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# Estimates of accessible food resources for pollinators in urban landscapes should take landscape friction into account

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**Abstract.** Maintaining biodiversity in urban landscapes requires a well-functioning green infrastructure for the landscape to remain ecologically functional. However, city planners often lack knowledge to identify how well different parts of the green infrastructure are connected, and tools to estimate the accessibility to important habitats for different species in urban areas are strongly needed. We compared the ability of three measures of available food resources, with increasing complexity, for explaining species richness and abundance of bees and wasps at 23 locations in an urban landscape in Sweden. Specifically, we tested (1) the summed amount of food habitat within a buffer circle, (2) the amount of food habitat weighted by distance, and (3) the summed amount of food habitat within an area created by cost-weighted distance based on the surrounding landscape friction. We tested two spatial scales (200 and 400 m). The results show that both the summed (1) and the weighted measures (2) were very poor in explaining species richness and abundance regardless of spatial scale, while we found significant relationships for both species richness and abundance with the friction-based measure (3) at both scales. For the friction-based measure, the relationships with both response variables were strongest at the smallest spatial scale (200 m). We conclude that bees and wasps are sensitive to barriers such as large roads and built-up areas when foraging in urban environments. This is important to consider when assessing the functionality of urban green infrastructure in order to not overestimate the available amount of habitat and how well different parts of the landscape are connected for these important pollinators.

**Key words:** Aculeata; green infrastructure; habitat fragmentation; landscape friction/resistance; road ecology; wild bees.

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## INTRODUCTION

As city regions around the world get increasingly populated, the land use requirements in and around cities also increase. This often occurs at the expense of urban green areas. It is assumed that rich biodiversity and cities are incompatible, but many cities have high species richness and several are located within globally recognized biodiversity hotspots making them important for conservation (Goddard et al. 2010, CBO 2012). Maintaining a high biodiversity is important, not only as it increases the possibility of preserving rare and endangered species, but also because a high biodiversity is crucial for ecosystem functioning and for delivering ecosystem services (e.g., Díaz et al. 2006). In addition, species-rich habitats are often more resilient in maintaining functionality and delivering ecosystem services after disturbance (e.g., Oliver et al. 2015). Maintaining biodiversity in urban landscapes requires a well-functioning green infrastructure so that the landscape remains well connected and ecologically functional, which is also stated in the EU Biodiversity Strategy (European Commission 2017). However, city planners often lack knowledge to identify how functional different parts of the green infrastructure are for certain species. Therefore, tools to estimate available habitat in urban areas are strongly needed.

Bees and wasps (Aculeata) serve as an example of a species-rich animal group providing important ecosystem services (Corbet et al. 1991, Harris 1994). Especially bees, but also to some extent wasps, are flower-visiting insects important for pollination of crops and native plants (e.g., Corbet et al. 1991, Steffan-Dewenter et al. 2005, Rader et al. 2016). Wasps are also predatory insects, potentially reducing populations of pest insects (Harris 1994). Bees and wasps often utilize habitats in urban areas, such as parks, flower-rich disturbed sites, roadsides, and flower-rich gardens (e.g., McFrederick and LeBuhn 2006, Goddard et al. 2010, Gunnarsson and Federsel 2014). Hence, there is a high potential in urban landscapes to benefit from the ecosystem services that these insects provide (Hall et al. 2017). However, maintaining such services in a sustainable perspective require an urban landscape where bees and wasps can easily move between important habitats. Most species are central-place foragers that have rather restricted foraging ranges around their nests (Steffan-Dewenter et al. 2001, Gathmann and Tscharntke 2002). Therefore, they may be sensitive to potential barriers such as large roads in the landscape (Andersson et al. 2017). This may explain why pollinator richness and abundance, and pollination success often decrease with increasing urbanization (Ahrné et al. 2009, Pellissier et al. 2012, Fortel et al. 2014), even if an alternative explanation for this pattern in warm areas also can be urban heat-island effects (e.g., Hamblin et al. 2017). However, our understanding of what drives richness and abundance patterns of bees and wasps in urban landscapes is still rather limited.

