analysis. Nevertheless, *P. icarus* seems to be a low to moderate disperser across both its native and introduced ranges.

Our recapture rate (2.2%) was low given that the butterflies did not disperse far between captures and in comparison with other MRR studies measuring butterfly dispersal (e.g., depending on the species: 4%–41% (Ricketts 2001); 2%–43% (Kuussaari et al. 2014)). It could be that the time between revisits was too long (~weekly) relative to their lifespan (i.e., individuals died before we could recapture them); however, their lifespan is uncertain. The longest time that we recorded between captures was 11 days, but this was only based on 103 recaptured individuals. It could also be that the extremely high densities of *P. icarus* adults in our MRR study region had a dilution effect making it difficult to recapture marked individuals. For instance, we captured and marked 4629 *P. icarus* adults in just 6 weeks, while Ricketts (2001) captured 1039 individuals of the same species in its native range in 10 weeks. Regardless, our recapture rate is still comparable with some previous butterfly MRR studies.

Implications

Our results have implications for habitat management and restoration as well predicting range expansion. First, our finding that *P. icarus* abundance was lower in grassier sites suggests that disturbed habitats could be restored with grass mixes to prevent the establishment of this non-native butterfly or reduce its abundance. Preserving forest fragments could also be an effective management strategy given the negative correlation that we observed between forest cover and *P. icarus* abundance. However, we note that negative impacts of *P. icarus* on native biota have not been assessed so the degree of management and restoration needed is uncertain.

Second, our study can inform future modelling efforts aimed at predicting range expansion. For example, the associations between *P. icarus* abundance and landscape composition reported here could be used to determine where range expansion is most likely to occur (i.e., in more urbanized landscapes with lower forest cover). These predictions could then be used to prioritize areas for control or assess potential negative impacts on native biota.

Although our results suggest that *P. icarus* is limited by the local-scale availability of its larval host, *L. corniculatus*, this plant species is widespread across Canada (Zandstra and Grant 1968; Turkington and Franko 1980) and thus may not limit future range expansion of *P. icarus*. Instead, range expansion may be constrained by the low to moderate dispersal ability of *P. icarus* adults. Still, range expansion could be facilitated by rare long-distance dispersal events and spill-over effects due to the extremely high densities of *P. icarus* individuals. Indeed, *P. icarus* has recently colonized sites in Toronto, Ontario (eButterfly 2020), over 400 km away from our study region. This could be the result of rare natural long-range dispersal, human-mediated dispersal via transport pathways, or independent introductions from Europe. Human-mediated long-range dispersal via highways has been implicated in the range expansion of another non-native insect in the United States: the emerald ash borer (*Agrilus planipennis* Fairmaire, 1888) (Muirhead et al. 2006). Future studies could use genetic analyses (e.g., Dincă et al. 2011) to determine the geographic origin, number of introductions, and genetic diversity of Canadian populations of *P. icarus*.

Conclusion

Overall, we found that anthropogenic disturbance at two spatial scales is an important determinant of *P. icarus* habitat

suitability in Montréal, Quebec, Canada. Building on this initial assessment of the ecology of *P. icarus*, modelling the trajectory of range expansion across Canada is needed. Further investigation into additional potential range-constraining factors (e.g., microclimate), especially larval preferences, would also be helpful.

Competing interests

The authors declare that there are no competing interests.

Funding statement

Funding was provided to H.M.K. by the University of Ottawa, and to H.M.K. and J. Kerr from the Natural Sciences and Engineering Research Council of Canada.

Acknowledgements

We thank S. Gilmour, E. Brown, A. Ouellette, and R. Ewing for help in the collection of field data, and J. Kerr and J. Bennett for guidance and advice. We are also grateful to the Société des établissements de plein air du Québec (SÉPAQ), the city of Montréal, and the city of Saint-Bruno-de-Montarville for permission to perform research on their sites.

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