

How movement across landscapes mediates species-resource interactions

by

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Abstract

This thesis explores how movement across spatially explicit landscapes mediates species-resource interactions. Firstly, I model pollinator foraging across agricultural landscapes, looking at the effect of different movement strategies on plant-pollinator dynamics. I also examine the effect of hedgerow spatial distributions and value on crop pollination. I find that a simple exponential foraging model serves as a reasonable approximation for more complex bee foraging, whether or not hedgerows are higher value than the crops that they surround. I find that when pollinators cannot nest in crop regions, crop pollination is more complete with increasing hedgerow size, with little effect of fragmentation. Secondly, I look at the evolution of over-exploitation of prey by predators in a patchy landscape with varying amounts of connectivity. I find that as the landscape becomes more structured, either through increasing the number of connected patches or decreasing the connectivity between patches, predator populations do not decline as much while evolving.

Keywords: landscape ecology; movement ecology; predator-prey; pollination; evolutionary ecology

Dedication

To my dog Banjo, who provided essential emotional support and levity, and who is very cute.

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Chapter 1

Introduction

Species interactions are complex narratives where the outcome depends on the arena in which they occur. This arena might include other species, seasons, variable population densities, and, what I will focus on here, the spatial landscape. The various characteristics of a landscape can have myriad effects on the population densities of species and the relationships between them. For example, the area and degree of isolation of a patch has a direct influence on the number of species that persist within that patch Macarthur and Wilson (1967). Similarly, the amount of movement across the landscape has important consequences for ecological communities. For example, the amount of movement between two isolated patches with different sizes and resources concentrations will change the number and types of species within each patch Macarthur and Wilson (1967). Landscapes can also impact the ecological relationship between a pair of species, such as a plant and its pollinator.

In the Chapter 2 of this thesis, I examine the complex relationship between wild pollinators and plants in an agricultural setting (or many species of plants and many species of pollinators). The amount of habitat dedicated to native flowers and the distance that crops are from these native flowers both tend to increase the presence of wild bees within agricultural landscapes (Garibaldi et al., 2011, 2013; Kremen and M'Gonigle, 2015; M'Gonigle et al., 2015). However it is not well understood how management that attempts to increase wild bee abundance might impact crop pollination; many studies suggest that native flower strips (hedgerows) increase crop pollination

(and, therefore, fruit production) while others show that they decrease crop pollination (Blaauw and Isaacs, 2014; Bishop et al., 2023; Clausen et al., 2022; Nicholson et al., 2019; Ricketts, 2004). Importantly, the spatial arrangement (e.g., many small vs few large) and location (e.g., within fields vs at field margins) of hedgerows may impact both pollinator population dynamics and the pollination services provided by those pollinators (Brosi et al., 2008; Keitt, 2009; Lonsdorf et al., 2009; Nicholson et al., 2019).

I explore the interaction between pollinator movement and landscape structure. Because pollinators are central place foragers (returning to their nest between foraging bouts), many important theoretical examinations of pollinators in agricultural landscapes assume that pollinator visitation simply declines exponentially with increasing distance from the pollinator's nest (Brosi et al., 2008; Keitt, 2009; Lonsdorf et al., 2009; Nicholson et al., 2019). While such an approach seems plausible, pollinator foraging behaviour is not random (Williams and Tepedino, 2003; Fragoso et al., 2021). There are also models of non-random foraging based on the distribution of resources on the landscape, though they look at a narrow measure of pollination services (Nicholson et al., 2019). Here I ask whether inferences about optimal hedgerow restoration design differ when one considers explicit models of pollinator foraging, rather than the traditional random foraging. I use a simulation model to compare a random diffusion-based model of pollinator foraging to progressively more complex foraging models. I also vary the landscape structure, specifically the proportion of landscape that is allocated to hedgerows and the spatial distribution of these hedgerows.

Eco-evolutionary feedback depends not only on the relationship between two or more species, but also upon the relationship between these species and their landscape. The number and connectivity of patches influences the outcome of evolution on key ecological traits, for example virulence & resistance (host-pathogen systems), cooperation, and attack rate (predator-prey systems) (Kerr et al., 2006; Fletcher and Doebeli, 2009; Eshelman et al., 2010; Leggett et al., 2017). In particular, in a single-well mixed patch, predators have been shown theoretically to evolve to over exploit their target prey, resulting in their own population decline (so-called adaptive decline) (Abrams, 2019). However in an empirical study on multi-patch systems in a plant-herbivore system (in which the herbivore is analogous to a predator, and the plant to prey) found that in some scenarios, high

rates of movement led to higher rates of population growth and reduced herbivore carrying capacities after adaptation (Bisschop et al., 2022). However, the exact relationship between the patch spatial connectivity and adaptive decline was not well resolved (Bisschop et al., 2022).

I use a predator-prey model to test whether predator evolution can lower population sizes and potentially lead to extinction of predators through the over-exploitation of their prey. I then ask whether dynamics in multi-patch landscapes might rescue predators from this effect. I then ask whether increasing or decreasing the rate of movement between patches might modulate the adaptive decline.

Both chapters in this thesis explore how movement across spatially explicit landscapes mediates species-resource interactions. In the first chapter I model pollinator foraging patterns across agricultural landscapes, looking at the effect of different movement strategies on the relationship between the pollinators and plants (hedgerow and crop). I also examine the effect of different spatial arrangements and relative values of hedgerows on the pollination of crops. In the second chapter I look at the evolution of over-exploitation of prey by predators in a patchy landscape with varying amounts of connectivity. In both cases I hope to provide useful predictions for resource usage in ecologically motivated scenarios.

Chapter 2

Spatial optimization of hedgerows under different assumptions of pollinator foraging

2.1 Introduction

Pollination represents an important ecosystem service for both wild plant communities and agricultural production (Potts et al., 2010; Ollerton et al., 2011). Thirty-five percent of crops grown for human consumption are dependent on animal pollinators (Klein et al., 2007). Crop pollination is performed by both wild pollinators as well as managed pollinators, such as the European honey bee (*Apis mellifera*) (Potts et al., 2010). However, populations of both wild and managed pollinators are declining globally (Potts et al., 2010; Goulson et al., 2015). Habitat loss, fragmentation, and degradation due to agricultural intensification and urbanization represent significant drivers of population declines (Potts et al., 2010; Goulson et al., 2015; Sánchez-Bayo and Wyckhuys, 2019). The conversion of landscapes to intensive agriculture has been highlighted as a significant driver of insect declines, including for Hymenoptera (Sánchez-Bayo and Wyckhuys, 2019). Even when honey bees are present in high abundance, wild pollinators still significantly contribute to pollination services of crops (Garibaldi et al., 2011). This service is highest when the agricultural landscape is geographically near to natural, florally diverse areas, and decreases with increasing isolation from these natural areas (Kremen et al., 2002; Garibaldi et al., 2011, 2013).

One method of incorporating natural habitats into agricultural landscapes is via planting of hedgerows. Hedgerows are typically strips of native, woody, flowering shrubs and trees at the edges of farm fields, where they usually do not remove arable land from production. They serve multiple functions such as signifying farm boundaries, providing wildlife habitat, managing livestock roaming, and mitigating soil erosion. In this study we use the term “hedgerow” as an umbrella that also includes various other natural habitat fragments or floral “enhancements” such as remnants of natural habitat that have not been converted for agricultural production or herbaceous annual flower amendments. Hedgerows have been shown to significantly increase occurrence of native bee and hover fly pollinators (Kremen and M’Gonigle, 2015; M’Gonigle et al., 2015).

While hedgerows bolster pollinator populations, they may not increase pollination services in agricultural fields if pollinators prefer to forage on those hedgerows over the adjacent crops. Optimal foraging theory posits that animals will forage in a manner that maximizes the reward gained per unit effort used to access that reward (Charnov, 1976). Because hedgerows are often chosen to contain plant species that are attractive to bees, it is probable that these plants are also highly rewarding. This could mean that hedgerows might even draw bees out of the adjacent croplands. Empirically, there is conflicting evidence. For example, hedgerows composed of large flowering shrubs in apple orchards were associated with decreased wild bee abundance when compared to unmanaged edges with similar floral cover and, overall, the hedgerows had no effect on fruit production (Bishop et al., 2023). Clausen et al. (2022) found that hedgerows were not associated with increased wild bee abundance or diversity, and did not offer increased foraging habitat, compared to remnant hedgerows and grassy margins. In contrast, wildflower plantings adjacent to cultivated highbush blueberry increased the presence of wild bees and syrphid flies in adjacent fields and, over several years, crop production was increased (Blaauw and Isaacs, 2014). Similarly, Ricketts (2004) found that tropical forest fragments within coffee plantations maintained pollinator visitation to coffee, though a riparian strip in the same area supported much lower pollination services. One potential explanation for the lack of consistency among these studies might be differences in the relative values of the hedgerows compared to the adjacent crops, or the spatial

arrangements and sizes of the amendments. For example, whether or not the hedgerows are situated at the margins of fields, as is typical, or are small inclusions within fields.

Existing spatial models of hedgerow design aim to identify the optimal size and distribution of natural habitat plantings in agricultural landscapes, as well as the amount of pollination services likely to result from these amendments (Brosi et al., 2008; Keitt, 2009; Lonsdorf et al., 2009; Nicholson et al., 2019). Using a one-dimensional spatial landscape, Brosi et al. (2008) concluded that the optimal farm layout should involve the inclusion of a few large natural patches as population reservoirs, as well as smaller, central patches to facilitate continuous pollination services throughout the field. Using a 2-dimensional spatial model, Keitt (2009) showed that, as long as the crops provide pollen as a food source for pollinators, up to 90% of agricultural land can be allocated to crop use. Both of these models assume simple models of pollinator foraging, namely that pollinators, which are central place foragers, exhibit simple foraging rules and an exponential decay of visit frequency as one moves away from the nest site (Brosi et al., 2008; Keitt, 2009; Lonsdorf et al., 2009). Central place foraging models have also been used to predict the change in pollination services with the addition of floral amendments and/or nesting amendments (Nicholson et al., 2019). Nicholson et al. (2019) used a linear predictive model to estimate the change in pollination services when either floral (foraging) habitat, nesting habitat, or both were added to a landscape. Based on a regression model built out of a central place foraging model that weighs distance travelled vs quality of habitat and maximum distance travelled, they found that hedgerows which, in their model, function only as a source of food resources (so, no nesting resources), distracted pollinators from foraging on and, therefore, pollinating crops (Nicholson et al., 2019). Nicholson et al. (2019) also found that, at a *landscape* level, changes in pollination services are relatively well modelled using a distribution of pollinators, where pollination rates decline exponentially with distance from the nest site. On a more *local* scale, however, they found a central-place foraging model that incorporated specific bee behaviours better captured rates of pollination services.

Here, we seek to understand how explicit foraging behaviours of pollinators might alter predictions of optimal designs of hedgerow and/or native flower plantings in agricultural landscapes. We use an individual-based simulation model to track both the population density of wild bees

and plants, and the associated pollination services they provide. We consider a series of increasingly complex foraging models, each incorporating additional aspects of bee behaviour and movement. In particular, we are interested in assessing how conclusions about optimal hedgerow design might differ when one uses an exponential-style central-place foraging model (as used in Keitt, 2009) versus more explicit rules-based foraging models, like that used by Nicholson et al. (2019). We contrast levels of provided ecosystem services across different hedgerow spatial distributions (size and degree of fragmentation) in order to assess how sensitive our conclusions are to attributes of the landscape.

2.2 Methods

We track the number of bees, wild plants, and pollinator visits to those plants across time over a set of agricultural landscape configurations. In order to make our findings comparable to earlier work, we largely base our model on that developed in Keitt (2009). The model was written and developed in R (Team, 2022).

Each season proceeds with the following sequence of events:

1. Bees forage across the landscape and some plants are pollinated.
2. Larvae and seeds are produced based on the outcome of the plant-pollinator interactions.
3. Plants, seeds, and nests experience background mortality.
4. Seeds disperse and then germinate into new plants.
5. Larvae disperse and new nests are recruited.
6. Plants and pollinators are censused.

We next describe each of these steps in more detail.

2.2.1 Landscapes

We simulate plant-pollinator dynamics across a landscape comprising a grid of 256×256 cells with wrap-around boundaries. Each cell is one of two types: crop or hedgerow. These cell types differ in the rewards they provide to pollinators and potentially in their suitability for nesting. We vary both the proportion of landscape that is hedgerow, as well as the spatial configuration of hedgerow cells across the landscape. Specifically, we consider both block and boundary arrangements (Fig. 2.1). We consider these to be the most realistic agricultural landscapes to test as large farm fields tend to have straight or gently curved layouts for efficient tractor usage. For each of these landscape types, we vary both the proportion of landscape that is allocated to crop versus hedgerow cells, and the degree of fragmentation. Fragmentation is measured as the number of patches that the landscape is broken into (blocks of crop or hedgerow, depending on the landscape type). Fragmentation has slightly different interpretations in the different landscape scenarios. In the boundary-type landscapes, increasing fragmentation increases the number of crop patches, with a continuous hedgerow border being maintained, whereas, in the block-type landscape, increasing fragmentation increases the number of hedgerow patches situated within a continuous field of crop cells.

2.2.2 Plants

Each cell in the landscape is occupied by a single plant. Crop cells are always occupied by crop plants, as they are assumed to be managed by farmers. Cells that are designated as “hedgerow” can contain a wild plant but may also be empty. Wild plants are only able to grow in hedgerow designated cells and rely on plant-pollinator interactions for reproduction. A native plant produces a single seed once it has been visited by a pollinator, meaning it is assumed to be pollinated once visited and no asexual reproduction of plants occurs. This seed disperses away from the parent plant with dispersal distances drawn from an exponential distribution and direction chosen at random. Specifically, a seed dispersal distance, d , which is drawn as

$$d \sim \lambda_{\text{plt}} e^{-\lambda_{\text{plt}} x} \quad (2.1)$$

where λ_{plt} denotes the mean dispersal distance. If a seed lands in a cell not designated for hedgerows (i.e., a crop cell) it is considered dead. Seeds experience background mortality prior to germination with probability δ_s and germinate with probability γ .

