FACULTY
OF SCIENCES

Flanders' Natura 2000 network is not effective in protecting beetles from climate change

Zaya Lips
Student number: 01900092

Supervisors: Prof. dr. Dries Bonte, Dr. Femke Batsleer
Counsellor: Garben Logghe

Master's dissertation submitted in order to obtain the academic degree of
Master of Science in Biology

Academic year 2023-2024

GHENT
UNIVERSITY

Table of contents

Introduction 3
Materials and methods 5
  Virtual species 5
  Basics of the model 6
  Landscape 7
  Different scenarios 8
  Survival linked to the thermal niche 8
  Fecundity 9
  Dispersal 9
  Data analysis 10
  Alpha diversity 11
  Bèta diversity 11
  Gamma diversity 12
  Functional diversity 12
Results 12
  Alpha diversity 12
  Bèta diversity 17
  Gamma diversity 18
  Functional diversity 18
Discussion 22
Acknowledgements 28
References 28
Appendix 33
  1. Sensitivity analysis 33
    Results 33
    Conclusion 35
  2. Functional diversity 35
    2.1 Coefficient of variation 36
    2.2 Mean of life-history traits 41
ODD protocol 46
  1. Purpose 46
  2. Entities, state variables, and scales 46
    Types of entities and their state variables 46
    Scale and extent 46

3. Process overview and scheduling Design concepts 46
4. Design concepts 47
    Basic principles 47
    Emergence 47
    Adaptation 47
    Objectives 47
    Learning 48
    Prediction 48
    Sensing 48
    Interaction 48
    Stochasticity 48
    Collectives 49
    Observation 49
5. Initialization 49
6. Input data 49
7. Submodels 50
    Creating the two different landscapes 50
    Species initialization 50
    Population initialization 50
    Determine which individuals will survive according to the environment temperature 50
    Individuals get offspring 51
    Dispersal 51
8. References 51

Introduction

Climate change is known to have disastrous effects on biodiversity (Koch et al. 2012; ; Newbold 2018, Short et al., 2016; Newbold 2018, Short et al., 2016). Most evidence is available for plants and vertebrates, with arthropods being heavily overlooked (Troudet et al., 2017), despite studies indicating the alarming rate at which these vertebrates are declining (Cardoso et al., 2020). This decline is not solely due to climate change, but rather an interplay of multiple stressors including habitat fragmentation, habitat loss, pollution, and insecticides (Wagner et al., 2021). Despite the recognition of this disturbing trend, little effort has been made to protect these species from extinction (Cardoso et al., 2011; D'Amen et al., 2013). For example, the IUCN Red List does not provide a realistic picture of the arthropod status (The IUCN Red List of Threatened Species, n.d.). For the red lists, a much higher percentage of vertebrates than invertebrates is covered to assess their conservation needs. This bias subsequently leads to less accurate conservation strategies for these understudied species. Because arthropods play a vital role in ecosystem functioning, such as nutrient cycling and pollination, fast intervention is needed (Ollerton et al., 2011; Yang & Gratton, 2014).

Species can adapt to climate change by range shift, acclimatization, and/or adaptation. How a species responds to this climate change depends on (genetic) trait variation such as dispersal, habitat breadth, thermal optimum, and fecundity (Richards et al., 2021; Lehmann et al., 2020; Pacifici et al., 2017; Richards et al., 2021). Therefore, incorporating species traits into distribution models will more accurately predict the ecological impacts of climate change. However, most studies are based on correlative approaches neglecting a mechanistic perspective to include traits and/or life histories (Green et al., 2022). Of these few studies including traits, most include only one, which is insufficient to explain complex responses to climate change. For example, patterns of range expansion observed in numerous species cannot be explained by a single trait (Chen et al., 2011: Comte et al., 2024). Furthermore, which traits and how they affect range expansion are species-specific. Therefore, a multi-trait approach is needed to make reliable predictions about ecological responses to climate change. By making these models spatially explicit, the results will be highly relevant for conservation decisions. In addition to more accurate predictions, these models also provide greater insight into how and why species differ in their ecological responses which currently, most studies fail to do so (Brown et al., 2014). These insights are important to better protect species by identifying which species are more vulnerable.