One of the most important factors for regulating populations of flower-visiting bees and wasps is the availability of food resources (e.g., Potts et al. 2003, Carvell et al. 2004, Roulston and Goodell 2011). Hence, estimates of available food habitat in different parts of the landscape can give indications on where the green infrastructure is functioning for these species. However, estimating available food habitat in the surrounding landscape can be done in several ways (e.g., Winfree et al. 2005). One of the most commonly used measures for quantifying important habitat in the surrounding landscape is the simple summation of the habitat area within a certain buffer radius around the focal location (e.g., Steffan-Dewenter et al. 2001, Bender et al. 2003, Bergman et al. 2004). Slightly more complex measures may take into account that the importance of the surrounding habitat decreases with increasing Euclidian distance from the location of interest, following, for example, a negative exponential function (as the connectivity measure in the classical incidence function model, Hanski 1994). Other even more complex measures also consider that the matrix may differ in permeability for the movements of the study species and that the landscape may contain barriers (Wiens et al. 1993, Adriaensen et al. 2003, Compton et al. 2007). These measures account for landscape friction by using cost-weighted distances rather than Euclidean distances (e.g., Adriaensen et al. 2003). Even if more complex measures are usually better in explaining species occurrence patterns (Moilanen and Nieminen 2002, Ranius et al. 2010), as they better reflect the movements of the focal species, the less complex measures often seem good enough (Prugh 2009, Ranius et al. 2010). The latter are generally also more practically applicable for landscape planners and field conservationists. However, in urban environments the less complex measures (based on the Euclidian distance) may become less reliable as, for example, roads and built-up land can function as barriers (Peralta et al. 2011, Andersson et al. 2017) that reduce the accessibility to some of the surrounding habitat. We are not aware of any study that compares how well different ways of measuring available habitat in the surrounding landscape explain patterns of species richness and abundance in urban environments.

The aim of this study was to compare the ability of different measures of available food resources for explaining species richness and abundance of bees and wasps at different locations in an urban landscape. We expected both richness and abundance to increase with increasing amount of food habitat in the surrounding landscape. We compared three types of measures with increasing complexity: (1) the summed amount of food habitat within a buffer circle (based on the Euclidian distance), (2) the summed amount of food habitat within a buffer circle but weighted by distance, and (3) the summed amount of food habitat within an area created by cost-weighted distance based on the surrounding landscape friction. We hypothesized that the explanatory power increased with increasing complexity of how the amount of food habitat in the surrounding landscape was estimated.

## METHODS

### *Field inventory of bees and wasps*

We performed an inventory of bees and wasps (Aculeata) during spring and summer 2015 using pan traps at 23 sites within Sollentuna municipality in southern Sweden. Sollentuna is part of the metropolitan area of Stockholm and is situated approximately 9 km north of central Stockholm. The sites were selected prior the field inventory using ArcGIS (Esri, Redlands, California, USA), and they were chosen to represent a gradient in urbanization. The average minimum distance between two sites was ~760 m.

To trap a representative sample of the species active at different time periods in the study area throughout the spring and summer, the field inventory was conducted at three occasions. The first inventory was conducted during the end of April, the second during the beginning of June, and the third inventory during the beginning of August 2015.

At each site, we placed three pan traps in a triangular setup on the ground, spaced with approximately 1 m. The pan traps consisted of 0.8 L aluminum boxes (without lid), and each was sprayed with either yellow, blue, or white paint (Westphal et al. 2008). The trap colors represented common floral colors in our study area. At each site, we used one pan trap for each color. The traps were filled with water and a drop of detergent was added in order to reduce tension of the water surface. The pan traps were placed at the sites during days with suitable weather conditions (sunny weather, light winds), and the traps were emptied and removed from the sites three–four days later (three days in April and June, and four days in August). All collected material was stored in ethanol. All bees and wasps where identified to species level.