2.2.3 Bees

We simulate female solitary bees. We assume that food, rather than the density of male bees, is the limiting resource for reproduction, although this may not be true at critically low population densities. We do not limit the density of bees across the landscape, and multiple bees may nest within the same cell. We contrast scenarios where bees are able to nest only in hedgerow cells to scenarios where they can nest in both hedgerow and crop cells. We assume bees forage under one of four increasingly complex models, which we describe in detail below. Based on the plant interactions experienced by a bee during a foraging bout and the foraging model, that bee may be able to reproduce after that foraging bout. Under all foraging models, the first bee to visit a given flower is able to produce a larva with probability ν , and after a single visitation the flower is assumed to be depleted of resources (nectar and pollen) and future bees that visit this flower receive no benefit. There is no explicit limitation on the number of larvae a bee can produce in a given season. The larvae disperse away from the parent nest in a random direction and with distance drawn from an exponential distribution

$$d \sim \lambda_{\text{bee}} e^{-\lambda_{\text{bee}} x}. \quad (2.2)$$

2.2.4 Foraging models

The foraging models discussed below begin with our implementation of the model used in Keitt (2009), herein referred to as “random foraging.” Subsequent models build on that initial model iteratively in an attempt to more closely approximate the foraging behaviour of bees. In all models, bees can either benefit from foraging on crops, or receive no benefit from foraging on crops. Bees are central place foragers, always returning to their nests between foraging bouts and this is reflected in all foraging models.

1. **Random:** Bees make $\beta * \tau$ visits to random cells around their nests, with distances drawn from an exponential distribution (Eq. 2.2) and direction drawn randomly. A bee is able to reproduce if it is the first to visit at least one flower (or potentially crop) cell.
2. **Directed:** Bees make $\beta * \tau$ visits, however, instead of choosing cells at random, we assume that they are able to survey some portion of the landscape and then decide where to move. Before a given movement, a bee surveys n_{cand} candidate cells. The probability a cell is drawn as one of the n_{cand} is specified by an exponential distribution centered at the bee's nest (Eq. 2.2). Relative quality of the sampled cells is based on how far away each is from the bee's current position, as well as the reward value (i.e., does the cell contain a wild flower, a crop plant, or nothing?). Assuming that the crop cells are valued at 1, the relative quality is calculated as:

$$\text{quality} = \begin{cases} \frac{1}{1+d} & \text{if cell is crop} \\ \frac{r}{1+d} & \text{if cell is hedgerow} \end{cases} \quad (2.3)$$

where r is the ratio of relative value of hedgerow cells to crop cells. The bee then visits the best of these candidates.

3. **Memory:** Identical to the Directed model except that here, when bees are ranking the n_{cand} cells they have surveyed, they devalue cells that they have already visited. Assuming that the crop cells are valued at 1, the relative quality is calculated as it was in the Directed model (Eq. 2.3) with the addition that, if they have already visited that flower, its quality is multiplied by a factor of μ ($\mu \leq 1$).
4. **Discernment:** Identical to the Directed model except that here, when bees are ranking the n_{cand} cells that they have surveyed, they devalue cells that they *or other bees* have visited during that season. Assuming that the crop cells are valued at 1, the relative quality is calculated as it was in Eq. 2.3, with the addition that, if a cell has already been visited by any bee, its quality is multiplied by a factor of μ ($\mu \leq 1$). Bees are able to assess the current relative value at a flower; that is, they can tell how many bees have visited the flower previously and consumed some of the available nectar (Goulson et al., 1998; Knauer and Schiestl, 2015).

2.2.5 Simulation decisions

We run the model for 50 generations and track the pollinator population (measured in density of potential pollination services across the entire landscape calculated as such: $\frac{N_{\text{poll}}[t] \times \beta \times \tau}{256 \times 256}$), the wild plant population density (measured by the proportion of the landscape occupied by plants), and crop visitation across the landscape (ecosystem services to farmer). We quantify crop visitation using three metrics:

1. The proportion of crop cells receiving at least one visit.
2. The average number of visits to crop plants per bee.
3. The total number of visits made to crop plants.

2.3 Results

We find that our implementation of the “random” foraging model corroborates earlier findings that, when pollinators cannot forage on crops, if the proportion of landscape that is hedgerow is below $\sim 40\%$, a pollinator population density threshold exists under which the bee populations go extinct (Fig. 2.2a-b; see Keitt, 2009). This threshold is higher when bees can only nest in hedgerow areas (blue lines, Fig. 2.2a-b). In contrast, when pollinators can forage on crops, over 90% of the landscape can be used for crop production without leading to extinction of bees (Fig. 2.3). When bees can also nest in crops, they no longer go extinct due to habitat loss (red lines, Fig. 2.3). In general, we find that, across all quantities of hedgerow that we examined, if hedgerow plants or pollinators drop below a critical threshold population size, both will go extinct unless the bees can forage on crops (Fig. 2.2, Fig. 2.3).

We find that how pollinators forage impacts the likelihood that they, as well as the wild flowers, go extinct. When pollinators are able to survey a subset of the landscape and choose among the surveyed sites (the directed model), extinction actually becomes more likely (occurs across a broader range of initial population sizes; compare second to first row of Fig. 2.2). At $\Lambda = 0.5$, 86% of runs go extinct under the random model, whereas 100% go extinct in the directed model.

In cases where species do persist, they do so at precariously low population sizes. This occurs because, when pollinators are able to choose flowers, but with limited information and memory, they revisit good resources that are close to their nests, to their own detriment. Not surprisingly, when bees are able to remember past cells they have visited (the memory model), extinction becomes less likely in the case of a 50% crop landscape (Fig. 2.2e,h). This effect is weak because, under this model, bees are not able to discern locations that other bees have already visited, so can still concentrate their visits among highly attractive, but depleted, locations. When bees can discern flowers that have already been visited by themselves or other bees (the discernment model), we no longer find extinction. With knowledge about the locations of their own previous visits and those of other bees', they are more likely to find the remaining unvisited flowers, even if those flowers are further away. In summary, our ecologically most realistic discernment foraging model generates population dynamics that are qualitatively similar to our least realistic random foraging model. In order to facilitate further comparison between these two models, we largely omit investigation of the directed and memory models, going forwards.

Across all foraging models we find that, when pollinators do not forage on crops, the risk of extinction of both plants and pollinators decreases as more of the landscape becomes available for forage and nesting (Fig. 2.2). Not surprisingly, across all of the above foraging scenarios, bee population sizes are lower when they cannot nest in crop fields and, thus, more susceptible to extinction (red lines show when bees can nest everywhere on the landscape, blue lines show when they are limited to only nesting in hedgerows Fig. 2.2).

When pollinators are able to forage on crops, the addition of hedgerows is most important if the crop fields are not suitable for nesting (final population densities for blue lines in panels with higher Λ are higher (Fig. 2.3). This is true even when crop plants are relatively less valuable foraging resources for the pollinators. Under the random foraging model, we do not see any cases of pollinator extinction across the different crop proportions we considered, although the wild plants in hedgerow areas may go extinct. Qualitatively, patterns are the same for the discernment model, though at lower population densities than the random model. Across both models, bee population

density is lower and trajectories are more likely to lead to extinction when bees cannot nest in crop fields.

When pollinators are able to forage and nest in crops, their population sizes remain high, even when the proportion of the landscape that is hedgerow is low (red lines in Fig. 2.3). In this case, individual pollinators are more evenly distributed throughout the landscape and this facilitates pollination of crop cells. It follows then that, when pollinators can nest in crop cells, the proportion of those crops that get pollinated is actually relatively insensitive to how much of the landscape comprises crop cells (red lines in Fig. 2.4). Conversely, when pollinators are only able to forage (but not nest) in crop cells, pollination services to crops are lower in landscapes comprising a high proportion of crop. This is because such landscapes support fewer pollinators and, further, those pollinators must travel greater distances to reach more interior crop cells (or from more interior hedgerow patches in the case of block-type landscapes). Despite this, the *per capita* rate of pollination to crops is higher in landscapes comprising mostly crop cells, as bees in these landscapes move out into the surrounding landscape after the nearby hedgerow resources are expended, under the discernment model. Under the exponential model, the increase in total pollination events to crops is also expected, as the distribution of visits, which are distributed randomly across the landscape, should track the proportion of landscape which is crop. Therefore as the proportion of landscape that is crop increases, the proportion of visits that a bee makes which land in crop cells will increase. Qualitatively, we find that the block and boundary-type spatial structuring of hedgerows does not impact pollination services across the proportion of landscape used for hedgerows (Fig. 2.4).

When pollinators are only able to nest in hedgerow cells, more fragmented landscapes (e.g., those with more smaller hedgerow blocks or farm blocks) experience higher *per capita* provisioning of pollination services (Fig. 2.5). Pollinators are limited in how far they are willing and/or able to fly and, therefore, if they must return to their nests between foraging bouts, they prioritize resources within that range. In landscapes comprising fewer larger blocks of crops, pollinators would need to travel too far to reach the plants in the centre of the blocks and, thus, the interior cells are less likely to be pollinated. If pollinators are able to nest everywhere then pollination remains

high. Just as with comparisons of pollination services across the proportion of landscape used for cultivation, we find the block and boundary-type spatial structuring of hedgerows does not impact pollination services across landscape fragmentation (Fig. 2.5).

The relative value to pollinators of the hedgerow cells compared to the crop cells does not significantly impact the pollination services provided to the crops (Fig. A.1). While surprising, this can be attributed to our discernment model approximating optimal foraging. As cells are visited by bees, they decrease in value and, thus, bees redistribute across the landscape. This means that, even in cases where hedgerows are highly valuable relative to crops (or vice versa where crops are highly valuable), once the nearby high value resources begin to deplete, bees will redistribute to previously lower value resources that have become relatively higher value due to remaining unvisited.

2.4 Discussion

We found that, when estimating pollinator population dynamics and pollination services across a landscape, the widely-used exponential foraging model (our “random” model) serves as a reasonable stand in for more realistic (and complex) bee foraging habits. This is true whether or not the plants within hedgerows are higher value than the crops that they surround. Further, we find that allocating less space to hedgerows only lowers pollination services to surrounding areas when pollinators cannot nest in crop regions. We also find that the per capita rate of crop pollination is more complete with increasing fragmentation of hedgerows, however the overall proportion of crops which are pollinated decreases.

While hedgerow amendments to farm fields are well accepted as a beneficial conservation practice for wild bees, a primary but less well-understood justification for their installation is that they may lead to provisioning of additional pollination services to crops. Whether or not pollinator spillover from hedgerows into farm fields results in increased pollination and, therefore, increased crop production is, however, contentious. There are empirical studies that show increased pollination

services to fields amended with hedgerows (Blaauw and Isaacs, 2014; Ricketts, 2004), as well as empirical studies showing no effect (Bishop et al., 2023).

Models of bee demography and foraging in agricultural landscapes have been used to make predictions about how hedgerow size, distribution, and composition may impact the ecosystem services delivered by wild bees. While important work, these earlier studies have generally used simplistic models of bee foraging that may not reflect how bees interact with floral resource landscapes. In earlier models (Brosi et al., 2008; Keitt, 2009; Lonsdorf et al., 2009), simulated bees that essentially diffuse from their nests into the landscape, stopping to forage randomly (i.e., bees pass over a landscape and randomly choose locations at which to stop, forage, pollinate, etc.). In contrast, Nicholson et al. (2019) modelled incremental changes in pollination rates associated with hedgerow additions both for “random” foraging as well as central place foraging, finding the approaches similar at large scales but central place foraging more closely matched empirical tests at local scales. Our goal here was to assess whether assumptions about pollinator foraging habits might alter the structure of optimal spatial distribution of hedgerows. We were inspired by Keitt (2009), who modelled bee movement distances using an exponential distribution (Eq. 2.2). Keitt (2009) found that when $\sim 60\%$ of the landscape was allocated to crop cultivation, pollinators are likely to go extinct if they are not able to forage on crops. In contrast, when pollinators can forage on (but not nest in) crops, the proportion of the landscape which can be used for crops increased to over 90% and when bees could also nest in crops, they no longer went extinct due to habitat loss.

We began by considering an exponential foraging model, similar to the one used by Keitt (2009). In line with Keitt (2009), we found that, when pollinators were able to forage, but not nest, in crop areas, there was a strong effect of both the spatial distribution and amount of hedgerow in the landscape. Specifically, landscapes with a high proportion of crops ($\sim 80\%$ in our case) received the highest total number of pollination events and also a high proportion of crop cells received at least one visit. We then compared this exponential model to other models, progressively adding layers of ecological realism. First, we considered our directed model, where pollinators choose the most valuable foraging site among a small subset of surveyed cells. Subsequently we used a mem-

ory model where pollinators again choose the relatively most valuable foraging site among a small subset of cells, devaluing sites that they have previously visited. For both of these models we did not explore the distribution of pollination services, as populations were non-viable in landscapes with low proportions of hedgerow when nesting was limited. It is likely that for both of those models, pollination services to crops would be limited, as the bees tend to choose to revisit the same set of nearby sites repeatedly. We then considered our discernment model, where pollinators choose where to forage based on the relative value of a given cell, determined by a combination of distance and previous visits by any bee. We found qualitatively similar patterns for the total amount of pollination, as well as per capita pollination, however, pollinator population sizes were lowered under this model and, consequently, the proportion of crop cells that saw at least one pollination event declined more notably as the total amount of hedgerow declined. The main resulting difference between the random model and the discernment model was a lower population density estimate with the discernment model and corresponding consequences from that. We find that, at least relative to the model developed within this paper, that the very simple exponential model for bee movement fairly approximates the results of more complex bee behaviour.

