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RESEARCH ARTICLE

Landscape composition and pollinator traits interact to influence pollination success in an individual-based model

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Abstract

1. The arrangement of plant species within a landscape influences pollination via changes in pollinator movement trajectories and plant–pollinator encounter rates. Yet the combined effects of landscape composition and pollinator traits (especially specialisation) on pollination success remain hard to quantify empirically.
2. We used an individual-based model to explore how landscape and pollinator specialisation (degree) interact to influence pollination. We modelled variation in the landscape by generating gradients of plant species intermixing—from no mixing to complete intermixing. Furthermore, we varied the level of pollinator specialisation by simulating plant–pollinator (six to eight species) networks of different connectance. We then compared the impacts of these drivers on three proxies for pollination: visitation rate, number of consecutive visits to the focal plant species and expected number of plants pollinated.
3. We found that the spatial arrangements of plants and pollinator degree interact to determine pollination success, and that the influence of these drivers on pollination depends on how pollination is estimated. For most pollinators, visitation rate increases in more plant mixed landscapes. Compared to the two more functional measures of pollination, visitation rate overestimates pollination service. This is particularly severe in landscapes with high plant intermixing and for generalist pollinators. Interestingly, visitation rate is less influenced by pollinator traits (pollinator degree and body size) than are the two functional metrics, likely because 'visitation rate' ignores the order in which pollinators visit plants. However, the visitation sequence order is crucial for the expected number of plants pollinated, since only prior visits to conspecific individuals can contribute to pollination. We

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show here that this order strongly depends on the spatial arrangements of plants, on pollinator traits and on the interaction between them.

4. Taken together, our findings suggest that visitation rate, the most commonly used proxy for pollination in network studies, should be complemented with more functional metrics which reflect the frequency with which individual pollinators revisit the same plant species. Our findings also suggest that measures of landscape structure such as plant intermixing and density—in combination with pollinators' level of specialism—can improve estimates of the probability of pollination.

KEYWORDS

agent-based model, habitat heterogeneity, movement ecology, Netlogo, patch size, visitation rate

1 | INTRODUCTION

The arrangement of plants in a landscape influences pollinator movements and plant–pollinator encounter rates (Cranmer et al., 2012). This influences visitation frequency and pollination success (Fortuna et al., 2008), which, in turn, affect plant fitness and yield. The level of a pollinator species' generalism affects which flower resources the pollinator can utilise and can therefore play an important role in modulating pollinators' responses to changes in the spatial arrangement of plants at the landscape level. Thus, the interactions between the spatial arrangement of plants and pollinator specialisation are expected to determine visitation rate and, ultimately, pollination success.

It is important to note that from a plant perspective, pollination success is not logically equivalent to the rate at which a plant is visited by a pollinator (King et al., 2013). A direct link between the two assumes that every individual insect which visits an individual plant will deposit conspecific pollen at each visit (Bascompte et al., 2003; Memmott, 1999). Such a scenario, however, is unlikely, because pollinators often visit several plants of different species between visits to conspecific plants. Moreover, pollen transfer is a highly stochastic and wasteful process (Johnson, 2010; Richards et al., 2009). Despite this, given the complexities of measuring effective pollination empirically, many researchers rely on visitation rate as a surrogate measure for pollination. Although visitation rate captures how often pollinator species visit or forage on a given plant species, and thus describe the importance of plants from the pollinator perspective, it disregards the *sequence* of flower visits by individual pollinators. This is a major shortcoming, given the crucial importance of this sequence in determining the chances of successful conspecific pollen transfer and pollination (King et al., 2013; Morales & Traveset, 2008). As a result, most plant–pollinator network studies using visitation rates do not accurately describe pollination success from the plant perspective (Armbruster, 2017; de Santiago-Hernández et al., 2019; Willmer, 2011).

The distinction between visitation rates and pollen transfer has been repeatedly stressed by several authors (King et al., 2013; Willmer, 2011), as has the importance of evaluating the link between the two. Nonetheless, studies attempting to fill this major knowledge gap are rare (Ballantyne et al., 2015, 2017). Some of the challenges in moving from visitation rate to better estimates of pollination success derive from the crucial distinction between pollinators as species and individuals (Cirtwill et al., under review). Effective pollination requires that a pollinator *individual* visits the same plant species consecutively, or at least repeatedly, during a plant visitation sequence. Yet, most field-based studies are unable to provide such detailed information at the level of the individual (but see, Arroyo-Correa et al., 2021; Dupont et al., 2014). Instead, information is provided at the level of species, genus or even family. Because of the difficulty in obtaining visitation sequences of individual pollinators (and hence their contribution to conspecific pollen deposition on plant individuals) from field data, the knowledge gap persists—despite recent efforts to disentangle mere visits from effective pollination (Arroyo-Correa et al., 2021; Ballantyne et al., 2015; King et al., 2013). Given the many challenges of assessing pollination success, even in a laboratory or greenhouse setup, the relationship between a given spatial configuration of plants, pollinator specialisation and pollination remains elusive and largely untested (Armbruster, 2017).

Individual-based models can circumvent some of the limitations faced by field studies because they allow the tracking of individual pollinators and their floral visitation through space and time (Newton et al., 2018). Individual-based models permit recording the time and location of all events taking place during a simulation, together with the identity of the individuals (e.g. plants and pollinators) involved in the event. Thus, a properly designed individual-based model can be used to simulate plant–pollinator interactions under a broad range of eco-environmental scenarios, while recording the complete sequence of floral visitation by pollinators and their exact spatio-temporal history. This, in turn, provides a unique opportunity to explore the dynamics of plant–pollinator interactions and disentangle the process of visitation from that of conspecific pollen transfer, therefore improving our understanding of the determinants of pollination success in a spatial context. Additionally, individual-based models are extremely flexible, providing users with freedom to design and manipulate simulation settings. Such flexibility allows the exploration of how variation in the emergent features of pollinator–plant interactions resulting from individual-level behaviour affects the pollination process by, for example, imposing different levels of specialisation for pollinators. Hence, these models can elucidate structure–function relationships and have the potential to catalyse the transformation of network approaches from descriptive to more predictive science (Arroyo-Correa et al., 2021).

In this study, we use an individual-based modelling approach to address how the spatial arrangements of individuals of different plant species within a landscape combine with pollinator specialisation to influence pollinator visitation rates. We further model the probability of conspecific pollen transfer in different visitation sequences to derive the expected number of plants pollinated. To do this, we formalise two functional metrics of pollination as well as visitation rate: *consecutive visits*, which describes the number of times an individual pollinator visits the same plant species twice in a row during a visitation sequence, and the *expected number of plants pollinated* based on pollen contributions from all previous visits to conspecific plants along a visitation sequence. The latter assumes a geometric decay of pollen (i.e. decrease in pollen transfer rates) between visits along the visitation sequence (Bateman, 1947; Harder, 1990).

We expect that the mean number of plants pollinated (per day) in our model differs between metrics considered. Trivially, we expect higher values for *visitation rate* than for *consecutive visits* and *expected number of plants pollinated*, because visitation rate includes all pollinator visits regardless of the position of plant species along each pollinator individual's visitation sequence. In contrast, we expect similar trends in consecutive visits and expected number of plants pollinated, as both these measures take the position of plant species visited along the visitation sequence (and hence the probability of conspecific pollen transfer) into account. A priori, we expected the level of pollinator specialisation to affect pollinator behaviour and plant–pollinator encounter rates, and hence our proxies for pollination. For specialist pollinators, nearly all visits will be consecutive visits to the same plant species. For more generalist pollinators, however, we expect our three proxies for pollination to differ substantially as more heterospecific plant visits occur. All three proxies for pollination are expected to vary in response to the spatial arrangement of plants in the landscape (i.e. with the level of plant intermixing). Furthermore, we expect the level of specialisation to interact with landscape structure in determining pollination success. For example, we expect more consecutive visits to the same plant species in landscapes characterised by no or low plant intermixing, especially for generalist pollinators.