### *Mapping potential food habitats*

To map potential food habitat, we mainly used the available biotope database in the municipality of Sollentuna, which has detailed information as it is based on classification using remote-sensing and interpretation of infrared aerial images. In combination with information on management from the municipality, we extracted five habitat types that we assessed to be flower-rich environments important for flower-visiting bees and wasps using GIS: (1) grasslands and shrublands with low-intensity management (Appendix S1: Table S1), (2) edges of forests and fields (10 m in width; Appendix S1: Table S1), (3) bedrock outcrops (warm openings in forests where, e.g., *Calluna* sp. are common; Appendix S1: Table S1), (4) home gardens classified as lush (with fruit trees and berry shrubs) and areas with cultivation of fruits and berries (e.g., allotments; Appendix S1: Table S1). For more details, see Appendix S1. In GIS, we then merged these habitats in the entire landscape into a single layer called food habitat.

### *Estimating available food habitat*

We compared the ability of three different measures of available food habitat, with increasing complexity, for explaining species richness and abundance of bees and wasps. For each measure (i.e., the explanatory variables), we tested two spatial scales. The first measure was a simple summation of food habitat in buffer circles surrounding the focal traps using the Euclidian distance (Table 1). We did the summation at buffer distance 200 and 400 m. These distances were based on earlier studies of foraging ranges (e.g., Gathmann and Tscharntke 2002) and distribution patterns in relation to landscape structures (e.g., Steffan-Dewenter et al. 2001) of the study species. As some of the traps were located relatively close to the municipality border, we could not test much larger distances (as land cover data outside the border was missing). However, these distances should capture foraging ranges of a large proportion of the species, even though some species probably forage over larger distances (e.g., Gathmann and Tscharntke 2002). The second

Table 1. Descriptions of the three measures of available food habitat. Also see Figs. 1, 2.

| Connectivity measure | Description |
|---|---|
| Summed | The total amount of food habitat within a buffer circle (based on the Euclidian distance). All food habitats within the buffer have equal weight. See Fig. 2a |
| Weighted | The amount of food habitat weighted by the Euclidian distance using a negative exponential function. The weight decreases with increasing distance. See Fig. 1 |
| Friction based | The summed amount of food habitat within an area created by cost-weighted distance based on the surrounding landscape friction. See Fig. 2b |