Using the exponential model of foraging movement, Keitt (2009) found that on landscapes simulated with a Gaussian wavelet pattern (complex landscapes with varying shapes of hedgerow evenly scattered throughout crops), the ideal distance between patches matched the mean dispersal distance of the simulated bees. In contrast, we found that there was little effect of shortening the distance between patches by increasing the fragmentation of the landscape (Fig. 2.5). As in previous investigations, we found that the spatial structure of hedgerow amendments on a landscape, when the proportion of landscape associated with these amendments is held constant, has little affect qualitatively on the distribution and amount of pollination services across the landscape (Keitt, 2009). Importantly, we found that, despite attempting to build a model with a more complex and accurate representation of the foraging of pollinators, our most ecologically realistic discernment model performs qualitatively similarly to the exponential model developed in Keitt (2009). This suggests that inferences made in earlier work that used simple exponential foraging models are likely robust to the inclusion of more complex foraging rules.

Nicholson et al. (2019) modelled the expected pollination services to blueberry (*Vaccinium sp.*) fields with the addition of hedgerows that either acted solely as a floral resource, as a nesting habitat, or as both. They found that adding large patches of floral resources as amendments to fields decreased pollination services relative to fields without those amendments. This was because pollinators were preferentially foraging on the floral enhancements. However, when fields were supplemented with foraging and nesting habitat, the reduction in pollination services disappeared. Finally, when they only added nesting habitat, pollination services increased. This agrees with our finding that, for crops that provide forage, adding nesting habitat in crop areas significantly increases pollinator population sizes and the resultant ecosystem services (Fig. 2.4, Fig. 2.5). In contrast, we do not find that pollinators seem to be significantly distracted by high value hedgerows which draw them away from the crops (Fig. A.1). This may be due to our assumption that only first visits to flowers provide pollinators with rewards (following Keitt, 2009), which strongly incentivizes dispersed foraging trajectories.

The general life-history model used within this study has some important limitations to explore in the future. For example, we have contrasted two scenarios: bees can nest in both hedgerow and agricultural cells or only in hedgerow cells. This distinction has a large effect on pollination services to crops; when bees are not able to nest in agricultural cells, they tend to have lower population densities and, consequently, provide less pollination services (Fig. 2.4, Fig. 2.5). However, actual insect pollinators have varied responses to nesting in fields that seem to be species and guild-specific. For example, stem-nesting bees (genus *Exoneura*) contribute to the pollination of *Rubus sp.* by nesting in the stems of those plants and visiting the flowers of those same plants (Coates et al., 2022). Despite being able to nest within the stems of crops in the fields, the abundance of *Exoneura* was higher with more native vegetation nearby (Coates et al., 2022). Similarly, ground nesting squash bees (*Peponapis pruinosa*) are able to nest within squash fields, however the extent to which they are successful at this varies. Squash bee nests have been shown to be negatively impacted by tilling in squash fields, with evidence for increased juvenile mortality and later emergence of juveniles (Ullmann et al., 2016). However, no effect of tilling on squash bees has been found in other instances (Esther Julier and Roulston, 2009). Among other bees, Tschanz

et al. (2023) compared the nest density of ground-nesting bees in tilled and no-till agricultural fields in Switzerland. They found no effect of tilling but did find that nest density declined exponentially as one moves from the farm edge into the field. In terms of amending habitat to increase nesting opportunities for ground-nesting bees (similar to recommendations by Nicholson et al. (2019)) hedgerows do not seem to increase rates of ground-nesting bees when compared to control edges of fields. Even though ground-nesting bees were found foraging on the floral resources supplied by hedgerows, the hedgerows did not appear to appreciably increase nesting habitat for ground-nesting bees Sardiñas et al. (2016).

In order to facilitate comparison to earlier work, we assumed that plants have a 20% probability of dying in a given season, which leads to an expected lifespan of 5 years. We also assumed that plants only reproduce if they have been visited by a bee. Both of these assumptions may limit applicability to managed hedgerows that are installed in agricultural settings. There, plants are often long-lived perennials and/or are replaced if they die are replaced. For example, within European cultural contexts hedgerows are typically dominated by mature woody shrubs and small trees, with lower herbaceous layers (Forman and Baudry, 1984; Vanneste et al., 2020). These plants, such as hawthorn (genus *Crataegus*), both survive for much longer than 5 years, on average, and are often able to reproduce asexually, either through apomixis or vegetative reproduction (Forman and Baudry, 1984; Vašková and Kolarčík, 2019). When plants are managed and/or long-lived, their population dynamics may be less coupled to the population dynamics of their pollinators and this may provide some degree of buffering against extinction of either species, as the food source provided by the plants would be less affected by short-term fluctuations in pollinator abundance. This effect could be explored in our model by exploring smaller values of plant annual mortality, δ_p . It would also be interesting to explore scenarios where plant reproduction is not be completely dependent on pollinator visitation.

We have examined 4 foraging models here, with each model progressively adding a layer of ecological realism. Our primary goal was to understand how these different models might alter population dynamics and, thereby, impact provisioning of pollination services. While the fact that different foraging models can impact total bee abundance is, in itself, an interesting and relevant

outcome, it complicates interpretation of our results for ecosystem services. For example, it might be desirable to compare the pollination services provided under different foraging models at *equal* bee population densities (effectively a per capita pollination services effect of the bees) and the resultant total amount of pollination given the absolute number of bees. Comparison of the per capita measurement of pollination services is sensitive to the overall density of bees on the landscape, because of the differing effects of competition in the exponential and discernment models. In the exponential model, bee foraging decisions are independent of other bees and, therefore, independent of density. In contrast, under the discernment model, bees prefer to visit cells that have not been exploited already by other bees. The result of this is that, across the two models, pollination services will scale differently with density. For example, the per capita rate of pollination under the discernment model tends to be higher when pollinators are only nesting in hedgerows, rather than nesting everywhere (Fig. 2.4, Fig. 2.5). While in contrast the per capita rate of pollination under the random model tends to be lower when pollinators are only nesting in hedgerows, rather than nesting everywhere (Fig. 2.4, Fig. 2.5).

Future avenues for helping understand the potential pollination services provided by hedgerow amendments via simulation or analytical models may use marginal value central place foraging models, as was done in Nicholson et al. (2019), to explore the optimal spatial arrangement of hedgerow field amendments. More specific estimates of the incremental increases in pollination services associated with the specific spatial design features of hedgerows in agricultural landscapes may provide actionable recommendations for farmers. Additionally, as Nicholson et al. (2019) predict that hedgerows distract pollinators from foraging on crops, comparing ecosystem services when the relative value of crops and hedgerows are similar (i.e., the crops and hedgerows are similarly valuable resources for the foraging bees) may provide a contrasting answer. Incorporating phenological coverage of both hedgerows and crops (that is, the proportion of the season that the target crops and hedgerows are flowering) and aligning this with potential pollinator foraging patterns may also help inform farmer decisions. Such that the temporal attractiveness of hedgerows over the growing season can itself be a design choice (M'Gonigle et al., 2017). For example, if crops and hedgerows are selected to not flower at the same time, hedgerows may not

distract bees from foraging on crops. Further, if the majority of the landscape is used for crops (with minimal hedgerows), that the bees can forage on, based on the simulation results presented here, bee populations will remain stable. However, many crops such as cherry (*Prunus sp.*) and blueberry (*Vaccinium sp.*) have limited flowering periods where outside of those periods bees must have additional floral resources to support their populations (Wood et al., 2018). Modelling could be used estimate the amount of floral resources required to support pollinator populations outside of target crop flowering seasons. Exploring how the spatial distribution of hedgerow design impact pollination services in empirical settings would be a natural next step for understanding the value of this critical restoration technique.

Table 2.1: Model parameters and model variables.

Symbol	Description	
Model parameters		
$N_{\text{bee}}[0]$	Initial pollinator population size	
$N_{\text{plt}}[0]$	Initial plant population size	
λ_{bee}	Average dispersal distance	16 cells
λ_{plt}	Average dispersal distance	16 cells
θ	Seed production probability	1
β	Number of visits per season	100
τ	proportion of season flowers are available	0.5
γ	Germination probability	0.5
α	Seedling survivorship probability	1
δ_{n}	Pollinator mortality rate	0.5
δ_{p}	Plant mortality rate	0.2
δ_{s}	Seed mortality rate	0.1
ν	Pollinator reproduction probability	0.2
r	Ratio of hedgerow to crop value	1.1
n_{cand}	Number of candidate cells surveyed	5
μ	Decay of nectar quantity	$\frac{2}{3}$
d	Distance	
Model variables		
Λ	proportion of landscape that is hedgerow	[0.02:1]
q	Number of fragments landscape is broken up by	[1,4,9,16,25,36]

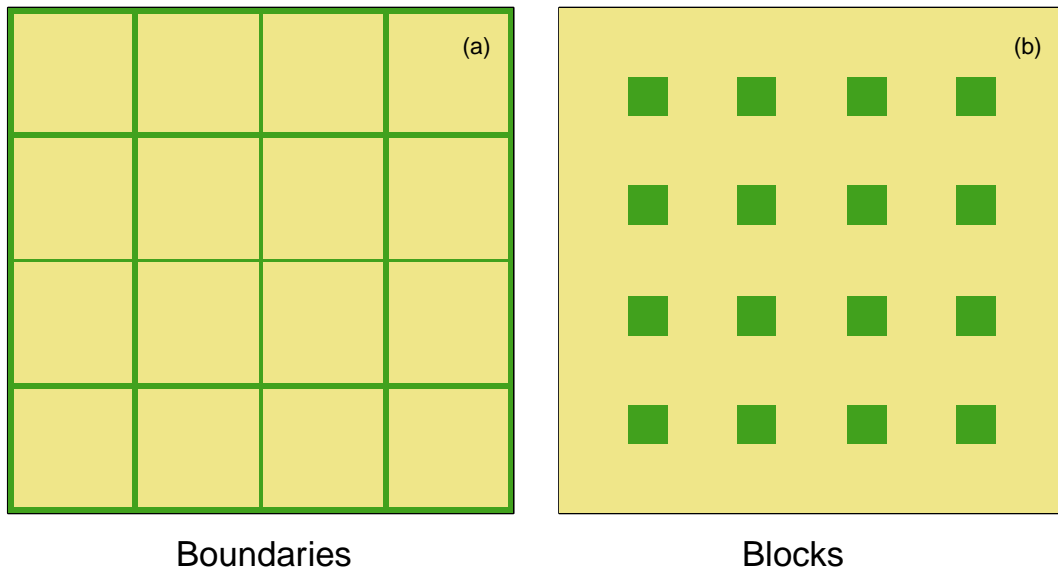


Figure 2.1: Sample 256×256 cell landscapes. Here, 90% of the landscape comprises crop cells (yellow) and the remaining 10% hedgerow cells (green). Boundary landscapes have hedgerows as edges around fields (a) while block landscapes have hedgerows as blocks within fields (b).

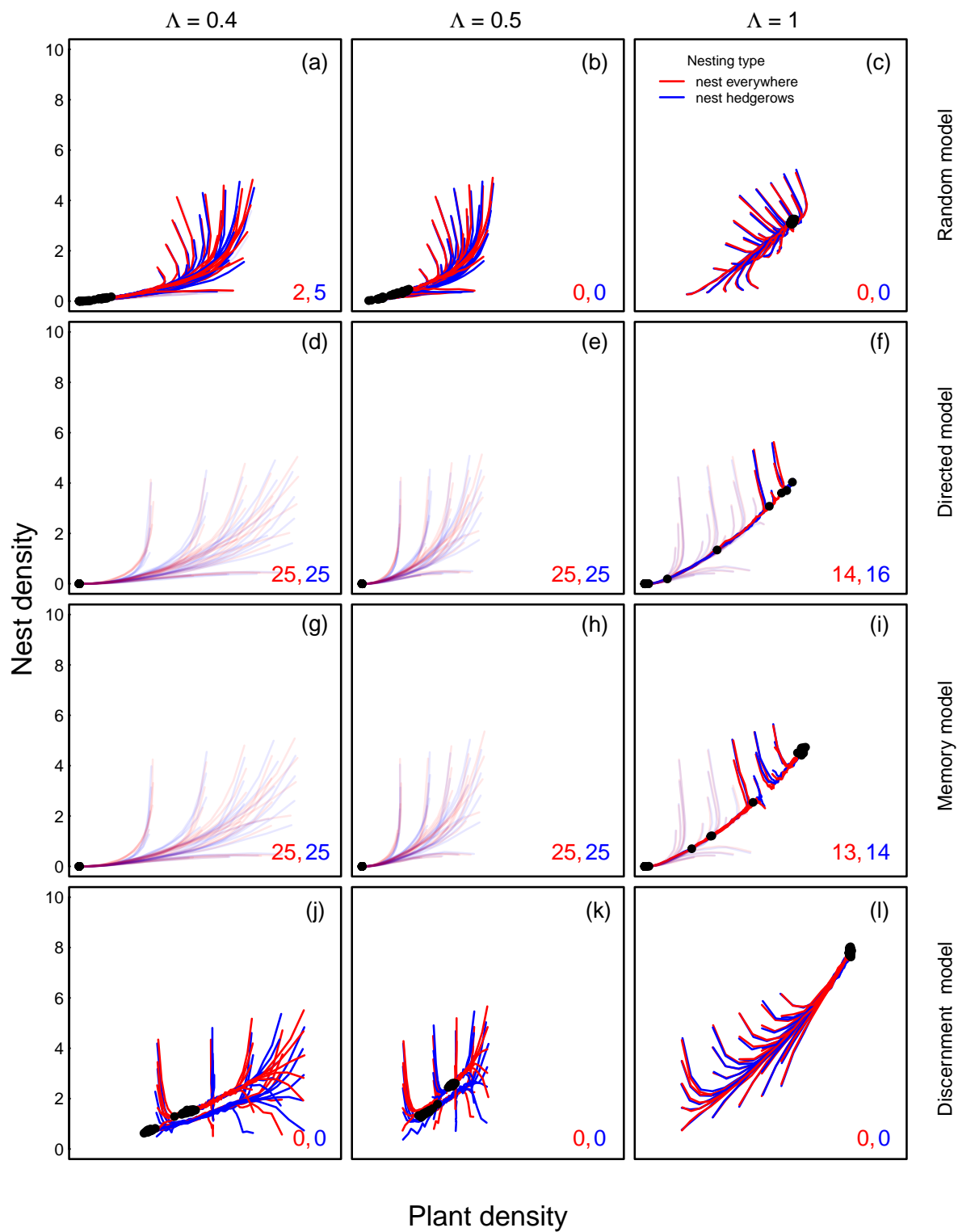


Figure 2.2: Plant density and pollinator scaled nest density ($\frac{N_{\text{poll}}[t] \times \beta \times \tau}{256 \times 256}$) trajectories through time under the random (panels a-c), directed (d-f), memory (g-i) and discernment (j-l) foraging models. Each panel shows multiple model runs across 50 seasons. In all panels the starting point of a time series simulation is unmarked and the endpoint is marked with a black circle. Red lines show model runs where pollinators can nest everywhere and blue lines show model runs where pollinators can only nest in hedgerow cells. Model runs that ultimately led to extinction of plants or pollinators are transparent. For all runs shown here, pollinators do not derive nutrition from crop cells. Additional parameter values are as shown in Table 2.1.