In particular, dispersal ability is an important trait to capture because of its contribution to many ecological processes (Travis et al., 2013). Dispersal consists of three main components: departure, transfer, and settlement (Clobert et al., 2004). These components can be associated with species-specific traits called dispersal syndromes, traits that are correlated with dispersal, but are also landscape dependent (Stevens et al., 2013). For example, a species may be highly dispersive, but if the landscape is of poor quality, its chances of finding suitable habitat are reduced. The inability to find a suitable habitat can lead to reproductive failure or even death. The dispersal capacity of a species can therefore be thought of as the ability of a species to spread. Spread depends on dispersal and population growth. These two factors are temperature dependent, but not necessarily in the same way (Amarasekare, 2024). This, combined with landscape effects, makes the dispersal capacity of a species difficult to predict under climate change.

Tracking of the climatic niche is an example of an ecological response where dispersal capacity plays an important role (Eiserhardt et al., 2013; La Sorte & Jetz 2012). In cases where acclimatization or adaptation is insufficient, colonization of new areas may be the only option to survive climate change. A decrease in dispersal capacity will inhibit the ability of a species to follow its climatic niche. In addition, the rescue effect allows metapopulation persistence by the colonization of individuals from other populations (Brown & Kodric-Brown, 1977; Lande et al., 1998). Small fragments can only support small populations, which increases their sensitivity to the effects of demographic stochasticity and reduces their genetic variance, which can ultimately lead to extinction. However, these processes can be prevented by the colonization of these small patches by individuals from other fragments. As the dispersal capacity of a species decreases, the occurrence of the rescue effect also decreases. Overall, the landscape seems to indirectly shape species' responses to climate change (Bonte et al., 2010).

The connectivity of a landscape is described by the interplay between the dispersal capacity of a species and the landscape itself, making it inherently species-dependent (Cheptou et al., 2017). As a result, it is not possible to determine a general connectivity value for a landscape. An important landscape characteristic influencing connectivity is fragmentation, which refers to the process by which habitats are divided into smaller, more isolated patches. Smaller habitat fragments support smaller populations which are more vulnerable to extinction (Cheptou et al., 2017). This is particularly detrimental if the rescue effect is reduced due to reduced dispersal capacity. The impact of fragmentation on biodiversity is however controversial. Some studies suggest that fragmentation benefits species diversity (Fahrig, 2017; Fahrig et al., 2019), while others dispute this claim (Fletcher et al., 2018). As a result, the effects of fragmentation on biodiversity remain controversial. However, fragmentation is often accompanied by habitat loss, and there is a general agreement on the negative effects of these combined factors on biodiversity. In the same way that the effects of fragmentation on biodiversity are not clear, the effects on dispersal are also complex. This makes it even more difficult to determine landscape connectivity for specific species. Although the effects of fragmentation on dispersal are not fully understood, dispersal between patches of a metacommunity is certainly necessary to maintain populations in the smaller patches (Brown & Kodric-Brown, 1977; Lande et al., 1998).

Because the effects of connectivity and fragmentation are species dependent, assessments of landscape connectivity should include multiple species (Cheptou et al., 2017). However, this is often not the case (Brodie et al., 2015). In addition to not including more than one species, most studies of fragmented landscapes use simple, unrealistic fragmentation patterns. Tao et al. (2024) have shown that the results of these studies are not generalizable to complex, realistic landscapes. Therefore, in addition to including multiple species in connectivity studies, the landscape should also be spatially explicit. This will make the results more robust for conservation strategies in that particular landscape.

The Natura 2000 network was created to increase the connectivity of Europe's valuable habitats with the goal of protecting threatened and valuable species (Natura 2000 - Environment - European Commission, n.d.). It has been suggested that this network was installed with a focus on plant and vertebrate protection, and therefore to be badly equipped to protect arthropods (D'Amen et al., 2013; Hernandez-Manrique et al., 2012). For this reason, we can also expect that arthropod hotspots may not currently fall under the coverage of the Natura 2000 network.

Coleoptera are one of the largest order of insects (Zhang 2011). Like other arthropods, their populations are declining, with dung beetles being one of the most affected taxa (Sánchez-Bayo & Wyckhuys, 2019). The order is not only large but also functionally diverse (McKenna et al., 2019). This explains their importance for ecosystem functioning. Bioturbation, seed dispersal, and decomposition are some examples (Nichols et al., 2008; De Vega et al., 2011). Despite their critical ecological roles, beetle species remain relatively understudied. Only grassland species will be studied as these species appear to be in even greater decline compared to other terrestrial arthropods (Seibold et al., 2019).