2 | MATERIALS AND METHODS

2.1 | Model characteristics

To address the effects of landscape structure on plant–pollinator interactions, we developed a spatially explicit individual-based model in NetLogo (Wilensky, 1999). The model landscape consists of 1 m × 1 m square patches (i.e. grid cells) covering a 600 m × 600 m large area. This landscape is divided into seven areas (hereafter called habitats), each containing a single plant species, except for one habitat which contains no plants and mimics areas in a landscape without plant species (Figure 1).

Within each habitat, a given proportion (f) of grid cells contains plants and the remaining proportion of grid cells ($1-f$) are empty. Plant densities vary among habitats and simulations. Furthermore, the density of flowers per plant species varies per individual and is randomly sampled from a uniform distribution with range U[4, 16]. Pollinators are also assigned random preferences for plants within their niche and can choose adaptively between plant patches based on the product of plant flower density and plant preference (see Supporting Information, Appendix 1 for examples of plant and pollinator input parameters, Tables 1 and 2). Consequently, less preferred plant species can be more attractive to pollinators if they contain more flowers than more preferred plant species with fewer flowers,

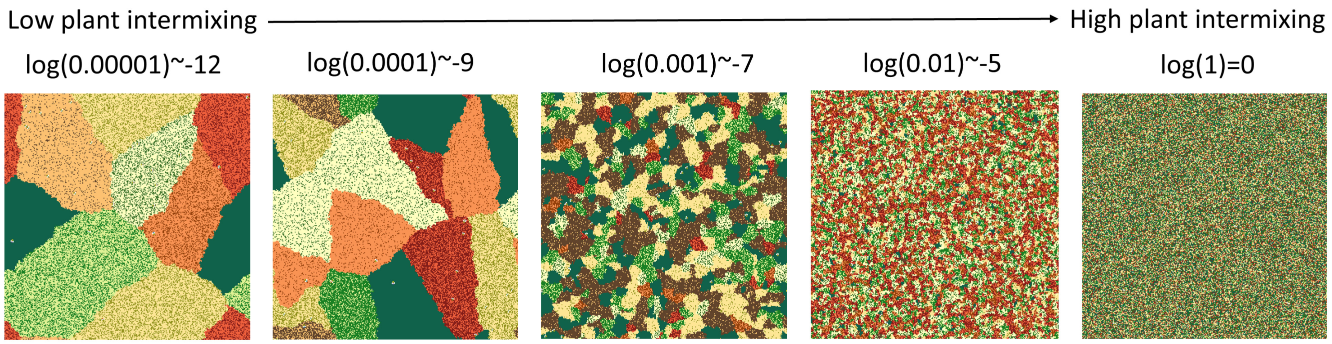

FIGURE 1 Illustrations of five random landscapes with varying levels of habitat plant intermixing. Each landscape contains seven habitats, of which six habitats contain one plant species each. The seventh habitat (dark green one) contains no plant species. The seed percentage, that is, the numbers above each panel, determines how finely grained (clumped or mixed) the plants are within the habitats. Low seed percentage numbers (e.g. 0.00001) generate relatively clumped plant habitats whereas intermediate (e.g. 0.001) and low (e.g. 0.1) seed percentage numbers generate smaller and more plant mixed habitats. Seed percentages equalling one result in maximum plant mixing where each grid is a small ‘habitat’.

TABLE 1 List of model parameters, their definitions and default values.

	Parameters	Definition	Possible values
Pollinators	Pollinator species	Pollinators are divided into species characterised by input parameter values	8
	Number of individuals	Number of pollinator individuals per pollinator species	10
	Sociality type	Pollinator species are divided into four sociality categories: 0 = solitary with no nest, 1 = solitary with nest, 2 = primitively and 3 = eusocial with nest	[0, 1, 2, 3]
	Degree	The pollinator degree (links) is the number of plants a pollinator could possibly visit (its fundamental niche), resulting from random assignment of potential feeding links to achieve a randomly selected network connectance (U[0.16,1]).	[1, 2, 3, 4, 5, 6]
	Preferences	Pollinator plant preferences determine which plants are actually visited, i.e. the realised niche of the pollinator species. They are assigned to the individual feeding links from a uniform distribution and sum to 1	U [0, 1)
	Body size	Pollinator body sizes (intertegular distance) are randomly sampled from a uniform distribution	U [1, 8]
	Perception range	Radius of pollinator perception range (patches)	4
	Perception angle	Angle of pollinator perception range (degrees)	180°
	Flight speed	The number of grid cells moved per time step depends on body size and sociality. Flight speeds (FS) are not constant but randomly sampled from a Poisson distribution with mean flight speed at every time step for every individual	see Appendix 2, Figure S1 for the flight speed distributions per pollinator species
	Movement and turning angle	Pollinators move in a correlated random walk with the turning angle drawn randomly from a normal distribution with mean 0 and standard deviation j	*j* = 90
Plants	Plant species	Plants are divided into different species or taxa	6
	Area	The landscape is divided into different habitats	7
	Plant density	A proportion of grid cells within an area containing a plant	U [0.1, 09]
	Flower number	Number of flowers per plant sampled randomly from a Poisson distribution	U [4, 16]

TABLE 2 Summary table of the GLMM output for the three pollination measures visitation rate, consecutive visit and expected number of plants pollinated, as a function of plant intermixing, pollinator degree including two-way interaction.

pollination ~ log (plant intermixing) * pollinator degree + (1|run)									
	Visitation rate			**Consecutive visits**			**Expected pollination events**		
Predictors	**Incidence rate ratios**	**CI**	***p***	**Incidence rate ratios**	**CI**	***p***	**Incidence rate ratios**	**CI**	***p***
Count model (Intercept)	2544.85	2356.52–2748.24	**<0.001**	3013.50	2758.05–3292.61	<0.001	1652.82	1514.64–1803.62	**<0.001**
seed [log]	1.15	1.14–1.17	**<0.001**	1.17	1.15–1.19	<0.001	1.14	1.12–1.16	**<0.001**
pol degree	1.05	1.04–1.07	**<0.001**	0.84	0.82–0.85	<0.001	0.96	0.94–0.98	**0.002**
seed [log]*pol degree	0.98	0.97–0.98	**<0.001**	0.95	0.95–0.96	<0.001	0.97	0.96–0.97	**<0.001**
Random effects									
σ2	0.59			0.74			0.71		
τ00 run	0.00			0.00			0.00		
N run	2000			2000			2000		
Observations	12,000			12,000			12,000		
Marginal *R*2/conditional *R*2	0.148/NA			0.083/NA			0.075/NA		

p-values in bold are significant (<0.05).

or vice versa. This assumption is supported by empirical findings that plants with high flower densities generally attract more pollinators (Fantinato et al., 2021; Leiss & Klinkhamer, 2005).