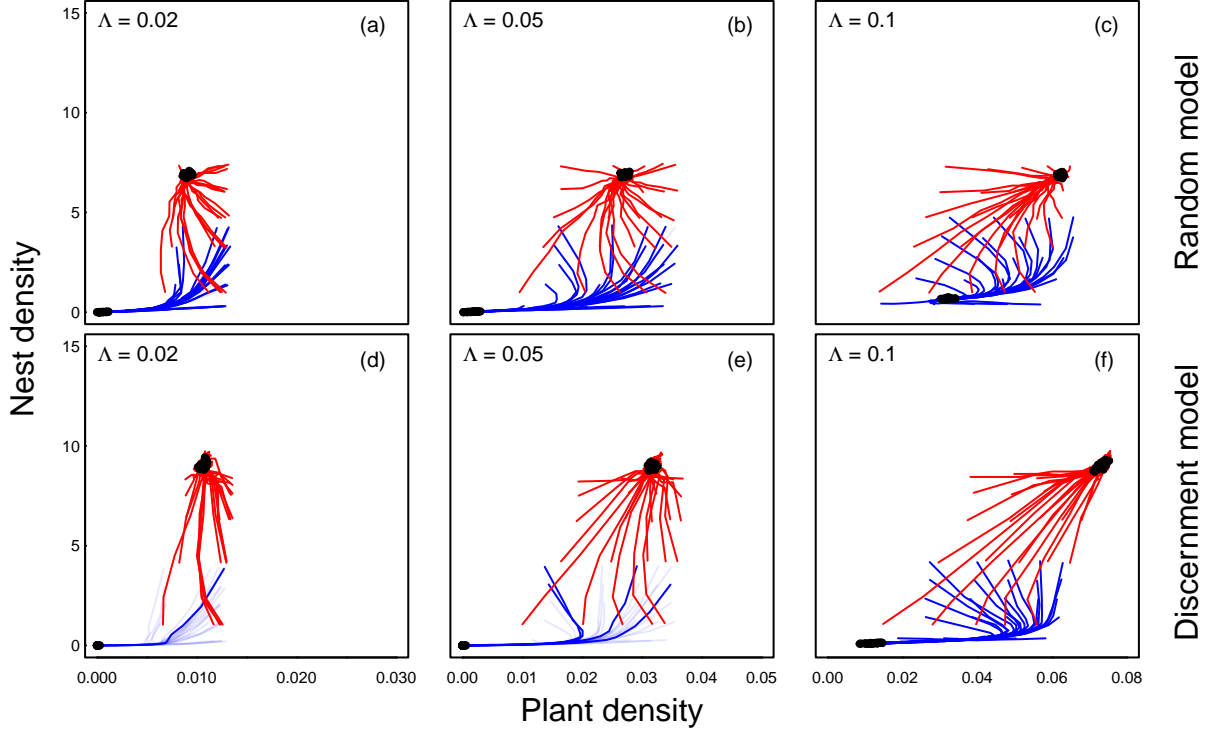


Figure 2.3: Plant density and pollinator scaled nest density ($\frac{N_{\text{poll}}[t] \times \beta \times \tau}{256 \times 256}$) trajectories through time under the random (panels a-c) and discernment (d-f) foraging model under a scenario where, in contrast to Fig. 2.2, pollinators *can* derive nutrition from crop cells. All other figure details are as in Fig. 2.2.

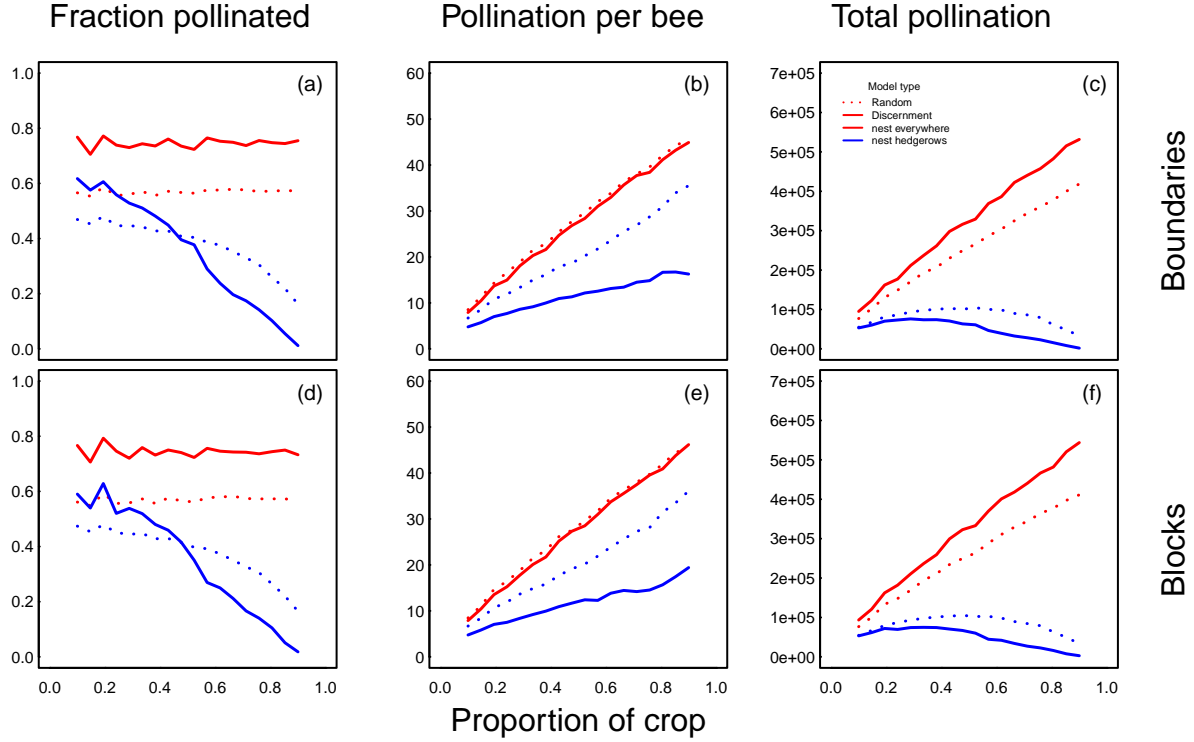


Figure 2.4: Ecosystem services provided to crop cells are relatively insensitive to whether pollinators forage according to a simple random model or a more complex discernment model. We measure ecosystem services as either the proportion of crops that receive at least one pollination event (panels a,d), the average number of crop plants pollinated by a given bee (panels b,e), and the total number of visits to crop plants (panels c,f). Qualitatively, the random and discernment model largely exhibit the same patterns of increase and/or decrease as the proportion of crop on the landscape increases. Rows present results for a boundary-type landscape (top row) or a block-type landscape (bottom row). Ecosystem services are calculated in the final season of a 50 season long model run. All other parameter values are as in Table 2.1.

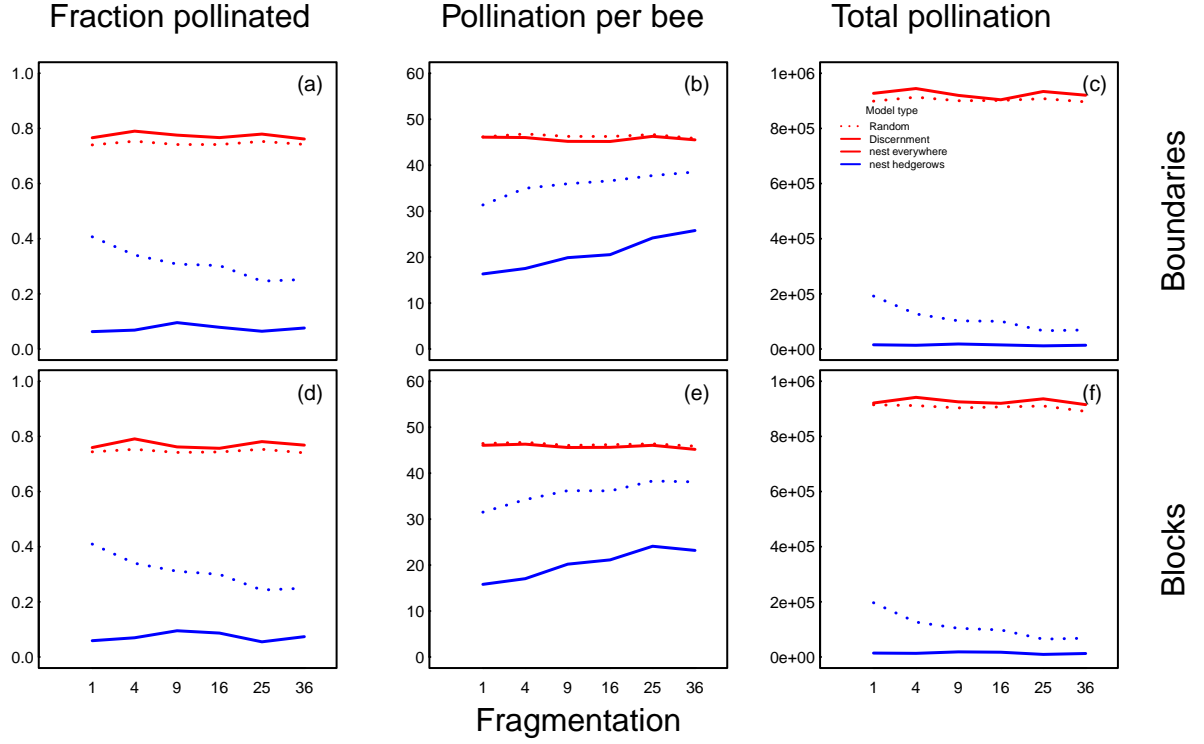


Figure 2.5: Ecosystem services provided to crop cells are relatively insensitive to whether pollinators forage according to a simple random model or a more complex discernment model. Panels here are all as in Fig. 2.4, except that we vary the amount of landscape fragmentation on the x -axis. All other parameter values are as in Table 2.1.

Chapter 3

Structured landscapes promote persistence by favouring prudent predators

3.1 Introduction

Adaptive evolution need not increase the size of a population. Rather, some phenotypes may increase the fitness of an individual, but lead to declines in equilibrium population size (so-called, “adaptive decline”; Abrams, 2019). Historically, this effect has been noted in cases where sexual selection leads to highly elaborate male ornaments that increase relative reproductive success but lower survival (Haldane, 1932). Sexually selected traits such as male aggression or harassment towards females can also lead to population declines under certain conditions. For example, in common lizards (*Lacerta vivipera*), male sexual aggression can be promoted by a small male bias in the adult sex ratio, resulting in decreased female survival and fecundity, which escalates the male bias, reinforcing the tendency towards aggressive behaviour (Le Galliard et al., 2005). In finches (*Carpodacus mexicanus*), males are more likely to feed near counterparts infected with the directly transmitted pathogen *Mycoplasma gallisepticum*, because these males are less sexually competitive due to their diseased condition, thus increasing the persistence and spread of *Mycoplasma gallisepticum* (Bouwman and Hawley, 2010) in the population. Sexual selection has also been found to result in higher extinction rates in animal-pollinated dioecious plants. Here, selection can favour showier flowers, but, because this effect is asymmetric across the sexes, males end up evolving

showier flowers, resulting in preferential visitation to male flowers by animal pollinators. As a consequence, there is a reduction in female reproductive success and an overall decrease in population size, which can lead to extinction (Vamosi and Otto, 2002).