Since landscape connectivity is species-dependent, we lack information on how understudied species experience a landscape (Cheptou et al., 2017). An effective method to address this problem is the virtual species approach (Wood et al., 2022). A virtual species is a combination of trait values that, when realistically assigned, represent real species, including those that are understudied. For instance, Santini et al. (2016) successfully predicted species' responses to climate change using this approach with only sparse data available on the species. To ensure realistic trait combinations, it is beneficial to include trait syndromes, which are traits that are closely related to each other. Since body size is closely related to many other traits, it serves as a good central trait for creating realistic virtual species (Woodward et al., 2005). This method will lead to reliable predictions for real communities. Another advantage of the virtual species' approach is its efficiency in covering a wide range of beetle traits with a relatively small number of modeled species. Additionally, it eliminates sample bias (Qiao et al., 2016).

We aim to assess the effectiveness of the Natura 2000 areas in Flanders in protecting Coleoptera from climate change. To achieve this, virtual species are created and simulated using an individual-based model. Two landscapes will be used to determine the effects of two contrasting conservation scenarios on the Flanders' beetle community. One landscape will include only the ecologically valuable grasslands within the Natura 2000 network present in Flanders, whereas the other landscape will include all valuable grasslands in Flanders. Each species is considered eurytopic for all the selected grasslands. Different heating scenarios are added to the model to study the effect of temperature on trait and species distributions under different management strategies. The effectiveness of the landscapes will be assessed by examining the alpha, bèta, gamma, and functional diversity of the beetle community. We expect low effectiveness in protecting Coleoptera from climate change, given the lack of focus on Coleoptera in conservation plans and the findings of previous studies (D'Amen et al., 2013; Hernandez-Manrique et al., 2012). Furthermore, we hypothesize that all diversity measures will be significantly higher in the landscape, including all Flanders' grasslands, as this landscape shows a higher level of connectivity, increasing its robustness to climate change.

Materials and methods

Virtual species

Virtual species are formed using real life-history traits of Flanders' beetles (figure 1), utilizing a dataset containing trait values from Western European arthropods (Logghe et al., 2024). The correlations between trait values were established through Bayesian regression models in R using the brms package (Bürkner 2017). Each trait was individually tested against another trait. A range of potential slopes and intercepts were obtained from these models. Only traits from grassland species were used since these species are the focus of our study.

Body size is closely connected to many other factors, such as fecundity, dispersal distance, and environmental temperature (Honěk 1993; Jenkins et al., 2007; Klok & Harrison, 2013; Shelomi, 2012). Therefore, we will only use the correlations between body size and other life-history traits to ensure realistic trait combinations. The other life-history traits selected, are thermal breadth, thermal optimum, dispersal capacity, and fecundity. First, a random body size for each species is selected from the trait dataset. Next, for each trait, random draws are selected from the combined posterior distributions of the slope and intercept. Using the randomly selected body size, slope, and intercept, trait values can be determined using equation 1. Consequently, a virtual beetle with five unique life-history traits is created. This process will be performed multiple times to simulate a beetle community.

$$Trait\ value = intercept + \log(size) * slope \quad (1)$$

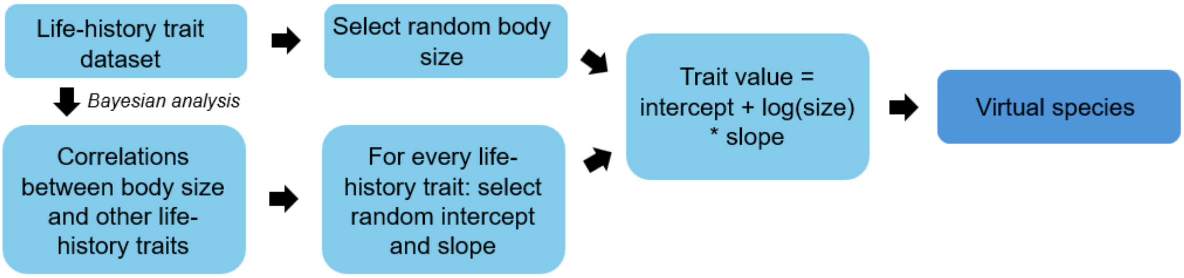


Fig. 1: Workflow to create a virtual species.