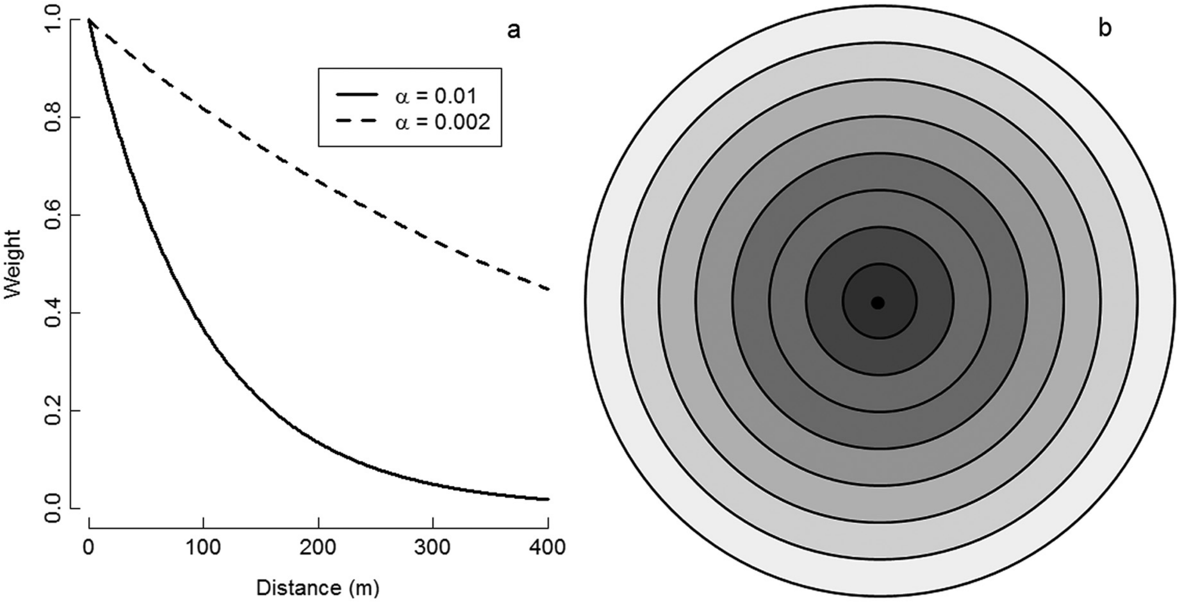

Fig. 1. (a) The spatial weighting given by the two different parameter values used in the connectivity measure based on the negative exponential function (weight = $e^{-\alpha \times \text{distance}}$), and (b) the eight 50 m wide buffer bands where the amount of food habitat was weighted based on the distance from the focal trap. The gray scale signifies an example weighting where bands close to the focal site (black dot) have higher weight (darker) than bands further away (lighter).

measure sums the food habitat in the surrounding landscape weighted by the Euclidian distance and is a very common measure in landscape ecology studies (e.g., used in the classical incidence function model; Hanski 1994). For this measure, we used the summed food habitat in 50 m wide buffer bands (up to 400 m) surrounding each trap (Samnegård et al. 2015) and calculated available food habitat ($\text{FH}_i$) as

$$\text{FH}_i = \sum_{j=1}^{n} e^{-\alpha \times d_{ij}} A_j$$

where $d_{ij}$ is the distance in meters between the focal trap $i$ and the middle of buffer band $j$, $\alpha$ is a parameter setting the spatial scaling (Fig. 1), and $A_j$ the amount of potential food habitat within band $j$ (Fig. 1). The number of bands ($n$) was eight (i.e., 400 m divided by 50 m). We tested two values of $\alpha$ (0.01 and 0.002) that give different weights to the surrounding landscape. The first, $\alpha = 0.01$, represents a steep dispersal kernel that gives relatively low weight (<0.14) for habitat >200 m away, while $\alpha = 0.002$ represents stronger dispersers with a corresponding weight of 0.67 at 200 m (Fig. 1). The third measure takes landscape friction into account, that is, that different land cover types are not equally permeable for the focal species (e.g., Adriaensen et al. 2003, Zeller et al. 2012, Fig. 2). This measure also can account for potential barriers in the landscape, which recently has been shown to affect the species composition of bees and wasps (Andersson et al. 2017). We first assigned friction values to all landscape types in the entire landscape using the detailed biotope map. Friction values were based on expert opinion and literature, and the result was a so called friction raster (Fig. 2, Appendix S1). The friction value represents the permeability of a raster cell for the movement of an individual of a species. It is not a measure of speed, but rather a measure for the reluctance or cost to use the landscape type for movement (e.g., Adriaensen et al. 2003). High friction values mean a higher cost for the species to move, and compared to, for example, a 200-m movement in friction 1 (no friction), it only reaches 100 m in friction 2 and 20 m in friction 10. Hence, with high friction (>40) even rather narrow (~10 m) landscape elements (if stretching across the landscape) can become complete barriers for the species when the maximum distance is 400 m. In this study, large roads, other paved ground, buildings, and open water were given friction values that make them complete barriers (Andersson et al. 2017). For details on how friction values were motivated, see Appendix S1. Then, we used the cost distance function in ArcGIS Pro 2.1.2 to calculate a cost-weighted area around each collection point based on the underlying friction in all directions. This creates a smaller and more asymmetrical area around each point (compared to a buffer circle that assumes no friction) where we then summed the amount of food habitat (Fig. 2).