Adaptive decline is also possible in predator-prey systems; recent theoretical work has shown that adaptive evolutionary change in the attack rate of a predator can suppress prey numbers sufficiently that their growth rate falls below its intrinsic maximum. Consequently, the populations of both prey and predators are smaller than they would be prior to predator evolution. This is true even when there is a trade off between the attack rate and mortality rate of the predator, which might be expected to otherwise limit the evolution of increasing attack rate (Abrams, 2019). In this model, predators and prey occupied a single well-mixed patch (Abrams, 2019). However, predator and prey may have distributions that are divided among multiple patches, with migration among them. Thus, eco-evolutionary behaviour predicted for a single patch model may not hold in a situation with multiple patches. Recent empirical work in a multi-patch plant-herbivore system (in which the herbivore is fulfilling the role of predator and the plant as prey) found that adaptive change to a novel food source in the herbivore sometimes led to a higher rate of population growth but a decreased herbivore carrying capacity (Bisschop et al., 2022). Here, the authors varied the sizes of patches, as well as the amount of movement among patches. While evolutionary outcomes differed across replicates, in some scenarios, high rates of movement led to reduced herbivore carrying capacities after adaptation, suggesting that this system might exhibit adaptive decline under certain conditions (Bisschop et al., 2022). Theory has shown that multi-patch dynamics can considerably alter the outcome of evolution of ecological traits. Spatial structure allowing relatedness within patches to exceed relatedness between patches, combined with different population sizes between patches allowing sink and source dynamics generates complex outcomes (Fletcher and Doebeli, 2009; Yang and Wang, 2011; Lion and Gandon, 2015).

There is an extensive literature on the evolution of prudence (reduction of virulence) in host-parasite systems. The primary difference between host-parasite systems and predator-prey systems is that parasites do not kill their hosts. However, insights gained from host-parasite studies can still help guide our predictions for the evolution of predator behaviour in predator-prey

systems, including predictions regarding the influence of spatial structure. Consistently, empirical studies have found that limited and local movement of pathogens leads to the evolution of more prudent pathogens (Kerr et al., 2006; Eshelman et al., 2010). Conversely, high rates of movement lead to the evolution of more virulent (less prudent) pathogens (Kerr et al., 2006; Eshelman et al., 2010; Semchenko et al., 2013; Tack et al., 2014; Carlsson-Granér and Thrall, 2015; Leggett et al., 2017). There are, however, exceptions. Vigneux et al. (2008) found that, under certain circumstances (namely, when host availability is low, relatedness within the pathogen population is high, and parasite movement is low), high virulence can evolve. While this result appears counter-intuitive, the reduction of in host conflict among bacterial strains due to high relatedness means that bacteria are participating less in interference competition with other genotypes, which would otherwise limit virulence. This points to relatedness as an important factor promoting the evolution of prudence in host-parasite systems. When movement among patches is limited, relatedness within pathogen populations is high and, thus, behaviour that limits host death (i.e., lower virulence) can be beneficial due to kin selection.

Reduced virulence in pathogens can be viewed as a cooperative trait: individuals that over-exploit their resource (“cheaters”) compete with less exploitative individuals (“cooperators”). Kin selection theory predicts that such cooperative traits should be more likely to evolve when relatives assort, which may depend on spatial structure. For example, Fletcher and Doebeli (2009) examined evolution of cooperation in a multi-patch framework and showed that spatial structure promoted the evolution of cooperation by allowing cheaters and cooperators to assort into separate patches. We might, therefore, anticipate that in multiple patch predator-prey systems, over-exploiting predators and less-exploitative predators could similarly assort into separate patches. If the patches containing more exploitative predators have reduced population sizes, they may contribute fewer migrant individuals to move among the meta-population of patches, thereby enabling persistence or even proliferation of less-exploitative predators.

Here, we use individual-based simulation models to investigate how the evolution of predator attack rate impacts the population dynamics of both predators and prey in an explicit meta-population framework. Building on the single-patch model of (Abrams, 2019) we develop a multiple-

patch model, and vary both the number of patches and the pattern of connectivity among those patches to examine the impact of spatial structure. We track the adaptive response of the predator's ecological traits (i.e., attack rate and death rate) and resulting impacts on population dynamics under these various landscape scenarios. We expect the magnitude of adaptive decline (i.e., the extent to which evolution lowers predator population size) will decrease as the landscape becomes more fragmented (i.e., increased number of patches or decreased connectivity among patches). With greater fragmentation, over-exploitation of prey is expected to be less advantageous because individuals are more likely to interact with their kin. Moreover, we expect that patches with less prudent predators will have lower population sizes and, therefore, contribute fewer migrants to the overall pool.

3.2 Methods

We consider a set of N patches, each potentially inhabited by some number of predators and/or prey. We model population dynamics within each patch using variations of discrete time Lotka-Volterra dynamics, with major differences being a logistic population growth for prey (in the absence of predation), as well as the addition of a prey handling time for predators. Events occur in the following order: movement among patches of predator and prey, consumption of prey by predators, reproduction of both predators and prey, and mortality of predators. We will describe each of these steps in more detail below. Table 3.1 provides a full list of parameters, their definitions, and their default values.

3.2.1 Predator-prey dynamics

We let $C[t, i]$ and $R[t, i]$ denote, respectively, the number of predators (consumers) and prey (resources) in patch i at time t . We assume that prey reproduction follows a logistic growth function. Specifically, the expected number of prey born per parent at time t in patch i is given by

$$\lambda_R[t, i] = r_i * \left(1 - \frac{R[t, i]}{K_i}\right), \quad (3.1)$$

where r_i denotes the intrinsic growth rate of the prey in patch i and K_i denotes the prey carrying capacity of patch i . We draw the actual number of offspring born from a Poisson distribution characterized by the expected number of prey, such that

$$R_{\text{born}}[t, i] \sim \text{Pois}[\lambda_R[t, i] * R[t, i]]. \quad (3.2)$$

After reproduction, prey (of all ages) are attacked and potentially eaten by predators. The number of prey attacked depends on both the predator attack rate, a , and the current densities of both the prey, $R[t, i]$, and the predators, $C[t, i]$. Specifically, the number of prey attacked in patch i is given by

$$R_{\text{attacked}}[t, i] = a * (R_{\text{born}}[t, i] + R[t, i]) * C[t, i]. \quad (3.3)$$

We assume that predators are limited in how many prey they can handle, such that the rate of consumption of prey declines with increasing prey abundance according to a Holling type II function. Specifically, the number of prey killed and eaten in patch i is given by

$$R_{\text{eaten}}[t, i] = \frac{R_{\text{attacked}}[t, i]}{1 + h * R_{\text{attacked}}[t, i]} \quad (3.4)$$

where h determines how quickly predators satiate with consumption of prey; when $h = 0$, predators consume all the prey they attack, whereas, for larger h , predators consume a smaller fraction of attacked prey.

Combining the above yields a recursion equation for the number of prey in patch i ,

$$R[t + 1, i] = R[t, i] + R_{\text{born}}[t, i] - R_{\text{eaten}}[t, i] \quad (3.5)$$

The birth rate of predators depends on the conversion efficiency c_r and the number of prey eaten $R_{\text{eaten}}[t, i]$. Specifically, the number of new predators born in patch i at time t is equal to

$$C_{\text{born}}[t, i] = c_r * R_{\text{eaten}}[t, i] \quad (3.6)$$

After reproduction, predators of all ages die at rate d . The number of predators that die in patch i at time t is equal to

$$C_{\text{died}}[t, i] = d * (C_{\text{born}}[t, i] + C[t, i]) \quad (3.7)$$

Combining the above yields a recursion equation for the number of predators in patch i ,

$$C[t + 1, i] = C[t, i] + C_{\text{born}}[t, i] - C_{\text{died}}[t, i] \quad (3.8)$$

3.2.2 Movement

Within each generation, before predation and reproduction occur, all predator and prey individuals undergo a cycle of movement. Prey and predator individuals leave their patch with probability m_C and m_R , respectively. The probability of moving to any other given patch is described by the patch connectivity scenario.

We consider three scenarios of patch connectivity.

1. **Universal:** all patches are equally connected, such that a moving individual is equally likely to move to any other patch. There is a $\frac{m}{n}$ probability of moving to a given patch. (Fig. 3.1a)
2. **Stepping stone:** patches are arranged linearly and movement only occurs between adjacent patches. Boundaries are wrap-around. There is a $\frac{m}{2}$ probability of moving to an adjacent patch. (Fig. 3.1b)
3. **One-way:** patches are arranged linearly, but movement only occurs in one direction. Boundaries are wrap-around. There is a m probability of moving to the next patch. (Fig. 3.1c)

3.2.3 Evolution

We initially consider model runs where both attack rate, a_i , and predator death rate, d_i , are fixed so that we can determine equilibrium mean population size. However, in order to model evolution (and, thereby, adaptive decline), we also consider model runs where these are evolving traits. Specifically, following Abrams (2019), we suppose that predator i is characterized by an evolving

quantitative trait x_i that determines both its attack rate and its death rate. We replace a and d by a_i and d_i , where

$$\begin{aligned} a_i &= c * x_i / (1 + \alpha * x_i) \\ d_i &= d_0 + d_1 * x_i \end{aligned} \tag{3.9}$$

Here, attack rate and death rate trade off against one another, such that individuals with higher attack rates will also have higher death rates. Attack rate increases with increasing x_i according to a saturating function (Holling type II function), while the death rate increases linearly with x_i . c is the success rate of attacks, α is the search time, d_0 is the intrinsic mortality rate, and d_1 scales the effect of trait x_i on death rate.

3.2.4 Simulations

For runs that allow for trait evolution of the predator (i.e., evolution runs), we follow the phenotypic value of trait x_i . In order to reduce computation time, we limit the number of distinct phenotypes at any given time to 10: no new mutations will occur until there are fewer than 10 distinct predator phenotypes. New predator offspring inherit their parental trait values. If there are fewer than 10 phenotypes in the population, then the remaining spots are filled by randomly selecting individuals to mutate (thereby producing new phenotypes). Mutant trait values are augmented by a value drawn from a Normal distribution centered at zero and with standard deviation σ_μ (any resultant negative trait values are set to 0).

All models were run in R version X Team (2022) and all code required to replicate the analysis is available upon request/available at X website.

3.3 Results

Our multi-patch model reproduces typical predator-prey ecological cycles and, with sufficient movement, cyclical dynamics across patches are largely synchronized (Fig. 3.2a). When evolution is permitted in the predator traits, we find that our model does indeed reproduce earlier findings of adaptive decline in predator prey systems (Abrams, 2019). Trait x_i , which is initially low, evolves

upwards, increasing both the attack rate, a_i , and the death rate, d_i and, ultimately, leading to a decline in the mean population sizes of both the predators and the prey (Fig. 3.2b).

Cyclical predator-prey dynamics are also impacted by the predator attack and death rates and, thus, by evolution in the predator. Specifically, when x_i is low, predators are relatively ineffective at catching prey, and thus predator-prey cycles are largely absent (left side of Fig. 3.2b). However, as x_i increases, and predators become more effective hunters, cycles emerge and grow in magnitude (right side of Fig. 3.2b). These large predator-prey cycles increase the opportunity for stochastic extinction of predators or both predators and prey (a point we will return to below).

We find that predator population size typically peaks at intermediate trait values (Fig. 3.3). All else being equal, we also find that the location of that peak depends on the number of patches. Importantly, the extent of adaptive decline, i.e., the difference in height between the peak and the evolutionary endpoint, decreases as the number of patches increases. Intuitively, this finding makes sense when one considers the potential negative consequences associated with a higher kill rate (and resultant smaller within-patch population size) in predators. In the single patch case, predators evolve to over-exploit their prey, quickly resulting in extinction, however as we extend the model to multiple patches the opportunity for recolonization exists. As predators in a given patch evolve higher attack rates, their population will consequently decline. In extreme cases this process could drive the predators in that patch extinct. Subsequent recolonization is then most likely to originate from a patch that has a high proportion of predators with lower trait values, as those patches will have higher within-patch population sizes and, thus, contribute more moving predators. In addition, even if predators do not go altogether extinct within patches, patches with lower average attack rates will still have larger population sizes and, therefore, movement will more often occur from patches containing prudent predators into patches containing exploitative predators than vice versa. Thus, exploitative predators will drive their populations down, only to be recolonized by prudent predators, thereby, limiting adaptive decline. The resulting spatial structure from differential movement will also mean that exploitative predators will experience greater kin competition, on average, than prudent predators and, thus, kin competition in multi-patch landscapes will also counter adaptive decline.

In line with the above, we also find that increasing rates of movement among patches promotes adaptive decline (Fig. 3.4). Higher rates of movement between patches homogenize the composition of the different patches, causing them to effectively behave more like a single large patch. This weakens the above-described effects of spatial structure that accompany a lower attack rate.

We next explore more complex spatial movement topologies. Specifically, we contrast our universal model (where individuals move to any other patch with equal probability, Fig. 3.1a) with more constrictive models where individuals can either only move to adjacent patches ('stepping stone,' Fig. 3.1b) or can only move to a single downstream patch ('one-way,' Fig. 3.1c). Because effects of movement topology are more likely to emerge in larger networks, where patches can be separated by more movement "steps," here we examine landscapes comprising 200 patches. In general, landscapes that limit movement tend to also limit adaptive decline (Fig. 3.5). Interestingly, the effect of landscape topology is most pronounced at intermediate levels of movement. This is because, when movement rates are low, few individuals disperse, and thus patches are relatively isolated from one another under all three topologies. In contrast, when movement is high, so many individuals move each generation that different topologies don't effectively limit movement between any set of patches.