Basics of the model

An individual-based model is created to simulate the effects of climate change on the virtual species using Python 3.10. This method is chosen for its ability to simulate population and community dynamics based on individuals' life-history traits in a robust manner (DeAngelis & Grimm 2014; Grimm et al. 2017). Interactions between beetle species are poorly understood in nature; therefore, species are simulated independently from one another. Additionally, we assume no competition due to the large grid cells relative to the small beetles and thus expect local niche segregation to occur.

Every run starts by creating a virtual beetle, as described above. Since we want to compare different scenarios with each other, we initialize the landscape at its carrying capacity, *K*. Thus, scenarios with the same landscape will always begin with the same population size. After initialization, the model loops through the following steps (Figure 2), with each loop representing a generation of beetles: assessing survival change according to the environmental temperature, surviving individuals get offspring, all the old individuals die, some offspring will disperse depending on cell density, and finally, the number of individuals above the carrying capacity die. These steps are closely related to the life-history traits assigned to the different species. Each run lasts for 100 generations, to allow the population to stabilize. For each run, the population size at the end of the simulation and the end positions of the individuals are obtained.

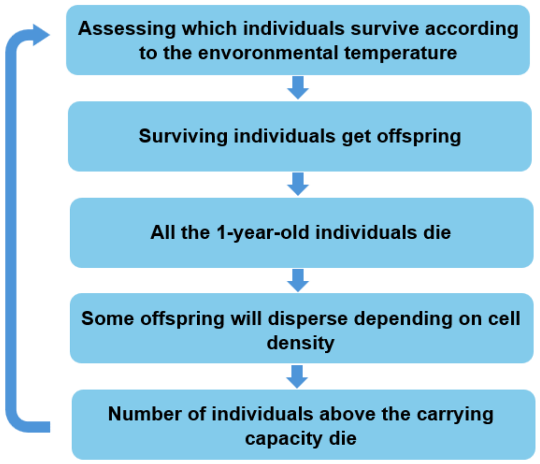


Fig. 2: Every simulation will loop 100 times through these steps.

Landscape

Two landscapes are used in the model (Figure 3). For the first landscape, we aim to include only the biologically valuable grasslands present in the Natura 2000 area in Flanders. For the second landscape, we aim to include all the biologically valuable grasslands present in Flanders. To create these landscapes, the geographic information system QGIS 3.24.0 is used. The datasets 'vogelrichtlijngebieden' and 'Habitatrichtlijngebieden, Toestand 18/01/2013' from Agentschap voor Natuur en Bos are used to create Flanders' Natura 2000 polygon layer. The dataset 'Biologische Waarderingskaart en Natura 2000 Habitatkaart, Toestand 2023 (BWK)' from INBO is used to select the correct habitat types (De Saeger et al., 2023, De Knijf et al., 2010). All three datasets can be found on www.geopunt.be.

Not all areas are suitable for grassland beetles; therefore, we include only ecologically valuable grasslands. This is based on the assumption that the number of species present in the less valuable grasslands will be negligible compared to those in the valuable areas. This also significantly decreases the running time of the model. Each species is considered eurytopic for all the selected grasslands.

We only want to include biologically valuable habitats therefore only the following grassland types are selected: species-rich permanent grassland (coinciding with the following BWK codes: hj, hp+, and hpr), semi-natural grasslands (ha, hc, hk, hm, hmm, hme, hmo, hn and hu), dry dune grassland (hd and had), Corynephorus canescens grasslands (hat), and Aira grasslands (hac) (De Saeger et al., 2023, Vriens et al., 2011). To determine the habitat types of the different polygons, we only use unit one of the polygon descriptions since this unit best describes the areas. Sometimes 'b' is added to the codes which describes the growth of young trees and shrubs which shows a decrease in the value of the grasslands. Since the polygon is still tagged as a valuable grassland, we also keep these habitat types. Lastly, the signs '+' or '-', are sometimes included in unit one. This sign describes how well a biotope is developed with '+' being a well-developed biotope and '-' describing a weakly developed biotope. As this factor is not important to our study, it will not be used for the selection of habitats. We considered the sign only for code hp, since polygons with code hp- or hp indicate species-poor grasslands. When all suitable grasslands are selected, we use only the polygons that overlap with the Natura 2000 area for the Natura 2000 landscape, whereas we use all selected grasslands for the other landscape.