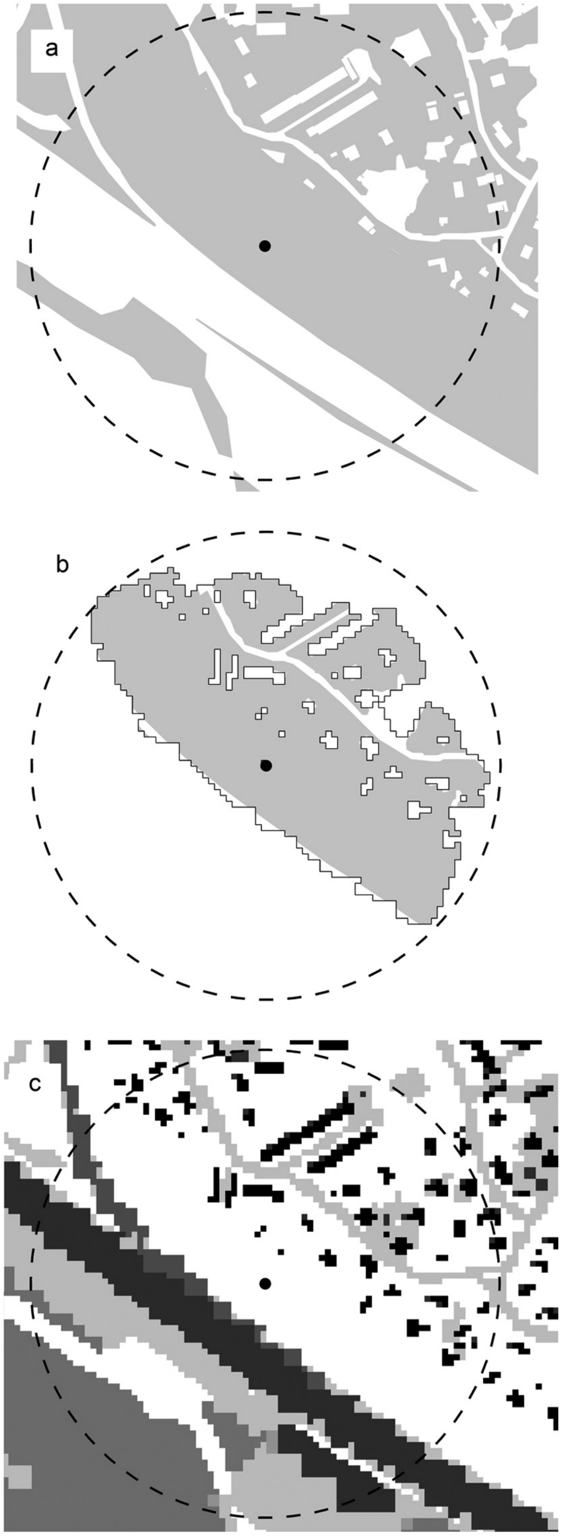

Fig. 2. A comparison between (a) the total amount of food habitat (gray area) within 200 m (broken line) around a study site (black dot), and (b) the food habitat (gray area) within an area created by cost-weighted distance (outer black line) based on (c) the surrounding landscape friction (increasing from light to dark). The gray area within the broken line in (a), hence, shows the available food habitat from the summed measure (Table 1), while the gray area in (b) shows the accessible food habitat from the friction-based measure. The high friction of a large highway (the E4) stretching across the landscape makes resources in the southwest unreachable, and local streets together with buildings reduce the access to resources also in the northeast.

As the results may be sensitive to the choice of friction values throughout the landscape (e.g., Zeller et al. 2012), we also tested two other sets of friction values. First, we decreased all friction values with 20% to test whether the results were sensitive to small adjustments of friction values in general (Appendix S1: Table S2). Second, we tested a very simplified version where we only assigned friction to roads, other paved ground and built-up land, while the rest of the landscape had no friction (value 1). This, hence, also tests whether the main effect of landscape friction is a result of roads and other paved ground being strong barriers. The two alternative sets of friction values were only tested for the spatial scale with the strongest relationship to species richness and abundance.

### *Statistical analysis*

For all statistical analyses, we used the statistical software R 3.4.2 with add-on library MASS (function glm.nb). We used pooled species data for each site (i.e., both from the three traps and from the three occasions) and analyzed species richness and abundance (as two separate response variables) in relation to the three measures of available food habitat using generalized linear models. We assumed a negative binomial distribution, as both response variables were over-dispersed counts, and used a log-link function. As explanatory variables, we tested each measure of available food habitat separately. We log-transformed and standardized all measures of available food habitat to improve normality and to make parameter estimates comparable. Moran's *I* tests suggested no spatial autocorrelation of the residuals from any of the tested models ($p_{\text{min}} > 0.20$).

To make sure that potential outliers with >50 species (one site) and >150 individuals (two sites) did not drive the obtained significant relationships, we also ran the analysis without these outliers. However, this did not affect the result much, and the significant relationships remained.