Three of the key traits of pollinator species that are known to affect their behaviour are body size, eusociality (Kendall et al., 2022) and foraging niche. Foraging range (FR) and flight speeds (FS) are based on body size and eusociality in our model, as foraging range scales positively with body size according to the allometric function:

$$FR = Y_0 * M^b, \tag{1}$$

where Y_0 is a species-specific constant, M is body mass and b is the allometric scaling exponent (Greenleaf et al., 2007; Kendall et al., 2019). Intertegular distance (ITD) is used as a measure of body size and corresponds to the distance between the wing bases (Cane, 1987). In addition to body size, foraging range also depends on pollinators' sociality (e.g. whether a pollinator is solitary or eusocial), that is, per unit body size (ITD), foraging ranges are larger an increase at greater rate with sociality (Kendall et al., 2022).

To account for the effect of sociality on foraging ranges, pollinators were divided into four sociality categories: solitary with no nest, solitary with nest and primitively and highly eusocial (with nest). The allometric scaling exponent (see Equation 1) differed between sociality categories based on empirical data (see Supporting Information, Appendix 2 for the equations used to calculate foraging ranges for the four groups). Highly eusocial pollinators (e.g. bees) exhibit significantly higher functional foraging ranges than either primitively eusocial (e.g. bumblebees) or solitary nesting bees (Hayes & Grüter, 2022; Kendall et al., 2022). In our study, we also included a solitary, no nest group category (e.g. flies or butterflies) which follow the same allometric relationship between body size and foraging range as solitary bees (Nieminen et al., 1999).

Maximum foraging range (i.e. maximum range from the nest) sets the upper boundary of the range that a pollinator will travel in our model. When a nesting pollinator exceeds its maximum flight range, it will immediately return to its nest (Figure 2). Nest type depends on pollinator sociality. Highly and primitively eusocial species will return to the same nest as their conspecifics whereas solitary species will return to their own individual nest. Pollinators will stay in their nest for as long as it takes to fly from the maximum foraging range back to the nest before they start a new foraging trip (Figure 2). Solitary pollinators without a nest will continue to search for more plants to visit in a correlated random walk. A correlated random walk is a random walk where the direction of a step is chosen by selecting random turning angles relative to the previous step. Small turning angles result in an almost straight line, whereas larger turn angles, closer to 90 degrees, result in agents turning their direction. In contrast to uncorrelated random walks, the correlated random walk results in a more purposeful movement pattern (O'Sullivan and Perry, 2013). The pattern of the correlated random walk is also influenced by the step length or flight speed (grid cells moved per time unit) which, in our model, varies between pollinator species.

The flight speeds (*FS*) are determined by a pollinator's body size and sociality (S), and calculated by dividing maximum foraging range by number of time steps *T* in a day (i.e. 600 time steps) multiplied by an average number of 10 daily pollinator flight trips (*FT*):

$$FS = \frac{FR}{T} * FT. \tag{2}$$

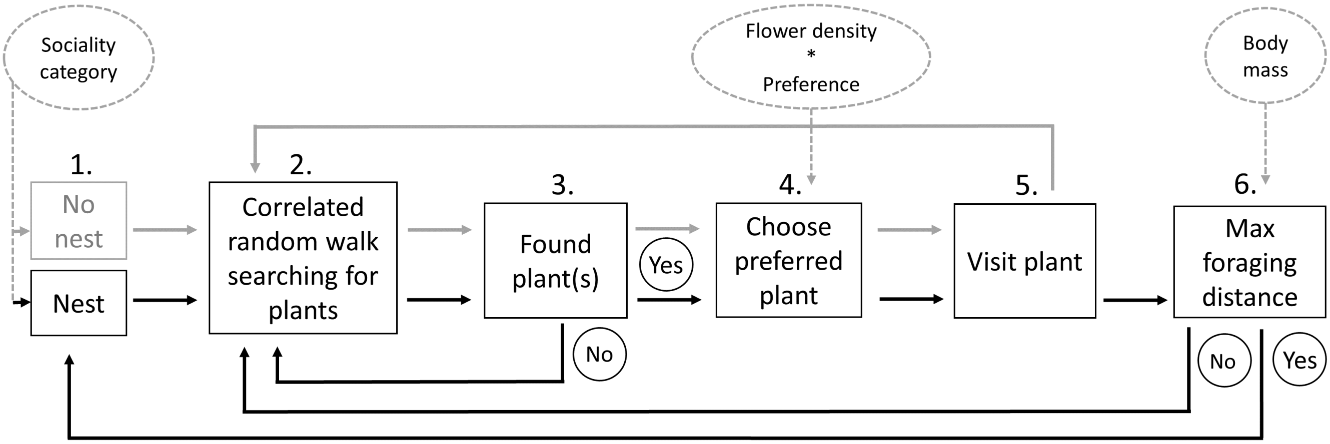

FIGURE 2 Flow diagram of pollinator visits to flowering plants. Step 1: for nesting pollinators, the simulation starts in grid cells containing a nest placed randomly in one of the seven habitats. For non-nesting pollinators, the simulation starts in a random grid cell in the landscape. Pollinators move in a correlated random walk (step 2) until they find one or several plants (step 3). If they find more than one plant, pollinators will choose the most preferred plant (step 4), which is the plant with the highest product of flower density and plant preference score. They move in a straight line to the chosen plant. Pollinators visit the preferred plant (step 5). These visits are recorded and form the bases for calculating visitation rate, consecutive visits and expected number of plants pollinated. If nesting pollinators reach their maximum flight distance (step 6), as determined by their body size and sociality category, then they return to their nest and start the pollination process all over again. Pollinators with no nest have no maximum foraging distance and continue in a correlated random walk. Nesting pollinators follow the black arrows, whereas non-nesting pollinators follow the grey arrows in the flow diagram.

This results in larger pollinators generally travelling faster than smaller pollinators in the same category, an assumption which matches both empirical and theoretical findings (Hirt et al., 2017). Flight speeds are not constant but randomly sampled from a Poisson distribution with mean *FS* at every time step for every individual (Appendix 2, Figure S1; Viswanathan et al., 1999). In our model, one time step represents 1 min and, as 1 day contains 10 h (i.e. a typical daily foraging hour for pollinators, Baldock et al., 2011), a day consists of 600 time steps. Simulations were run for 1 day. The main adaptive steps undertaken by pollinators are illustrated in Figure 2 and outlined in the overview, design concepts and details (ODD) protocol (Supporting Information, Appendix 3).

Another important trait determining a pollinators' foraging behaviour is their degree, or the number of plant species within their fundamental dietary niche. Generalist pollinators have a high degree and can potentially visit many plants, although they have different preferences for each plant within the niche and therefore may act as specialists if they encounter an abundant, highly preferred plant. Pollinators with a degree of 1 are obligate specialists. In each simulation, the fundamental niches of all pollinators (the set of plant species they can visit) and their relative preferences for each plant species were randomly assigned. The relative preferences vary between 0 and 1 and always sum to one. These parameters shape the realised niche (plant visits) of each individual pollinator.

To select a plant from its niche, the pollinator assesses all plants within its perception range, (determined by the radius and angle of perception). It then chooses the most attractive one as defined above, following Benadi and Gaeger (2018), and moves in a straight line to the chosen plant (Figure 2). If more than one plant is equally attractive, the pollinator randomly chooses one among them. If no flowers are within a pollinator's perception range, it continues to move in a correlated random walk, with turning angles drawn from a normal distribution with mean (0) and standard deviation (90) until it perceives at least one plant from its niche (Table 1). After each visit, the plant loses one flower unit and pollinators move at least one step in a correlated random walk, mimicking the realistic scenario where a pollinator is unlikely to return to the same nectar-depleted plant which it has just left.