Next, a grid is constructed of the two different landscapes with cells of 1 × 1 km^2. The total landscape is 237 × 91 km^2. The grassland cover percentage is calculated for each cell. Carrying capacity is determined by multiplying this percentage by ten. Thus, the maximum carrying capacity per cell is ten individuals per species. This amount is low for computational reasons, but will still lead to reliable predictions, as we assume numbers in reality are a multiple of this computational number of individuals. The landscape with only Natura 2000 grasslands has 669 cells with a carrying capacity of at least one, while the other landscape contains 2278 of these kinds of cells.

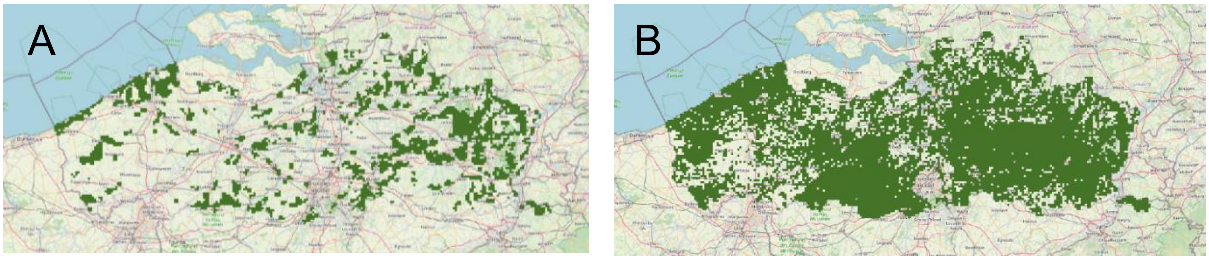
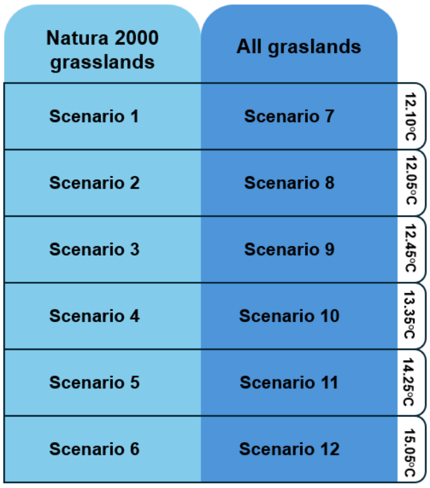


Fig. 3: The two different landscapes used in the model. A: only the valuable grasslands present in the Natura 2000 area of Flanders. B: All the valuable grasslands present in Flanders.

Different scenarios



Natura 2000 grasslands	All graslands	
Scenario 1	Scenario 7	12.10°C
Scenario 2	Scenario 8	12.05°C
Scenario 3	Scenario 9	12.45°C
Scenario 4	Scenario 10	13.35°C
Scenario 5	Scenario 11	14.25°C
Scenario 6	Scenario 12	15.05°C

Fig. 4: Every virtual species will go through these twelve different scenarios.

Six different environmental temperatures, based on the IPCC report (IPCC 2022), are modeled in combination with the two different landscapes, resulting in 12 different scenarios. Each virtual species goes through all of these scenarios (figure 4), simplifying comparisons. As mentioned, one landscape includes only the suitable grasslands present in the Natura 2000 area of Flanders, whereas the other landscape includes all the suitable grasslands present in Flanders. The six different environmental temperatures are based on the Shared Socioeconomic Pathways (SSPs) defined by the IPCC Sixth Assessment Report (IPCC 2022). The first temperature is the average temperature of Flanders from 2023 (KMI 2024). The other temperatures are the expected changes in average temperature by 2081-2100 based on the 2021 report of the IPCC. This leads to the following environmental temperatures, 12.1°C, 12.05°C, 12.45°C, 13.35°C, 14.25°C, and 15.05°C respectively linked to following scenarios, current average temperature, SSP1-1.9, SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5. Temperature is always homogeneously modeled across landscapes.