## RESULTS

In total, we captured 953 individuals of 110 Aculeata species (Appendix S2: Table S1) at the 23 sites. Among the sites, species richness and abundance ranged 2–59 species (median = 12) and 2–220 individuals (median = 23), respectively. The trap catches in total comprised 62 species of bees (Anthophila), consisting of Apidae (19 species), Halictidae (17 species), Andrenidae (13 species), Colletidae (six species), Megachilidae (six species), and Melittidae (one species). The remainder of the trap catches consisted of various wasp species, such as Crabronidae (18 species), Pompilidae (14 species), Vespidae (seven species), Chrysididae (four species), Sphecidae (three species), Tiphidae (one species), and Ampulicidae (one species).

The summed amounts of food habitat within the 200 and 400 m buffers around each site were on average 36.7% and 33.6% of the buffer area, respectively, while the corresponding values for the accessible food habitat, based on the friction-type measure, were 17.5% and 11.7%. For the weighted measure, the amounts of food habitat with $\alpha = 0.01$ were on average 16.7% of the 200 m buffer area, while for $\alpha = 0.002$ it was 20.3% of the 400 m buffer area.

There were clear differences between the three measures of available food habitat in explaining species richness and abundance. Both the summed and the weighted measures were very poor in explaining the two response variables regardless of scale (Tables 2, 3), while we found strongly significant relationships for both species richness and abundance with the friction-based measure at both spatial scales (Tables 2, 3, Fig. 3). For the friction-based measure, the relationships with both response variables were strongest at the smallest spatial scale, that is, at 200 m, based on the higher explained deviance (an analogue to $R^2$) and lower Akaike's information criterion values (Tables 1, 2).

Having 20% lower friction gave a very similar result as the original friction, with strongly significant relationships with both species richness and abundance (Appendix S2: Table S3). Also for the very simplified friction-type measure (i.e., only including friction of roads, other paved ground, and built-up land), the significant relationships to both species richness and abundance remained, but the explanatory power was lower (Appendix S2: Table S3).

## DISCUSSION

We show that estimates of available food resources for important pollinators in urban landscapes

Table 2. Parameter estimates, Akaike's information criterion (AIC) values, and the explained deviance of models for species richness with different types of connectivity measures as explanatory variables.

| Connectivity measure | Parameter estimate (SE) | *P*-value | AIC | Explained deviance (%) |
|---|---|---|---|---|
| Summed 200 m | 0.18 (0.18) | 0.31 | 169.4 | 2.9% |
| Summed 400 m | −0.24 (0.17) | 0.16 | 168.0 | 8.5% |
| Weighted ($\alpha$ = 0.01) | 0.05 (0.18) | 0.77 | 170.1 | 0.3% |
| Weighted ($\alpha$ = 0.002) | −0.20 (0.17) | 0.25 | 168.7 | 5.9% |
| Friction based 200 m | 0.54 (0.17) | **0.001** | 162.4 | 27.8% |
| Friction based 400 m | 0.46 (0.17) | **0.006** | 164.7 | 20.6% |

*Note:* Significant (<0.05) *P*-values in bold.

Table 3. Parameter estimates, Akaike's information criterion (AIC) values, and the explained deviance of models for abundance with different types of connectivity measures as explanatory variables.

| Connectivity measure | Parameter estimate (SE) | *P*-value | AIC | Explained deviance (%) |
|---|---|---|---|---|
| Summed 200 m | −0.005 (0.24) | 0.98 | 223.2 | 0% |
| Summed 400 m | −0.28 (0.23) | 0.23 | 221.4 | 6.5% |
| Weighted ($\alpha$ = 0.01) | −0.07 (0.24) | 0.77 | 223.1 | 0.2% |
| Weighted ($\alpha$ = 0.002) | −0.26 (0.23) | 0.27 | 221.8 | 5.3% |
| Friction based 200 m | 0.76 (0.22) | **<0.001** | 215.9 | 24.4% |
| Friction based 400 m | 0.72 (0.22) | **<0.001** | 216.9 | 21.3% |

*Note:* Significant (<0.05) *P*-values in bold.

should not be based on methods only using the Euclidian distance. Specifically, we show that it is important to take landscape friction and barrier effects linked to roads and built-up land into account. Our results therefore suggest that knowledge of potential barriers is crucial for our understanding of green infrastructure and assessments of ecosystem services in urban landscapes.