2.2 | Pollinator species specialisation

To ensure a variety of pollinator specialisation levels, we simulated networks with varying levels of connectance. Connectance, the proportion of potential links that actually occur, is equivalent to the average degree of all pollinators in the system divided by the number of plants. A network with lower connectance therefore contains more specialists and a network with a connectance of 1 contains only generalists able to visit all plants (see Supporting Information, Appendix 4, Figure S2 for example of networks). We simulated networks with connectance values randomly chosen from a uniform distribution between 0.166 (minimum connectance) and 1. Each plant and insect species was required to have at least one interaction to ensure that simulated networks had no disconnected plant species or pollinator species. Pollinator species' *niches*—the set of plants they are able to visit—are derived from these random networks and the degree of each insect is the number of plants in its niche.

In practice, a pollinator may be more specialised than its degree would suggest if it has a strong preference for some plant(s) in its niche. To simulate this effect, we assigned preferences for each plant in each insect's niche. If the insect had a degree of one, the preference for the single plant in its niche was one. If the insect had multiple plants in its niche, a preference was randomly drawn for each plant from U [0, 1). Preferences were then rescaled to sum to 1 for each pollinator. Because of these preferences, an insect may not visit all plants in its niche if more preferred plants are available, and the input preferences for a plant species may differ from the realised preference, the proportion of visits made to the plant species (Supporting Information, Appendix 5, Figure S3). Note that the availability of preferred and non-preferred plants depends on plant flower density, plant intermixing in the landscape and the insect's detection range and insects may therefore also visit less preferred plants if its most preferred plant is not available.

2.3 | Simulation experiments

To test the effect of landscape and pollinator specialisation on pollinator visitation rates and pollination probability, we generated random landscapes with varying levels of plant intermixing using a landscape diversity model (Santos et al., 2020; Wirth et al., 2016). The level of plant intermixing is controlled by a variable called 'seed percentage' (Figure 1). Low seed percentages (0.00001–0.001) create clumped, unmixed landscape structures whereas high seed percentages (0.01–1) create thoroughly mixed structures (see also, Supporting Information, Appendix 6, Figure S4, for the relationship between plant intermixing [log] and size of the habitats [log]). Landscapes with different structures were created by randomly sampling seed percentages from a beta distribution, ensuring that seed percentage values covered the whole range between 0 and 1 and that sufficiently many simulations had less mixed landscapes (seed percentages < 0.01: 50%). The arrangement of habitats between runs with the same seed percentage can differ but have the same average habitat size (i.e. amount of grid cells per habitat). The simulated landscapes consist of seven types of habitats: six containing one plant species each and one being empty. The number of habitats was kept constant between simulations.

To capture the effects of variation in landscape structure on plant–pollinator encounter rates and pollination success for different species of pollinators and plants, we randomly varied five variables between each simulation ($n = 2000$): density of plants within habitats, pollinator body sizes, pollinator degree, pollinator plant preferences and nest locations (Supporting Information, Appendix 1, Table 1). Plant density within a habitat was randomly drawn U [0.1, 0.9]. A plant density in a habitat of 0.1 corresponds to a 10% of the grid cells within that area containing a plant, while the remaining grid cells

(90%) are empty. Differences in plant density simulate differences in plant availability at a given point in time irrespective of whether this difference results from plant rarity or spatio-temporal (phenological) turnover in plant composition. To explore the impact of landscape structure on pollinators' movement patterns, we modelled the relationship between foraging range and pollinator body sizes (ITD) based on allometric functions and empirically derived pollinator body sizes (Kendall et al., 2022). For each pollinator, we randomly assigned ITDs from a uniform distribution with range [1, 8]. Although pollinator body sizes may not be uniform in nature, we chose to sample from a uniform distribution in order to obtain a broad range of pollinator sizes and to avoid dominance of pollinators of certain body size.

2.4 | Pollination measures

We used three distinct measures of pollination to assess how pollination varies with habitat structure and how this change is reflected by the definition of these measures (Figure 3). Note that while we model individual insects, we estimate pollination at the species level (i.e. the total pollination service provided to plant *i* by insect *j*). The first measure, visitation rate, is a count of all visits to a plant species by individuals of a pollinator species during a visitation sequence. This measure is similar to the visitation rate commonly used in empirical plant–pollinator network studies in that it counts all pollination visits by a pollinator to a plant per sampled time unit (here a day) but ignores a pollinator's plant visitation sequence.

To account for a plant's position along pollinator individuals' visitation sequences and thereby improve our estimation of pollination, we calculated two additional pollination measures. First, we calculated consecutive visits, that is, the number of times an individual pollinator visited two individuals of the same plant species in a row, with no visits to other plant species in between. Second, we calculated the expected number of plants pollinated by assuming that conspecific pollen may still be transferred to conspecific plants if other plant species are visited in between visits to conspecific plants (see Supporting Information, Appendix 7, Figure S5 for a worked example). In calculating the latter, we assume that the probability of conspecific pollen deposition declines consistently with the number of steps between a pair of visits to conspecific plants along a pollinator's visitation sequence. This decline occurs because some donor pollen will be lost during transport or while visiting heterospecific stigmas. Following Bateman (1947), this decline in pollination probability was modelled as a geometric decay process. For this, we evaluated the probability that a visitation event resulted in successful pollination according to the following procedure.

For each pollinator individual of a given species in each simulation, we recorded the exact sequence of individual plants visited as $\{p_1, p_2, \ldots, p_n\}$, where p_i is the identifier of the i-th plant individual visited. We then considered each pair of potential pollen donor and pollen recipient individuals, that is, for each p_i visited plant individual with $i = \{0, \ldots, n-1\}$, we computed the probability of successful transfer from p_i to each one of the subsequent j-th conspecific plant individuals in the visitation sequence (i.e. for all p_j individuals with $j > i$).

We computed the probability p_{ij} as:

$$p_{ij} = 0 \text{ if } p_i \text{ and } p_j \text{ belong to different species;}$$

$$p_{ij} = (1-a)^{(j-i)} \text{ if } p_i \text{ and } p_j \text{ belong to the same plant species.} \quad (3)$$

The parameter *a*, which is bounded in [0, 1], determines how the probability of successful pollination decays as the number of intermediate, heterospecific visits in between the target donor p_i and the target recipient plant p_j increases. To avoid adding species-specific bias to our modelling outcome, we held the geometric decay value fixed between species. However, in real-world pollinators, this decay constant may vary between pollinator species due to traits such as pollinator hairiness (Stavert et al., 2016), or due to specific trait matching between a pollinator and plant. We tested the geometric decay process with other geometric decay values (Supporting Information, Appendix 8, Figures S6 and S7). A small decay constant (e.g. 0.1) will resemble the visitation rate metric, as little pollen will be lost between visits, whereas a large decay constant (e.g. 0.9) mimics species that are poor pollinators. We set *a* to 0.3, that is for every visit along the visitation sequence pollination probability declines with 30%. This value is based on empirical observations (Holmquist

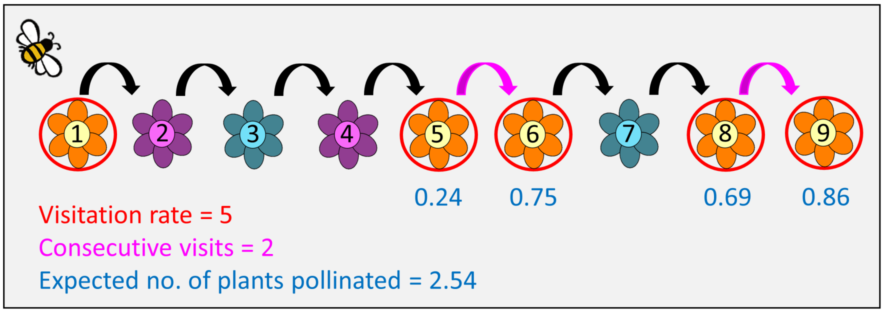

FIGURE 3 Conceptual figure showing estimates of pollination using visitation rate (red circles) and consecutive visits (magenta arrows) to the orange flower by a pollinator individual during a visitation sequence. Together, these visits translate to an expected number of plants pollinated (cyan numbers). The three pollination proxies are thoroughly defined in the text, and a worked example for expected number of plants pollinated is presented in Supporting Information, Appendix 7, Figure S5.

et al., 2012). Our model did not explicitly incorporate species-specific variation in pollinator effectiveness, but such variation could be included as species-specific or individual-specific geometric decay values (see Supporting Information, Appendix 8). Nonetheless, we did incorporate flower constancy implicitly, by modelling variation in pollinator preferences. As a result, the proportion of visits made to a plant species (the effective or realised niche) can be higher than the input preference, the fundamental niche (see examples of individual pollinator visitation sequences in Supporting Information, Appendix 5).