Survival linked to the thermal niche

Each individual receives a fitness value between one and zero. However, fitness only represents survival associated with the thermal niche in our model. Nevertheless, this value is important for local demography since only after assessing survival via fitness, an individual can reproduce and disperse (Figure 2). Once an individual survives, reproduction and dispersal depend only on the life-history traits fecundity and dispersal, respectively (see further). The fitness value depends on two life-history traits (thermal optimum and thermal breadth) and the environmental temperature in the grid cell. Since thermal breadth and optimum are constant for individuals of the same virtual species, their fitness will only vary if the environmental temperature is different. Survival chance, on the other hand, will be more stochastic, as it is only partially influenced by fitness. Randomization is done by generating a random number between one and zero for each individual. If this number is lower than the individual's fitness, the individual is removed from the model. Thus, the higher the match between the environmental temperature and an individual’s thermal optimum, the higher its chance of survival will be.

Many studies have documented the generality of left-tailed skewed thermal niches (Roitberg & Mangel 2016; Ruel & Ayres 1999). Thereby, the performance of an individual decreases faster when the environmental temperature is above its optimum than when the environmental temperature is below its optimum. We want to include this observed asymmetry in the calculation of an individual's fitness to make the model more realistic (figure 5). Therefore, we use an analogy to the Morse potential function to calculate the fitness, as seen in Terry et al. (2024).

$$G_{Mor}(E) = R_{max}\left(1 - \frac{\left(1 - e^{a(E-\phi)}\right)^2}{a^2 W^2}\right) \quad (2)$$

The value *a* determines the asymmetry of the niche and is set to 0.1 since this provides a realistic temporal niche for beetles (Buckley et al., 2022; Terlau et al., 2023). A sensitivity analysis will be performed to test the effect of this factor (appendix 1). R_{Max} describes the local intrinsic growth rate of an individual at its thermal optimum. In the model, R_{Max} is equal to one. Therefore, the survival probability of an individual will be equal to one when the environmental temperature and its thermal optimum are the same. E is the parameter for the individual's thermal optimum, whereas W describes the thermal breadth of the individual.

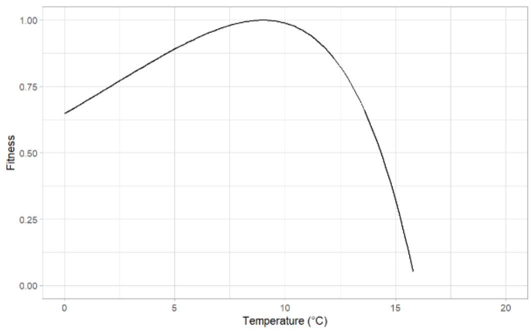


Fig. 5: Example of a species fitness curve using equation 2 where E = 9 and W = 10.

Fecundity

In the model, we assume no partner limitations; therefore, we model only females. Since we do not include genetics in the model, this assumption should not pose problems regarding the reliability of the results. As mentioned above reproduction is determined in part by fitness and hence by thermal optimum and range. This is because fitness partially controls whether an individual reaches reproductive age. However, if an individual reaches this age, the number of offspring, λ, depends solely on the life-history trait fecundity. Some beetle species are k-strategists, producing few offspring with higher survival rates. While many other beetle species produce hundreds of eggs, only a small portion of them will successfully hatch and reach reproductive age. These are r-strategists. To minimize the running time of the model, λ will only represent the offspring who reach adulthood under demographic stochasticity and selection. Therefore, we take the base ten logarithm of the fecundity value of the individual. Taking this logarithm will result in a proportionally greater effect on higher fecundity values (r-strategists) compared to lower values (k-strategists). To get the final λ one is added to the transformed fecundity value this ensures an average of two offspring per individual. This approach avoids modeling species with declining populations only because of a low average number of offspring, independent of the environment. The number of offspring per individual of the same virtual species is constant. Thus, demographic stochasticity is added by taking a Poisson distribution to determine the final number of offspring per individual. Offspring inherit the life-history traits and position of their parent. In a later step, the offspring will be able to disperse.