### *Comparing measures of available food resources*

Our results suggest that more complex measures of available food resources are better in explaining species distribution patterns compared to simpler measures, which agrees with our hypothesis and earlier work on other insects in non-urban habitats (Moilanen and Nieminen 2002, Ranius et al. 2010). The reason is most likely that complex measures are more ecologically realistic and better capture how species move in the landscape. However, the commonly used distance-weighted measure (e.g., Hanski 1994, based on the Euclidian distance) was not better than simple summations of habitat in buffer circles in our urban landscape study area, which disagrees with earlier studies (Moilanen and Nieminen 2002, Ranius et al. 2010). Our results instead strongly suggest that estimates of available food resources for important pollinators in urban environments should be based on the cost distance (e.g., Adriaensen et al. 2003) rather than the Euclidian distance, to account for differences in matrix permeability. Potential barriers, such as large roads, seem to be particularly important to consider as the simplified friction-type measure (where we only had friction for roads, other paved ground and built-up land) also significantly explained both species richness and abundance. The barrier effect of large roads agrees with recent research showing clear differences in species composition of bees and wasps between two sides of a large highway (Andersson et al. 2017). Reasons for this could be that the bees and wasps avoid crossing large roads during their regular foraging trips due to a hostile environment or that, when trying to cross the road, the mortality increases due to collisions with vehicles (Skórka et al. 2013, 2015, Baxter-Gilbert et al. 2015). Measures that do not take landscape friction into account most likely overestimate the amount of accessible food habitat (Fig. 2) as they include habitat that is not reachable for the insects (in our study, we found an overestimation with 2.1–2.9 times for the two distances tested). In urban landscapes with many potential barriers, the measures based on the Euclidian

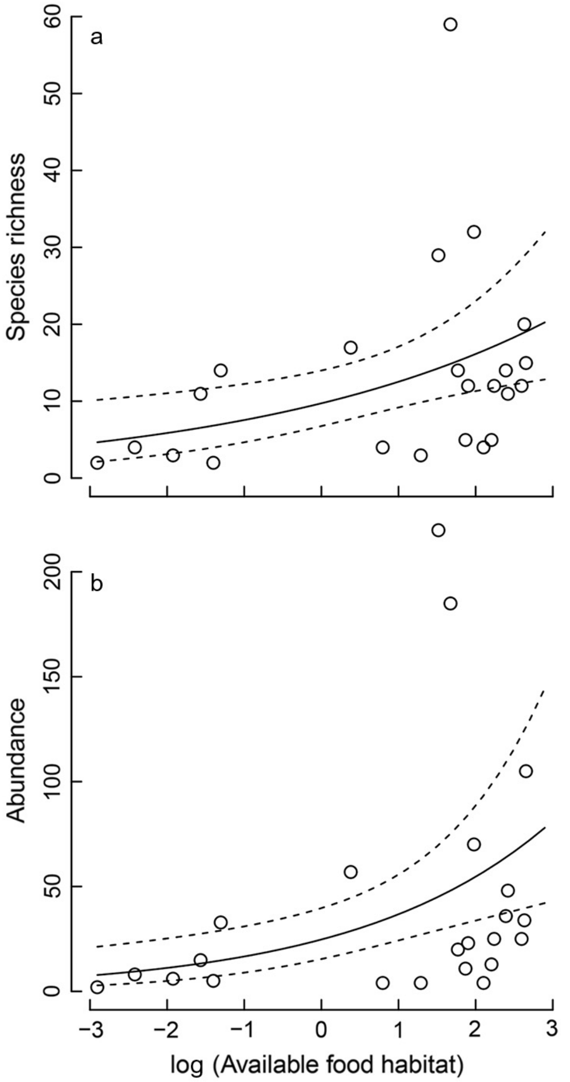

Fig. 3. Species richness (a) and abundance (b) in relation to the available food habitat within 200 m, based on the connectivity measure including landscape friction. Points represent raw data, and whole lines mean predictions (broken lines are 95% confidence intervals) from the fitted negative binomial models.

distance are therefore not suitable for assessing, for example, green infrastructure and the potential for the ecosystem service pollination. Moreover, there is a risk of false conclusions regarding the importance of food resources for pollinators in urban landscapes when only analyzing the relationship between species distributions and less complex connectivity measures (such as summations in buffer circles).