We also test for adaptive decline across varying parameter combinations in order to ensure that our results are not overly dependent on the particular parameter combinations we present in the main text. We find that, while the absolute amount of adaptive decline does depend on chosen values of parameters such as r , h , and b , the pattern of proportionally less adaptive decline in landscapes with more patches generally remains true. Each parameter affects the amount of adaptive decline differently. For example, as handling time is increased, the amount of adaptive decline generally decreases as handling time limits the amount of prey a predator can consume, and therefore limits over consumption. Conversely, adaptive decline stays relatively stable with increasing prey growth rate, as this trait primarily modulates the frequency and amplitude of predator and prey population cycling, rather than affecting the mean population sizes. Adaptive decline actually increases with increasing conversion efficiency, as conversion efficiency magnifies the effects of over consumption of prey on the population dynamics of the predators. At the up-

per and lower limits of parameter values where model runs occur without immediate extinction, population sizes can fluctuate dramatically and produce extreme (but not ecologically relevant) adaptive decline (e.g., 100% and -100% decline). Here, the predator typically persists at borderline extinction conditions with transient and large fluctuations in population size prior to extinction (Fig.S1, Fig.S2, Fig.S3).

3.4 Discussion

We have shown that meta-population dynamics can impact the extent of population decline in predators corresponding with the evolution of ecological traits such as attack rate (so-called adaptive decline). In particular, we find that landscapes containing more patches, and therefore, more opportunity for spatial aggregation among patches, generally exhibit less adaptive decline. Further, in a multi-patch landscape, reduced movement between patches, either via lower movement rates or via a less connected landscape, also limit the extent of adaptive decline. Interestingly, effects of landscape structure are most notable at intermediate rates of movement, such that the frequency of movement between patches is low enough that there is spatial differentiation among patches, but high enough that within-patch dynamics are correlated across patches. In addition to novel findings, our analyses confirmed earlier findings by Abrams (2019) that selection on a predator trait that modulates both its death rate and its attack rate can lead to adaptive decline.

While theoretical studies of adaptive decline in the ecological literature are relatively recent and few, there are important parallels between adaptive decline theory and theory developed to study both host-pathogen co-evolution and the evolution of cooperation. More prudent predators in our model can be viewed as “cooperative”: because they consume fewer prey, they exert weaker competitive effects on their patch cohabitants than exploitative predators. Given this, theoretical insights regarding when cooperation is favoured or disfavoured should also be relevant to understanding adaptive decline. Conditions under which cooperation would be expected to evolve would, by analogy, also be those conditions under which prudent predators would evolve, leading to less adaptive decline. (Fletcher and Doebeli, 2009) showed that positive assortment between cooperator genotypes is a necessary requirement for cooperation to evolve. When populations are

structured and interactions are local, cooperative individuals are more likely to interact with other cooperators and, therefore, share the benefits they produce. Assortment can emerge as a consequence of spatial landscape structure that limits movement/dispersal. Indeed, in our model, we find that landscapes that limit movement among patches favour more prudent predators (less adaptive decline), as patches containing more of these prudent predators benefit from greater prey numbers. There is also empirical support for this finding in host-parasite systems; using *E. coli* Berngruber et al. (2015), showed that less virulent (or more prudent) bacteriophage strains are favoured when they are able to cluster spatially in a low disturbance environment. Similarly, Kerr et al. (2006) found that when the movement of host *E. coli* and viral pathogen T4 coliphage between subpopulations was restricted, the evolution of prudent pathogens was favoured. Conversely, when movement between the subpopulations was high a more virulent pathogen was favoured (Kerr et al., 2006).

Kin selection theory has shown that high relatedness within a population can facilitate the evolution of altruistic behaviours (Hamilton, 1963; Fletcher and Zwick, 2006). More generally, even in the absence of explicit kin selection, the assortment of those carrying altruistic genotype and those receiving the benefits of altruism allows for the evolution of altruism. Limited movement between patches in our meta-population means that individuals are, in general, more likely to stay near where they were born, which means that relatedness will be higher within patches than between patches. Accordingly, individuals that have lower attack rates are likely to be in patches with other individuals of low attack rates, and therefore benefiting from the restrained predation. This assortment of low attack rate predators within patches incentivizes cooperative behaviour which, in the context of a predator, may manifest as the evolution of restraint in the exploitation of its prey. We can see this in our model in the single patch case. Here, predators tend to evolve towards over-exploitation, to their own detriment. However, in a meta-population of connected patches, with limited movement, we see the evolution of more restrained predators that exhibit little to no adaptive decline.

Empirical results from pathogen-host and herbivore-plant systems also align well with our results. For example, Eshelman et al. (2010) show that in spatially structured populations of *E. coli*, unre-

stricted movement favours high virulence, high infectivity strains of phage T4, while restricted movement favours low virulence and infectivity. Tack et al. (2014) found, contrary to their predictions, that there was no difference in virulence between the two landscape types with differing amount of spatial structure. However, this latter study used coevolving host and pathogen populations, and thus the host may have evolved stronger resistance in response, neutralizing what would have otherwise looked like increased virulence in the pathogen. By surveying patches of *Viscaria alpina* with varying amounts of isolation, (Carlsson-Granér and Thrall, 2015) investigated how landscape structure impacted both the evolution of pathogen infectivity and host resistance in *Microbotryum violaceum* and *V. alpina*, respectively. They found that landscapes that were more continuous (i.e. *V. alpina* patches that were better connected to neighbouring populations) led to both higher parasite infectivity as well as higher host resistance (Carlsson-Granér and Thrall, 2015).

The evolution of prudent predator behaviour maintains predators at or near their maximal population size. The degree to which prudent predator behaviour evolves is dependent on the spatial structure of the landscape they inhabit. Our finding that adaptive decline is less severe in complex landscapes with limited connectivity suggests that occurrences of extinction through adaptation are likely to be rare in nature because actual landscapes are often complex and comprise interconnected metapopulations. Additionally, in empirical systems prey are able to evolve counter-defenses to their predators, such that, as the attack rate of the predator increases, so does the evasion rate of the prey. This process can limit the outcome of adaptive decline in the predators (Abrams, 2019). Only under fairly specific scenarios might we expect to see adaptive decline in actual predator-prey situations, and identifying such scenarios could be an interesting avenue for future empirical work. Microcosm evolution experiments (e.g., the rotifer-alga predator-prey system) could be used to explore adaptive decline under more realistic conditions.

Our work has implications for the land management of specialist predators. Assuming that fragmented patches are connected to some extent by movement of predator and prey, increased fragmentation (i.e., an increased number of patches of habitat on a landscape, independent of total habitat quantity) has been linked to potentially positive ecological responses, such as increased

species richness at a landscape level (Fahrig, 2017). One proposed hypothesis is that multiple patches, with limited connectivity, can actually stabilize predator prey dynamics (e.g., see Hufaker, 1958). Our work here provides an additional mechanism whereby multiple patches might maintain greater abundances of both predators and prey. However, it is also well understood that fragmentation can imperil species for a variety of reasons including associated habitat loss, risk of stochastic extirpation of small, isolated populations, and inbreeding depression (Crooks et al., 2017). When small populations are effectively isolated from one another adaptive decline may represent yet another risk. We have shown that such populations are especially prone to adaptive decline and possibly even extinction.

Table 3.1: Model parameters and model variables.

Symbol	Description	$n_p \leq 8$	$n_p = 200$
Model parameters			
N_{pred}	Initial predator population size	500	
N_{prey}	Initial prey population size	1000	
K	Carrying capacity of prey	2×10^5	
d_0	Mortality probability	0.1	
d_1	Slope of mortality probability modifier	0.5	
α	Saturation rate for attack rate modifier	100	
σ_μ	Width of mutational effects distribution	0.001	
m_R	Probability of a prey moving	1×10^5	
r	Intrinsic growth rate of prey	0.15	
b	Conversion efficiency of predator	0.1	0.25
c	Attack rate of predator	0.01	0.015
h	Handling time	0.1	0.04
n_p	Number of “patches” in our simple landscapes	[1,2,4,6,8]	200
Model variables			
x	Value of trade off trait	[0.01, 1×10^{-3} , 1×10^{-5} , 1×10^{-8}]	
m_C	Probability of a predator moving		

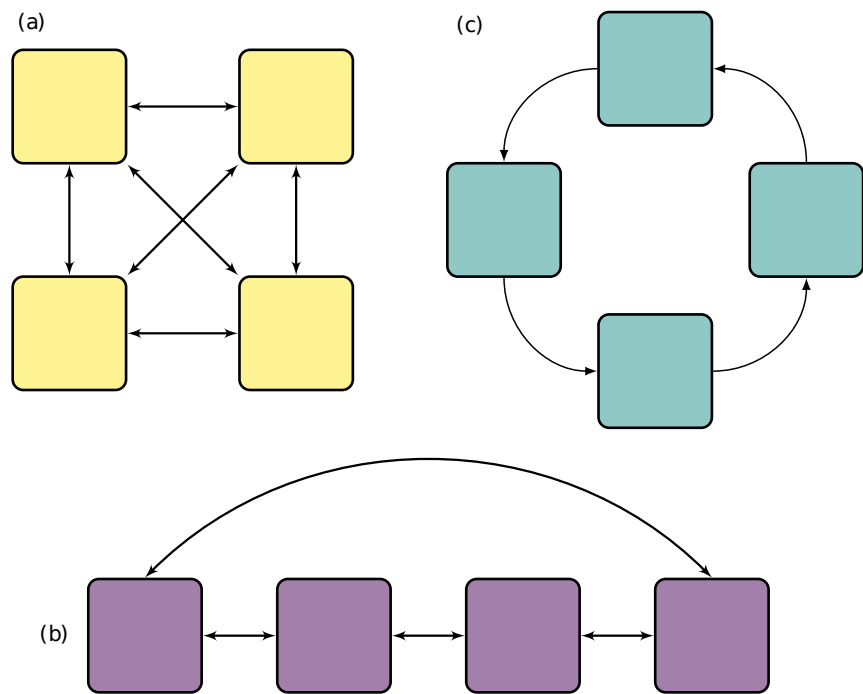


Figure 3.1: Graphical representations of the available movement patterns across the three spatial structures: (a) universal (b) stepping stone (c) one-way.

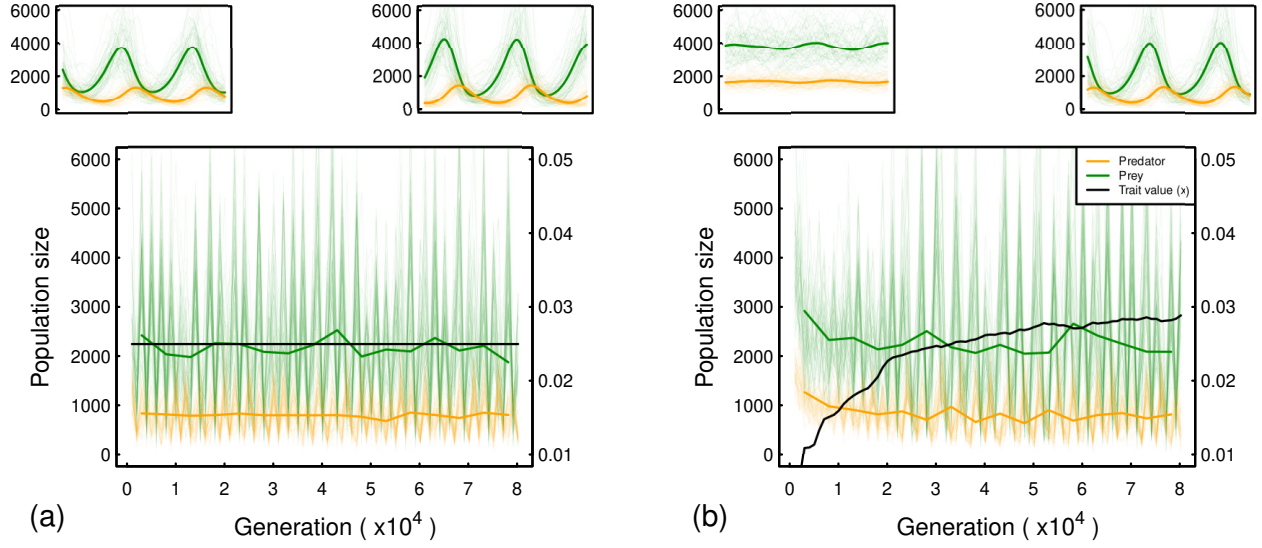


Figure 3.2: Predator and prey cycles tend to synchronize across patches through time (generations) (a) without and (b) with evolution of the predator trait (x_i). Evolution of predator traits leads to larger amplitude cycles but lower mean population sizes of both prey and predators. Small top panels show the first and last 200 generations of each main panel. The green and orange lines show the population size within a patch of the prey and predators respectively, average population size across patches are represented by the bold green and orange lines, with the main panels showing a simple running average with a width of 5000 generations. [$r = 0.1, b = 0.27, k = 4 \times 10^4, n_p = 65, c = 0.015, h = 0.03, d_0 = 0.05, d_1 = 0.5, \alpha = 100, m_C = 1 \times 10^{-3}, m_R = 1 \times 10^{-2}$]