Next, we aggregated all the p_{ij} values computed across all visitation sequences by a pollinator species for a given plant individual *v*. We then used those values to quantify the overall probability that the target plant individual was successfully pollinated during the simulation by a pollinator species. Assuming that a given plant individual had been visited *n* times by a pollinator species in the simulation, we associated with that plant the corresponding list of probabilities $\{p_{v1}, p_{v2}, \ldots, p_{vn}\}$. Thus, for each i-th visit of a target pollinator species to a plant individual *j*, the probability that the visit does not result in successful pollination would be equal to $(1 - p_{ji})$. The product of all $(1 - p_{ji})$ values for all the *i*-th visits received by the *j*-th plant corresponds to the overall probability that none of the visits result in successful pollination. Therefore, the probability that the plant will be successfully pollinated will be equal to 1 minus the probability that all pollination attempts fail, that is:

$$P_j = 1 - \prod_{i=1}^{n} \left(1 - p_{ji}\right). \tag{4}$$

We summed the *Pj* values for all *j* individuals belonging to the target plant species to obtain an estimate of the number of individuals (of that plant species) successfully pollinated by the target pollinator species within a simulation. Finally, we averaged these values to obtain the mean expected number of pollinated individuals of a plant species by pollinator species per simulation (Supporting Information, Appendix 7, Figure S5). The resulting pairwise plant–pollinator pollination probability estimates were further averaged per plant species per simulation and then used in the statistical analyses.

2.5 | Statistical analyses

To resolve how pollinator specialism (i.e. degree, the number of plants a pollinator could feasibly visit) affects the amount of pollination service that species delivers in different landscape structures, we modelled each proxy for pollination per plant species as a function of log plant intermixing, of pollinator degree (mean degree of the focal plant's pollinators) and of the two-way interaction between these main effects using three GLMMs. To test how pollination relates to the average specialisation of all pollinators in the network, we fitted a similar series of three GLMs including plant intermixing, connectance and the interaction between them (Supporting Information, Appendix 9). Furthermore, to investigate how a plant's density and the specialism of its pollinators might interact to affect pollination, we fitted an additional set of models including pollinator degree (the mean degree of the focal plant's pollinators), plant density and the two- and three-way interactions between these main effects using three GLMMs. To account for differences in pollinator parameters (e.g. pollinator plant preferences, sociality category and body sizes) among simulations, *run* (i.e. simulation number) was included as a random effect in all GLMMs. The raw values behind the predicted relationships between pollination proxy, pollinator degree and seed percentage can be found in the Supporting Information, Appendix 10, Figures S9–S11. To explore how the other traits included in our model affect pollination, we fitted a supplemental similar series of GLMMs relating pollination to body size and sociality category, a measure of how movement patterns (no nest vs. nesting, foraging distance and flight speeds) associated with these traits influence pollination metrics (Supporting Information, Appendix 11, Figure S12).

Due to overdispersion in the data, we used a negative binomial distribution with a log-link function to estimate the mean and the dispersion in the GLMMs. Because we were interested in the change in pollination metrics per original unit, we did not scale the predictor variables. To evaluate the goodness of fit of the negative binomial regressions, Nagelkerke's pseudo-*R* squared were calculated (Nagelkerke, 1991). All computations and statistical analyses were performed in R version 4.1.2 (R Core Team, 2021) using custom-written code and available R packages. Generalised linear models were fitted using the nb.glm() function in the R package MASS (Venables & Ripley, 2002). The generalised linear mixed effect models were fitted using the GLMMTMB R package (Brooks et al., 2017). Residuals were checked with the R packages PERFORMANCE (Lüdecke et al., 2021) and DHARMa (Hartig, 2019). Connectance was calculated using the BIPARTITE R package (Dormann et al., 2009). Data were processed and figures plotted using tidyverse (Wickham et al., 2019).

3 | RESULTS

3.1 | Performance of visitation rate as a proxy for pollination

Our three proxies for pollination responded quite differently to changes in landscape and pollinator specialisation. In particular, visitation rate nearly always increased with plant intermixing (Figures 4a and 5a) regardless of pollinator degree (except for pollinator degree 6). Consecutive visits and expected conspecific pollen transport had varying responses depending on pollinator degree (Figure 4b,c). In general, the number of consecutive visits and expected number of plants pollinated showed more similar trends to each other than to visitation rates. Visitation rate nearly always overestimated the number of pollination visits compared to the more functional metric,