### *Spatial scale*

We found a stronger explanatory power for the smallest spatial scale (i.e., when setting the maximum distance to 200 m), which indicates that the overall community of wild bees and wasps may have rather limited foraging distances in urban landscapes. This agrees with earlier studies of foraging ranges and distribution patterns of wild bees in other environments (Steffan-Dewenter et al. 2001, 2002, Gathmann and Tscharntke 2002), even if the ranges may differ considerably between species. Usually, it is the smaller species that have the most restricted foraging ranges (Gathmann and Tscharntke 2002, Greenleaf et al. 2007, Tscheulin et al. 2011) and are therefore most negatively affected by barriers (Andersson et al. 2017). In the planning of green infrastructure, it is therefore important to consider a rather small spatial scale, in order for the green infrastructure to be functional also for the poor dispersers. Including more of the community (i.e., more species) may increase the ecosystem service pollination, as it is likely to increase with increasing pollinator richness (e.g., Klein et al. 2003, Hoehn et al. 2008).

### *Accounting for landscape friction in insect movements*

Landscape friction has been used rather extensively in landscape ecology (mainly for mammals, birds, and amphibians), but potential effects on insect movements are still underrepresented (Zeller et al. 2012), but see, for example, Jha and Kremen (2013) and Jha (2015). Our results suggest that accounting for landscape friction when quantifying available habitat in the surrounding landscape is important for insects (here bees and wasps), at least in urban landscapes. Previous studies suggest that landscape friction may be less important in non-urban landscapes, as distribution patterns of flying insects in such landscapes often is well explained by rather simple measures (e.g., Moilanen and Nieminen 2002, Ranius et al. 2010). However, studies of butterflies in natural landscapes have suggested that the dispersal between habitat patches can be strongly affected by matrix permeability (e.g., Roland et al. 2000, Ricketts 2001), and several habitat types could potentially function as dispersal barriers for pollinators. Examples are large continuous agricultural fields that offer few foraging opportunities and dense forests with a cold microclimate (Ricketts 2001, Jauker et al. 2009). We believe that the effects of landscape friction on insect movements and distributions need further investigation to potentially increase our ability to assess and understand connectivity in general. This should include studies in both urban and non-urban landscapes and of other species groups (Jauker et al. 2009). To increase our ability to set appropriate friction values, which today mainly is done by expert opinion (Zeller et al. 2012), we need more studies that estimate insect movements in different environments (e.g., Ricketts 2001). Even if we show that our results are mainly dependent on strong barriers, the loss of explanatory power when testing the simplified friction-type measure indicates that friction of other land use types also matters.

## CONCLUSIONS

Estimates of available food resources for bees and wasps in urban landscapes should take landscape friction into account, rather than only using the Euclidian distance. This is important to consider in order to not overestimating the available amount of food habitat and how well different parts of the landscape are connected for these important pollinators. Knowledge of potential barriers is crucial for our understanding of green infrastructure and assessments of ecosystem services in urban landscapes. This knowledge contributes to the development of methods for assessing green infrastructure in urban planning, which is an important step in the EU biodiversity strategy 2020 that is currently being implemented in, for example, Sweden. The demand for reliable analysis tools is high for municipalities and county boards to identify areas with high potential for biodiversity and how these are linked together at the landscape level (Zetterberg 2011). Our study concludes that less complex, but commonly used, measures to quantify important habitat for pollinators (e.g., summations of habitat within a buffer radius) may fail to identify such areas and links in urban environments. When assessing green infrastructure and the ecosystem services pollination in urban landscapes, we thus may require more complex measures that account for landscape friction.

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