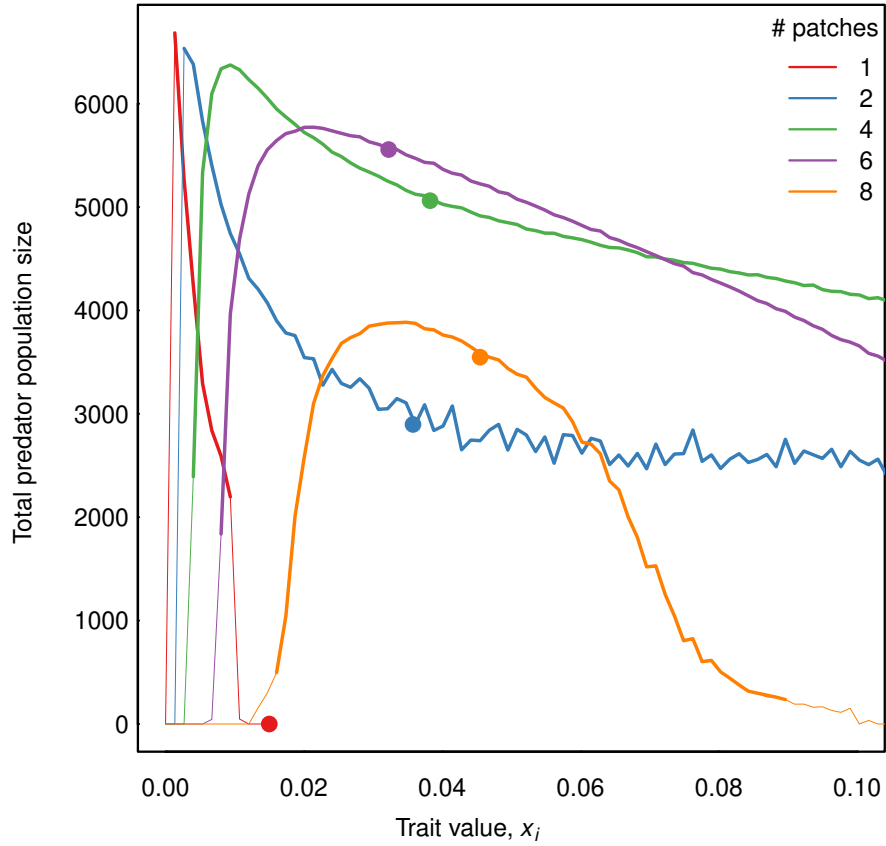


Figure 3.3: Predator population size peaks at intermediate predator trait values and adaptive decline is most pronounced in landscapes with few patches (different curves depict landscapes comprising different numbers of patches). Curves show mean population size calculated across model runs of 10,000 generations with no evolution. Curves are shown over the range of trait values for which predator populations persisted, with the thin lines representing regions where populations go extinct. Coloured points show population sizes at evolved trait values for model runs where traits were free to evolve. Visually, adaptive decline can be quantified as the vertical distance between the peak of each curve and the corresponding point of the same colour. With only a single patch, evolution led to trait values that ultimately drove predators extinct (extreme adaptive decline), and thus the red point is shown at a population size of zero. Parameters are as in table 1, $n_p \leq 8$. For each line with n_p the carrying capacity, K , is divided by n_p .

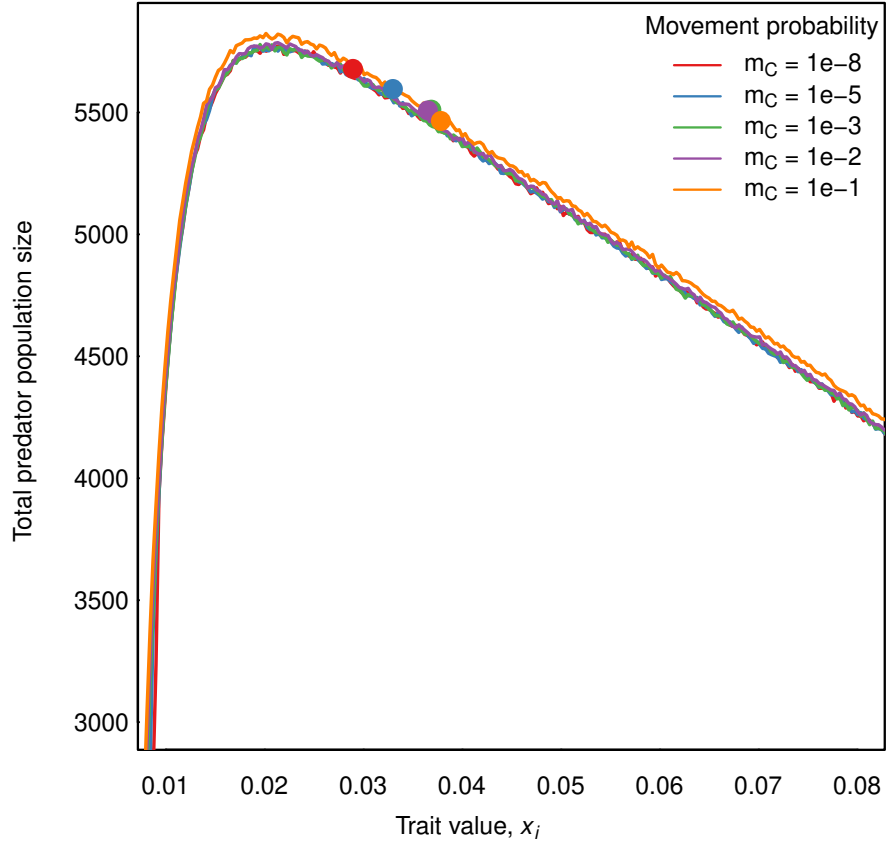


Figure 3.4: Predator population size is insensitive to rates of movement between patches, however, adaptive decline is greatest when movement rates are highest. As in Fig. 3.3, curves show mean population size calculated across model runs of 10,000 generations with no evolution and coloured points show population sizes at evolved trait values for model runs where traits were free to evolve. All parameters, aside from predator movement rate and patch number ($n_p = 6$), were as in Fig. 3.2.

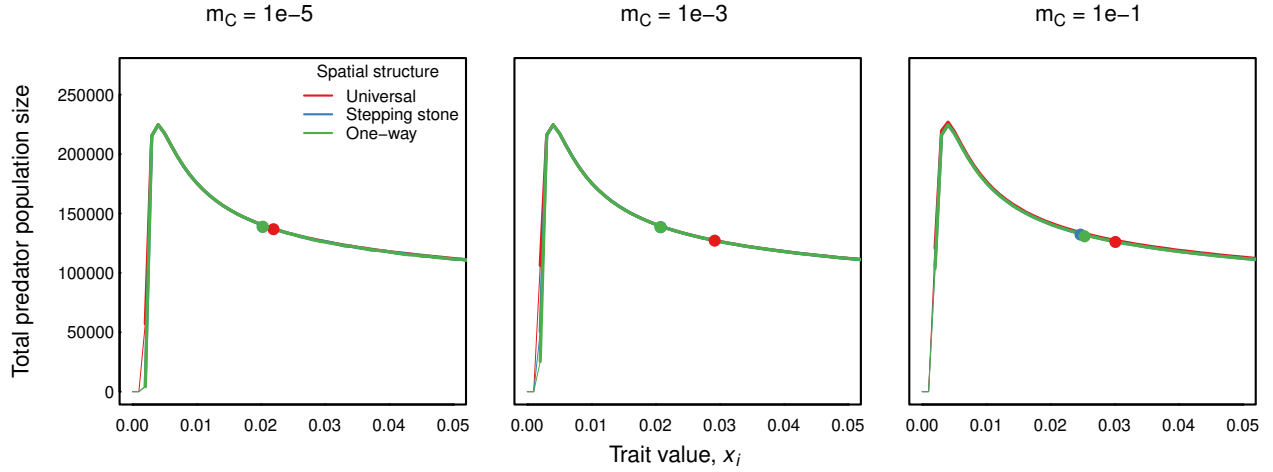


Figure 3.5: In addition to being insensitive to rates of movement, predator population size is insensitive to the spatial structure of patches. As in Fig. 3.4, adaptive decline is greatest when movement rates are highest. Comparing across spatial structures, adaptive decline is highest when the spatial structure is the least restrictive ('Universal'). The effect of spatial structure is most pronounced at intermediate amounts of movement, and is less noticeable at the extremes of both high and low movement. As in Fig. 3.3, curves show mean population size calculated across model runs of 10,000 generations with no evolution and coloured points show population sizes at evolved trait values for model runs where traits were free to evolve. Parameters are as in table 1, $n_p = 200$.

Chapter 4

Conclusion

I set out to explore the relationship between species-resource interactions and the landscape those interactions play out on. Two very different models were used to accomplish this; Firstly I used a series of models of pollinator foraging across agricultural landscapes to see how assumptions around pollinator movement change predictions of optimal hedgerow design when seeking spillover pollination of crops from wild pollinators. I found that when moving from the random model to models where pollinators preferentially forage in higher value locations increases risk of extinction due to over-exploitation of those areas. However this effect is recovered from when pollinators can assess whether or not those locations have been depleted by previous visits. I found that the simple, random model is acceptable at estimating pollination when compared to a model with more complex foraging dynamics. In general, when pollinators can nest in and forage on crops, there is little effect associated with hedgerow size and placement, even when plants within hedgerows are of higher value to pollinators than the surrounding crops. When pollinators are not able to nest in crops, I found that the per capita rate of pollination increases with increasing fragmentation and decreasing hedgerow landscape proportion. However the overall proportion of crops which are pollinated decreases due to pollinator population declines, with this effect being significantly more dramatic when looking at the proportion of landscape which is used for hedgerows. Secondly, I used a classic model of predator-prey to explore eco-evolutionary feedback, and how predictions change when landscapes have complex spatial structure with multiple patches with varying amounts of movement between them. In the case of the adaptive decline

model I find when the predators are in a single well-mixed patch, that the predators will evolve to over-exploit their prey and drive themselves extinct similar to Abrams (2019). With more patches they no longer drive themselves extinct and in fact see less population decline from their theoretical maximum. When movement between those patches decreases they see less adaptive decline and vice versa. The effects of more complicated landscape structure are most notable at intermediate rates of movement, such that the frequency of movement between patches is low enough that there is differentiation among patches, but high enough that patches remain correlated with each other.

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Appendix A

Supplementary Figures

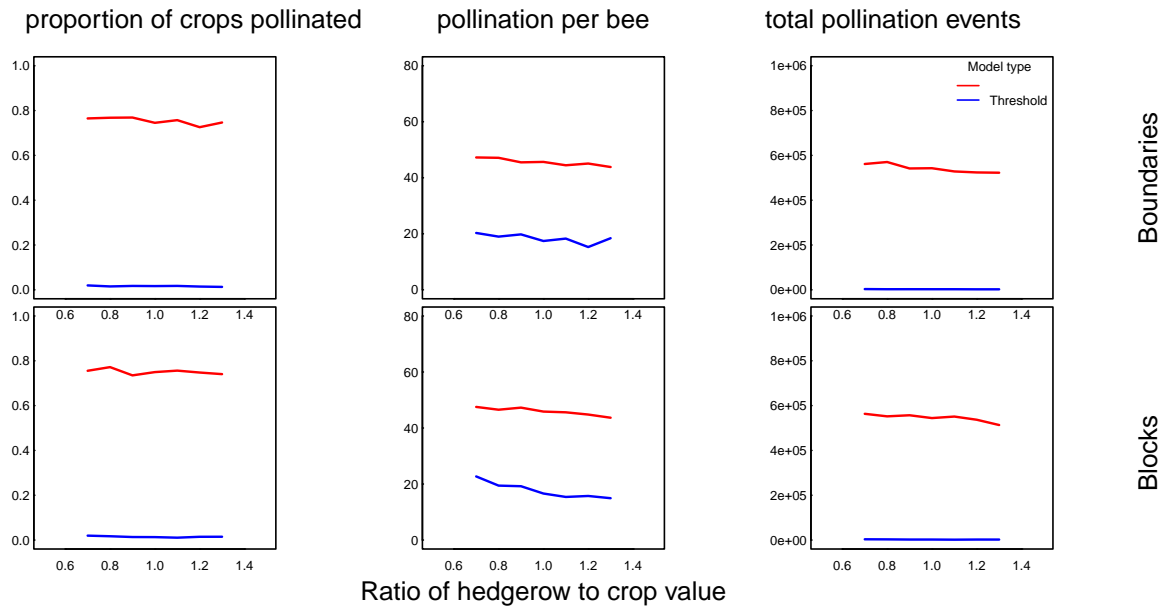


Figure A.1: Ecosystem services provided to crop cells are relatively insensitive to the ratio of the value of plants within hedgerows to the value of crop plants when pollinators forage according to a more complex discernment model. Panels here are all as in Fig. 2.4, except that we vary the relative values of the two resource types on the x -axis. All other parameter values are as in Table 2.1.