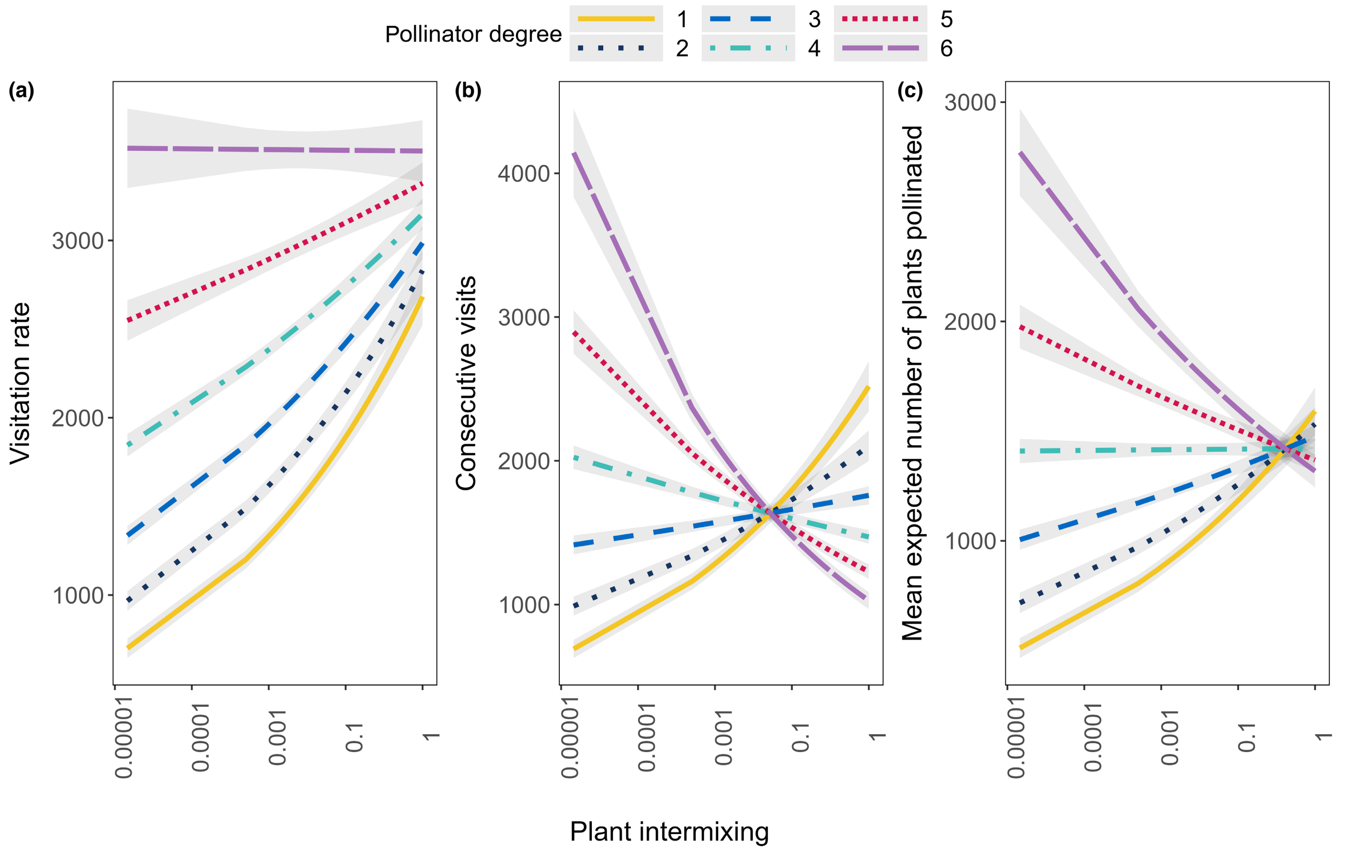

FIGURE 4 GLMM predicted mean pollination measures for the three pollination measures per plant species: (a) mean visitation rate, (b) mean consecutive visits and (c) mean expected number of plants pollinated as a function of the combined effects of plant intermixing and mean degree of a plant's pollinator (indicated by line colour and linetype). The shaded grey areas indicate the confidence intervals of the predictions. The plant intermixing values on the *x*-axes are log transformed, but the original values are shown in the figure. Consult figure 1 for more details on the plant intermixing variable, seed percentages and the resulting landscape structure.

expected number of plants pollinated, in particular in intermixed landscapes and for generalist pollinators.

3.2 | Pollinator specialisation determines differences between metrics

Degree, as a measure of pollinator species specialisation, strongly affected the responses of all three metrics to changes in the landscape (Table 2). Generalist pollinators tended to make more visits (purple, long-dashed line Figure 4a), but their number of consecutive visits to the same plant species depended strongly on the level of plant intermixing (Figure 4b). Generalist pollinators also had high expected numbers of plants pollinated in habitats with low plant intermixing (Figures 4c and 5c). Interestingly, Figure 4a shows that in terms of number of visits to plants, generalists with a degree of 5 and 6 are less affected by landscape structure than pollinator species with a lower degree. Specialist insects had much lower visitation rates but made many more consecutive visits in landscapes with high plant intermixing, leading to high numbers of expected plants pollinated (Figure 4). Connectance—as a measure network-level specialisation—similarly affected all three metrics (Supporting Information, Appendix 9, Figure S8).

3.3 | Specialisation interacts with plant density in determining pollination outcomes

As with plant intermixing, specialisation (pollinator degree) also interacted significantly with plant density (Table 3). The three-way interaction between these variables was only significant for consecutive visits and expected number of plants visited (Table 3).

Visitation rate generally increased with increasing plant intermixing and increasing plant density, but this increase was stronger at high plant densities and for more specialist pollinators (Figure 5a). For specialists, the number of consecutive visits and expected number of plants pollinated followed the trend of visitation rate (Figure 5b,c).

For generalists, conversely, the number of consecutive visits decreased with increasing plant intermixing (Figure 5b) and the expected number of plants pollinated shows a similar, but less severe trend (Figure 5c). The difference between these two proxies strongly illustrates the tendency for generalists to visit conspecific plants non-consecutively in mixed landscapes. For most pollinators

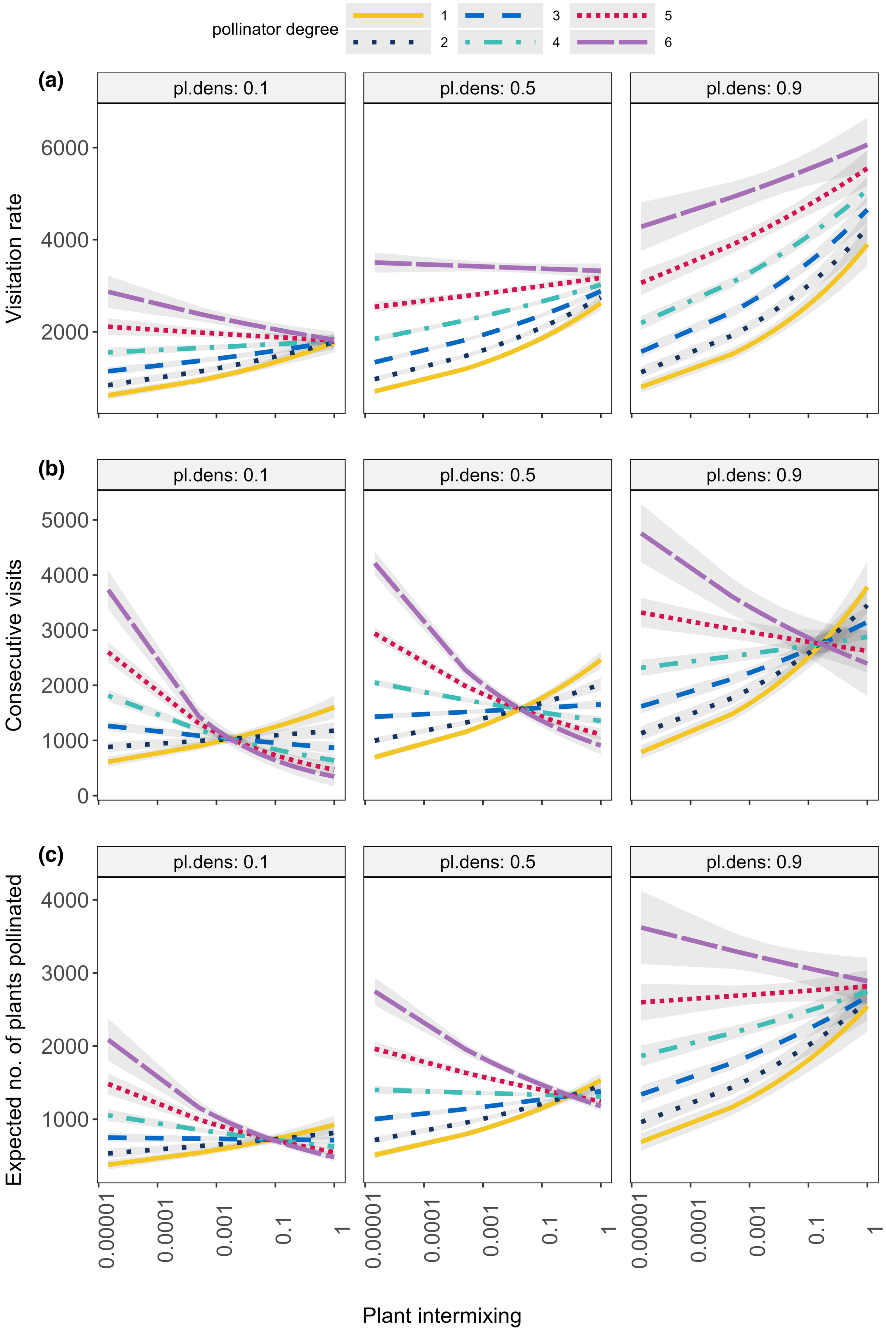

FIGURE 5 GLMM predictions of changes in pollination measures per plant species for (a) visitation rate, (b) consecutive visits and (c) expected conspecific pollen transfer as a function of plant intermixing, pollinator degree (mean degree of a plant's pollinators; line colour and linetype) and varying plant density levels (0.1, 0.5 and 0.9). The shaded grey areas indicate the confidence intervals of the predictions.