Dispersal

To realistically simulate the movement of an individual, the life-history trait dispersal is used, which is valued between one and zero. In the trait database the dispersal value represent the relative mobility of a species in comparison with species of the same order, which is in most cases based on the wing load of the species. This trait includes the probability of dispersal, as well as the distance traveled. A value of one means a species will travel far and/or has a high probability of dispersal. We use the Pareto distribution to represent these two factors (García & Borda-de-Agua, 2017).

$$Y = \frac{\frac{\alpha-1}{\alpha} * X\_mean}{U^{\frac{1}{\alpha}}} \quad (3)$$

X_mean represents the average distance traveled by a virtual species. This value is calibrated using the maximum known dispersal distance of Flanders' beetle species. In this case, a dispersive ladybug species typically traveled 18 km (Jeffries et al., 2013). Multiplying the dispersal trait value of the virtual species by 18 gives the value for *X_mean*; therefore, the most dispersive virtual beetle, with a dispersal value of one, can travel an average of 18 km. Since individuals from the same species will obtain the same dispersal curve (figure 6), we include the random value *U* in the equation. *U* represents a random value between one and zero and is used to add stochasticity to the model; thus, individuals of the same species will not disperse the same distance. Finally, *α* determines the curve's tail. We want a heavy fixed tail; therefore, this value was set to two. This type of tail leads to the inclusion of rare long-distance dispersal events in our model, which is important for correctly assessing. landscape connectivity (Saura et al., 2014). These rare long-distance dispersals have also been documented for beetles (Trotter et al., 2023; Elek et al., 2014). A sensitivity analysis will be performed to test the effect of α (appendix 1). Dispersal direction is completely random and differs for each individual. When an individual crosses the borders of the landscape, they are removed.

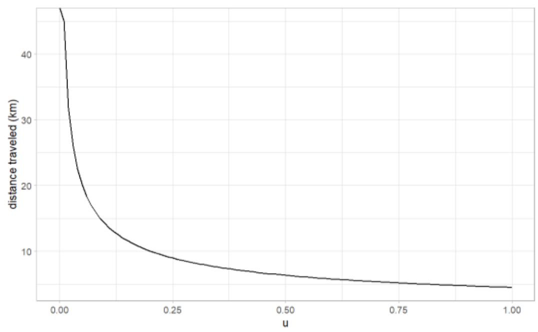


Fig. 6: Example of a dispersal curve using equation 3 with *X_mean* = 9 km.

The probability of dispersal is partly included in the Pareto distribution but depends mostly on the carrying capacity of a cell. When local populations exceed the *K* of their cell, individuals disperse away from the cell until the carrying capacity in that particular cell is reached. Which individuals disperse out of the cell is completely random. Since an individual can only disperse once and the direction is completely random, there is a probability that an individual will not reach a suitable cell and die. After all dispersal events have finished, the *K* of each cell is again checked. This is necessary since individuals who dispersed in the previous step could have reached another full cell. For each cell, all individuals above the *K* are removed from the model. Which individuals are removed is again completely random, thus not based on arrival time.

Data analysis

Each run consists of only one species (figure 7). Since we want to investigate diversity measures between the different scenarios, we need to create beetle communities. A simulated community is created by merging 100 virtual species. This is replicated three times to have independent replicates on the emergent properties of the species dynamics, which results in a total of 300 modeled species. This is a simplification of the more than 4000 beetle species present in Flanders. However, this model aims to cover the trait diversity observed in Coleoptera and not the species diversity. Since many species have similar traits, a community of 100 beetles should be sufficient to cover this trait diversity. This amount was also verified by plotting 100 random body sizes from the trait database which resulted in a normal distribution, as observed in the real beetle community.