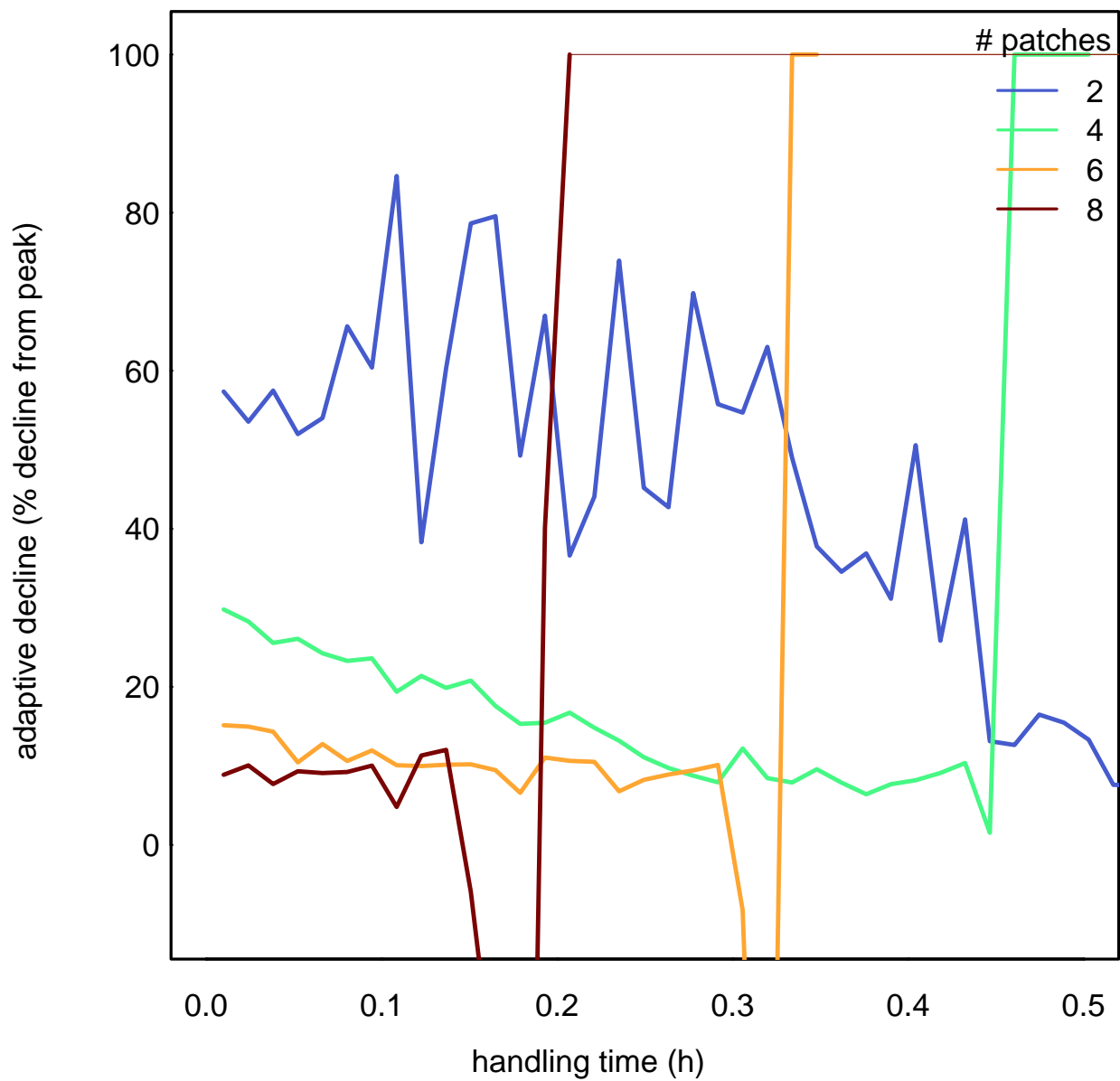


Figure A.2: The amount of adaptive decline as a function of the handling time for 2,4,6,8 patches. Parameters are as in table 1, $n_p \leq 8$. For each line with n_p the carrying capacity, K , is divided by n_p .

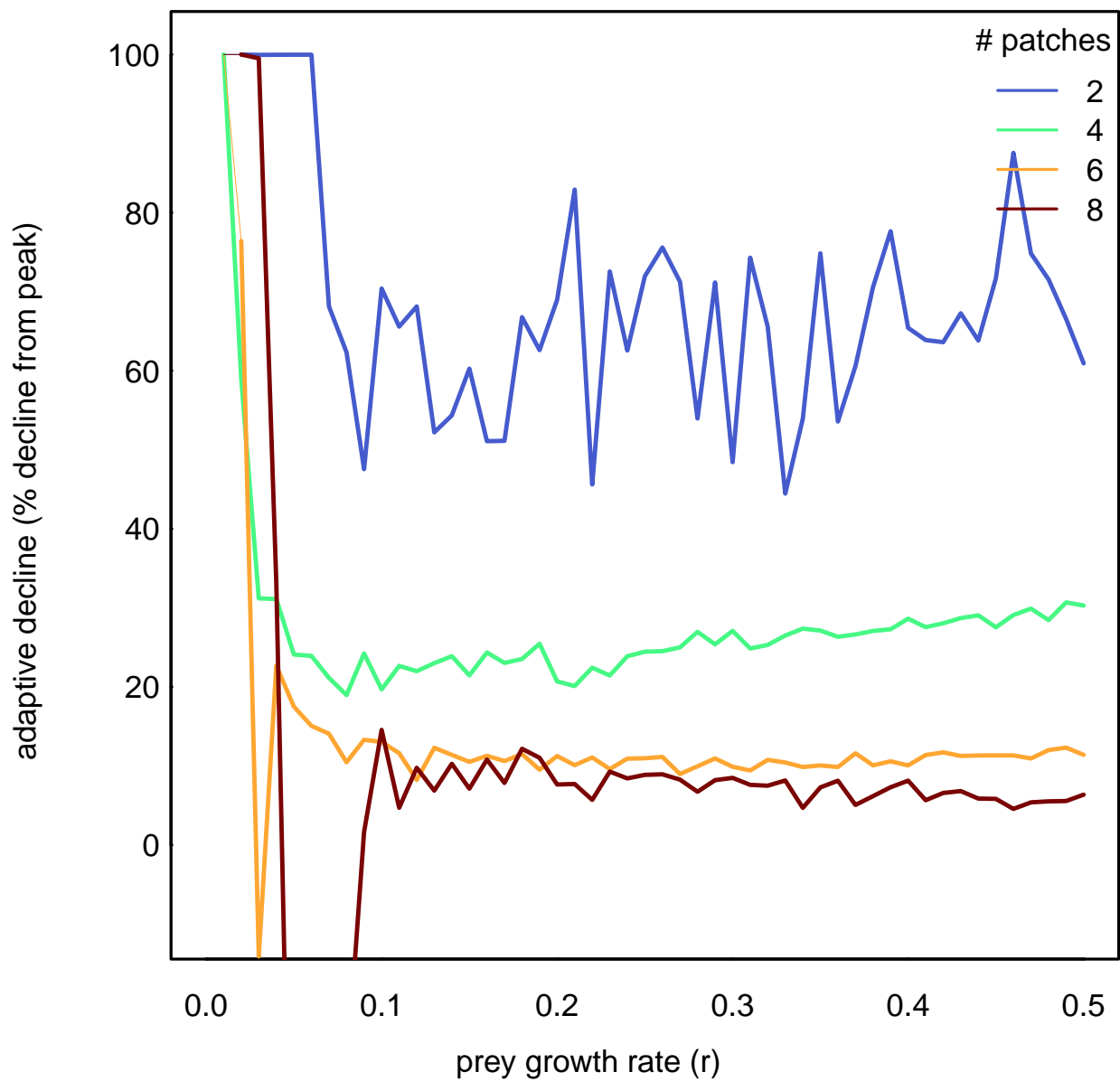


Figure A.3: The amount of adaptive decline as a function of the intrinsic growth rate for 2,4,6,8 patches. Parameters are as in table 1, $n_p \leq 8$. For each line with n_p the carrying capacity, K , is divided by n_p .

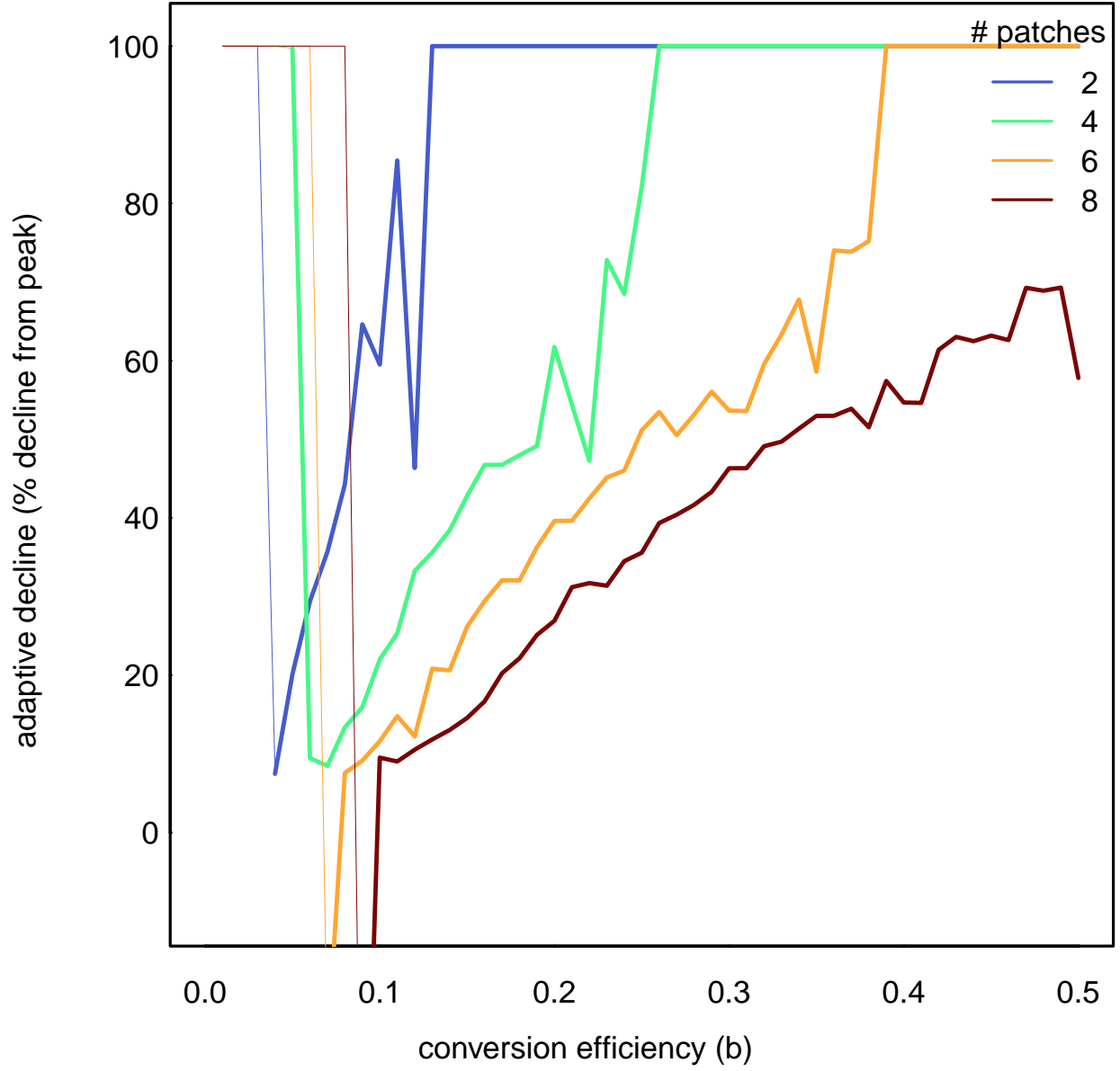


Figure A.4: The amount of adaptive decline as a function of the conversion rate for 2,4,6,8 patches. Parameters are as in table 1, $n_p \leq 8$. For each line with n_p the carrying capacity, K , is divided by n_p .

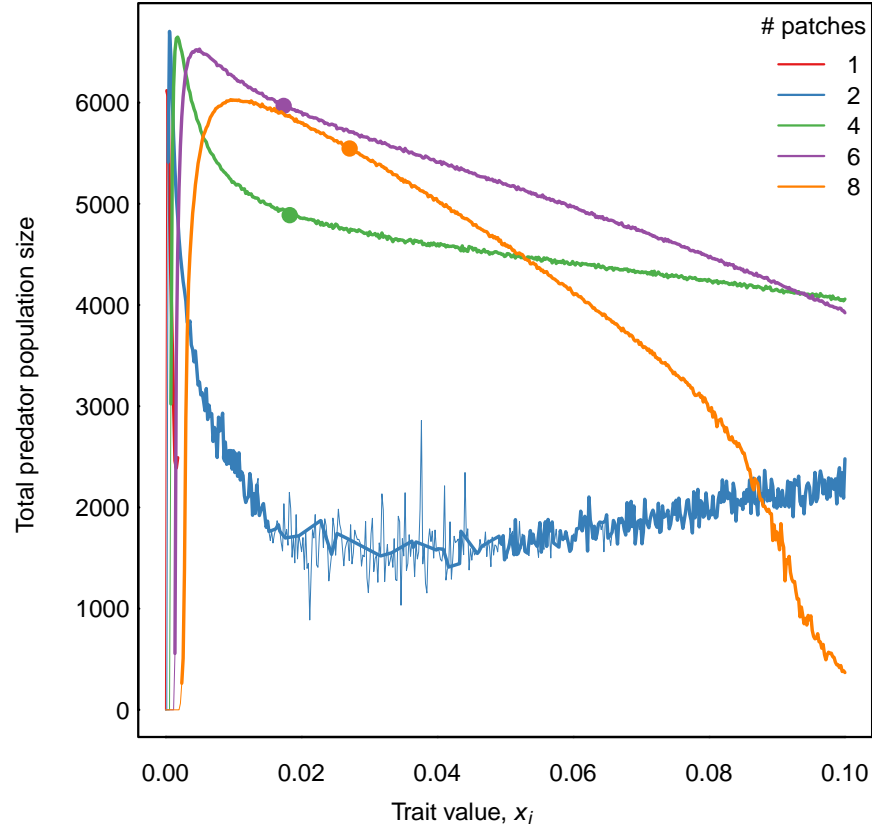


Figure A.5: Predator population size peaks at intermediate predator trait values and adaptive decline is most pronounced in landscapes with few patches (different curves depict landscapes comprising different numbers of patches). Curves show mean population size calculated across model runs of 10,000 generations with no evolution. Curves are shown over the range of trait values for which predator populations persisted, with the thin lines representing regions where populations go extinct. Coloured points show population sizes at evolved trait values for model runs where traits were free to evolve. Visually, adaptive decline can be quantified as the vertical distance between the peak of each curve and the corresponding point of the same colour. With only a single patch, evolution led to trait values that ultimately drove predators extinct (extreme adaptive decline), and thus the red point is shown at a population size of zero. Parameters are as in table 1 except $c = 0.05$ and $\alpha = 500$. $n_p \leq 8$. For each line with n_p the carrying capacity, K , is divided by n_p .