(degree 1–4), at high plant densities (0.9), expected number of plants pollinated increased with plant intermixing as with visitation rate (Figure 5c), indicating that the visitation sequence has less of an impact on the expected number of plants pollinated when flowers are abundant.

4 | DISCUSSION

By constructing an individual-based model, we were able to formalise and explore the effects of landscape structure and pollinator specialisation on pollination outcomes in spatially explicit landscapes. While we started from a relatively simple model, we managed to test fundamental predictions hard to address for empirical research—and found support for each. Overall, we found visitation rate to be only weakly related to the metrics of consecutive visits and expected number of plants pollinated. Moreover, each proxy for pollination responded differently to pollinator specialisation and landscape structure (plant intermixing). We also found that pollinator specialisation and landscape structure interact to shape pollinator behaviour: for example, in landscapes where plant species are highly intermixed, movement by generalists often occurred between heterospecific rather than conspecific plants (including less-preferred plants) whereas specialists kept moving between conspecific plants even though these journeys were longer. The spatial arrangement of plants is therefore important in shaping pollination

TABLE 3 Summary table of the GLMM output for the three pollination measures: visitation rate, consecutive visit and expected number of plants pollinated, as a function of plant intermixing, mean degree of a plant's pollinator (pol degree) and plant density (pl dens) including two- and three-way interactions.

pollination ~ log (plant intermixing) *pollinator degree*plant density + (1|run)									
	Visitation rate			**Consecutive visits**			**Expected pollination events**		
Predictors	**Incidence rate ratios**	**CI**	***p***	**Incidence rate ratios**	**CI**	***p***	**Incidence rate ratios**	**CI**	***p***
Count model (Intercept)	1599.69	1332.93–1919.82	**<0.001**	2010.40	1629.20–2480.79	**<0.001**	948.46	771.07–1166.67	**<0.001**
seed [log]	1.12	1.08–1.15	**<0.001**	1.15	1.11–1.19	**<0.001**	1.12	1.09–1.16	**<0.001**
pol degree	1.00	0.95–1.04	0.887	0.72	0.68–0.75	**<0.001**	0.86	0.82–0.91	**<0.001**
pl dens	2.44	1.75–3.41	**<0.001**	2.24	1.52–3.29	**<0.001**	2.91	1.99–4.25	**<0.001**
seed [log]*pol degree	0.97	0.97–0.98	**<0.001**	0.94	0.93–0.95	**<0.001**	0.96	0.95–0.97	**<0.001**
seed [log] * pl dens	1.05	1.00–1.11	0.064	1.04	0.98–1.11	0.193	1.03	0.96–1.09	0.407
pol degree * pl dens	1.11	1.02–1.20	**0.015**	1.31	1.19–1.44	**<0.001**	1.22	1.11–1.33	**<0.001**
(seed [log] * pol degree) * pl dens	1.01	0.99–1.02	0.405	1.02	1.01–1.04	**0.003**	1.02	1.00–1.03	**0.022**
Random effects									
σ2	0.57			0.70			0.67		
τ00 run	0.00			0.00			0.00		
N run	2000			2000			2000		
Observations	12,000			12,000			12,000		
Marginal *R*2/conditional *R*2	0.205/NA			0.191/NA			0.194/NA		

p-values in bold are significant (<0.05).

success in networks with a given level of specialism. Below, we will examine each finding in turn.

4.1 | Performance of visitation rate as a proxy for pollination

Across landscapes of different composition, we found clear differences in the pollination patterns between visitation rate and consecutive visits and expected number of plants pollinated. These differences reflect the fact that visitation rate ignores the sequence of visitation by individual pollinators, a key part of the pollination process (Ne'eman et al., 2009). As preceding visits to pollen donors might have been to heterospecific plant individuals, the probability of conspecific pollen transfer between flowers of the same plant species, and hence successful pollination, can be relatively low despite a high visitation rate. Indeed, empirical studies have shown that higher visitation rates in landscapes with mixed plant species may increase heterospecific pollen deposition and lower conspecific pollen transfer because of pollinators switching between plants (Morales & Traveset, 2008).

Our results suggest that visitation rate provides an unreliable proxy of plant pollination; that is, higher visitation rates do not directly translate into more conspecific pollen reaching a plant. While it has been empirically shown before that visitation rate overestimates pollination (de Santiago-Hernández et al., 2019), our model opens for explorations of how landscape configurations and pollinator traits interact to influence effective pollination based on individual-level pollinator visitation sequences and how they unfold in a spatial context. This allows assessing under exactly which circumstances (landscape configurations and pollinator degrees) visitation rate severely overestimates or may even approximate effective pollination. Hence, our general finding does come with two explicit caveats. There are situations in which visitation rate still parallels pollen transfer with reasonable accuracy. For example, if pollinators are highly specialised on a given plant, then the total number of visits will be closely related to the number of consecutive visits, which will reflect pollen transfer rates. In our simulations, this was the case for highly specialised pollinators (similar slopes in yellow solid lines in Figure 4b,c). Moreover, in landscapes with high plant densities, the ease of detecting nearby conspecific plants resulted in high visitation rates, many consecutive visits and higher estimated pollen deposition for generalists as well as specialists (Figure 5a–c, panels to the left). Thus, visitation rate can be used with greater confidence in highly specialised or very plant-dense systems. Another example where visitation rate could be a good proxy for pollen deposition is in plant species whose flowering periods do not overlap with the peak flowering time of the plant community, for example, plant species that flower at the beginning or end of the community's flowering season. Dominance in flowering by one plant in a community will lead to more consecutive visits to this flower species and hence to higher expected number of plants pollinated.

Second, we stress that pollen transfer is but one among several functional outcomes of plant–pollinator interactions. From an insect perspective, counts of visits to flowers and links describing what flowers are visited and with what frequency can provide perfectly valid representations of expected nutrient intake by pollinators regardless of visit order. Thus, we do not question visitation-based network representations as such, but aim to bring clarity to what ecological processes they truly represent.

4.2 | Pollinator specialisation determines differences between metrics

Pollinator specialisation strongly shapes the way in which landscape structure affects plant–pollinator interactions. High plant specificity (pollinator specialisation) implies a low frequency of pollinator switching between plant species, even when plants are highly intermixed. This means that most of each pollinator's visits are to the same plant and that visitation rate, number of consecutive visits and expected number of plants pollinated all show similar trends (similar slopes in yellow solid and black dotted lines in Figure 4a–c). Low plant specificity (generalisation), in contrast, implies the potential for frequent switching between plants. This means that pollen deposited during any given visit is likely to be mixed; in empirical studies, heterospecific pollen may constitute up to 70% of the pollen load (Arceo-Gómez et al., 2019). Heterospecific pollen deposition may decrease plant fitness and reproduction through several mechanisms, including the clogging of stigma, allelopathic inhibition of pollen tube growth, takeover of ovules etc. (Morales & Traveset, 2008), resulting in decreases in plant reproductive success (Ashman & Arceo-Gómez, 2013). Nonetheless, some studies also report positive (facilitative) effects, suggesting that impacts may vary between plant species and habitats (Morales & Traveset, 2008). For example, one recent study found increasing conspecific pollen loads on stigmas with increasing heterospecific pollen diversity, possibly reflecting higher per-flower pollinator visitation rates in more plant-diverse communities because of increased pollinator recruitment. The effects of these increased visitation rates can surpass the dilution effect of heterospecific visits (Gavini et al., 2021). Such effects may be particularly pronounced in harsh environments (e.g. at high altitudes), which are relatively poor in terms of both plant and pollinator species (Gavini et al., 2021). Another mechanism that may reduce the negative impacts of heterospecific pollen loads is pollen specificity mediated through pollen–pistil interactions making the sequence of prior visitation by the pollinating agent less important (Broz & Bedinger, 2021).

4.3 | Specialisation interacts with landscape structure in determining pollination outcomes

Co-flowering of nearby heterospecific plants can induce pollinator-mediated competition (Tiusanen et al., 2020; Waser, 1978). Rare plant species may be more vulnerable to competition in plant intermixed landscapes because visits to rare flowers are likely to be followed by pollen-wasting visits to other plant species (Palmer et al., 2003). Our model corroborates this finding as pollen transfer among less-abundant (densities <10%) plant species declined with plant intermixing unless pollinators were highly specialised (Figure 5, panels on the left). This implies that rare plant species can maintain reproductive success and co-exist with more abundant plant species despite their low densities in inter-mixed plant landscapes, if they are associated with specialised pollinators. Such a relation appears very interesting because, while it is often assumed that specialism is a cause of rarity in plants and pollinators, our results suggest that rarity itself may favour specialism (Goulson et al., 2005). Our model also shows that if plants are rare but clumped together in space, it could be an advantage for such plants to be associated with pollinator generalists, since rare plants may be harder to encounter by chance. Being able to visit alternative plants may allow generalists to perform relatively many conspecific visits and hence transfer conspecific pollen between individuals of these rare but spatially aggregated plant species.

Intriguingly, at very high plant densities, generalist pollinators with degree 4 can behave like specialists (Figure 5 panels on the right), as the number of visits and the expected number of plants pollinated increased with plant intermixing for both generalists and specialists. This is likely because generalist pollinators make more consecutive and near-consecutive visits to their preferred plants when these plants grow at high density.

As well as with specialisation and landscape structure, the other traits we included in our model (body size and sociality) influenced pollinator behaviour and the amount of pollination that results from it (Supporting Information, Figure S12, Appendix 11). In particular, smaller pollinators tended to make more consecutive visits to the same plant species while larger pollinators tended to achieve higher numbers of effective pollination events. This is likely because, in our model, small pollinators tend to remain within the same patch of plants while larger pollinators may frequently change patches, visiting different plant species. The different trends for consecutive visits and expected pollination with respect to body size also highlight the importance of considering the whole visitation sequence, not merely the immediately preceding visit. Unless the rate of pollen loss between visits is very high, a visit to the same plant species with two or three stops to other plant species in-between may still provide an important pollination service. We also note that, while pollinator size and sociality affected all three of the pollination metrics, different insect taxa tended to respond to changing plant intermixing in similar ways. This implies that a model which incorporates insect traits, but neglects landscape structure is unlikely to predict pollination successfully.

The mechanisms by which landscape composition and pollinator specialisation interact to shape pollination may become increasingly important as anthropogenic changes such as land-use conversion and climate change disrupt co-evolved plant–pollinator associations. For example, specialist pollinators may decline at the expense of generalist pollinators (Biesmeijer et al., 2006; Goulson et al., 2005). According to our model, this can result in increasing heterospecific pollen transfer and hence an overall decline in pollination success. At a larger scale, this may influence plant population dynamics, abundances and distributions (Ashman et al., 2020).

5 | CONCLUSIONS

The analyses presented in this study clearly demonstrate that the choice of pollination metric, and its underlying assumptions, affects the interpretation of the ecological impact. For example, pollination success, measured as *consecutive visits* and *expected number of plants pollinated*, may decrease in landscapes with higher plant intermixing—even if visitation rate increases. Generally, direct counts of the classic visitation rate overestimate proxies for pollination which include information about a pollinator individual's visitation sequence. This overestimation is particularly severe in highly mixed plant landscapes and for generalist pollinators. Hence, measures more reflective of the functional, individual-based aspects of plant–pollinator interactions and pollination should ideally be applied to assess the consequences of pollinator traits from a plant perspective. Importantly, this does not invalidate the utility of plant–pollinator networks as such since they provide valuable descriptions of insect nutrition and its sources across plant species. Recording insect visits also narrows down the field of potential pollinators of a given plant species. However, in order to grasp pollination from the plant's perspective, we should ideally supplement visitation-based methods with observations of proxies closer to pollen transfer. While following insects in the field is vastly more complex than simulating them in silico, we see three particularly promising avenues for future research. First, rates of pollen transfer can be mimicked by rates of transfer for dyed particles (Carper et al., 2016; Howlett et al., 2017; Schmidt-Lebuhn et al., 2019). By dyeing plants of different species with different colours, one can then estimate rates of conspecific pollen transfer under field conditions. Second, the pollen loads carried by individual pollinators carry information on their visitation history, and thus of their movement trajectories. Such pollen loads can be dissected by either traditional microscopy (Orford et al., 2015; Tiusanen et al., 2020) or by rapidly emerging methods for the DNA metabarcoding of pollen loads (Bell et al., 2017; Lowe et al., 2022). Third, our simulations yield conveniently testable predictions: that the composition of pollen loads of a given pollinator species should vary with differences in the spatial arrangement of plants in the landscape and pollinator traits, reflecting differences in individual pollinator movement trajectories. We hope and trust that future studies will follow these leads, and bridge work in silico to outcomes *in natura*.

AUTHOR CONTRIBUTIONS

Susanne Kortsch, Giovanni Strona, Alyssa R. Cirtwill and Tomas Roslin conceived the project. Leonardo Saravia and Susanne Kortsch designed and developed the individual-based simulation model. Liam

Kendall provided data and allometric functions to parameterise the model. Giovanni Strona and Susanne Kortsch wrote the algorithms on pollination success and performed the simulations. Susanne Kortsch analysed the data in close consultation with all co-authors. Susanne Kortsch, Alyssa R. Cirtwill and Tomas Roslin wrote the first draft of the manuscript. All authors contributed to manuscript completion and revision.

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CONFLICT OF INTEREST STATEMENT

We declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The individual-based *NetLogo* model (Saravia & Kortsch, 2022), data and R scripts are downloadable from GitHub: https://github.com/skortsch/NLmodelAnalyses via NLmodelAnalyses-v1.0.0, Zenodo: https://doi.org/10.5281/zenodo.6701564.

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SUPPORTING INFORMATION

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

Appendix 1. Examples of parameter values.

Appendix 2. Body size, foraging range and flight speed.

Appendix 3. Overview, Design concepts, Details protocol.

Appendix 4. Examples of network connectance, pollinator degree and preferences.

Appendix 5. Pollinator visitation sequences and fundamental vs. realized niches.

Appendix 6. Relationship between seed percentage and habitat size.

Appendix 7. Expected number of plants pollinated.

Appendix 8. Geometric decay constants and expected no. of plants pollinated.

Appendix 9. Relating pollination to connectance.

Appendix 10. Raw values behind the relationship between pollination visits, plant intermixing, and pollinator degree.

Appendix 11. Relating pollination to body size and pollinator sociality.

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