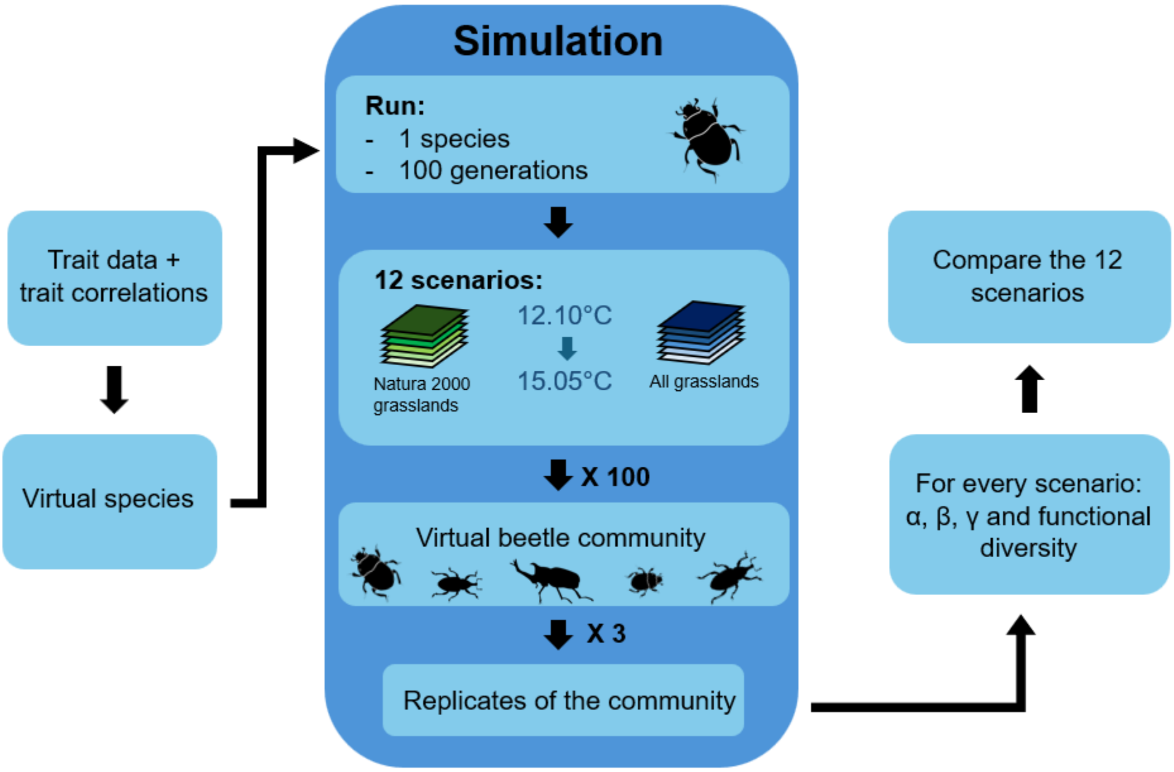


Fig. 7: Schematic representation of the methods.

All calculations are performed using R 4.1.2 with the packages ggplot2, dplyr, tidyr, forcats, betapart, and vegan (Wickham 2016, Wickham et al., 2021, Wickham 2021, Wickham 2021, Baselga et al., 2023).

Alpha diversity

First, we calculate alpha diversity at the cell level. For each cell, the number of different species is counted; this number represents the alpha diversity and is independent of the number of individuals per species. This value is averaged across the replicates to obtain the final alpha diversity value per cell. Heatmap for different scenarios are created using these alpha diversity values. Next, the average alpha diversity for each scenario is calculated. Therefore, for every scenario separately, all the alpha diversity values at the cell level are added up. This sum is then divided by the number of cells with a carrying capacity of at least one. Depending on which landscape is used this number of cells will differ. This value is again averaged across the three replicates.

Bèta diversity

We examine bèta diversity by plotting the distance decay in dissimilarity, as this method has proven to be powerful for ecological studies (Graco-Roza et al., 2022; Morlon et al., 2008). Hereby, the similarity between communities is calculated along the spatial distance. Therefore, two different matrices are calculated. The first matrix is a dissimilarity matrix, which is calculated using the Sorensen dissimilarity index and the function beta.pair from the R package betapart (Martín-Devasa et al., 2024). Next, a distance matrix is calculated, which contains the Euclidean spatial distances between the cells, using the dist function of R. The distance decay for each scenario is calculated using the function decay.model of the R package betapart. We choose to use the exponential model type following Martìn-Devasa et al. (2024). For each scenario, the distance decay in dissimilarity is plotted. These functions are the result of taking the average between the replicates for every scenario.

Gamma diversity

Gamma diversity is calculated by counting the number of species still present at the end of a run. This is done separately for each scenario and is independent of the population size. The average between the different replicates is calculated to obtain the final gamma diversity of each scenario.

Functional diversity

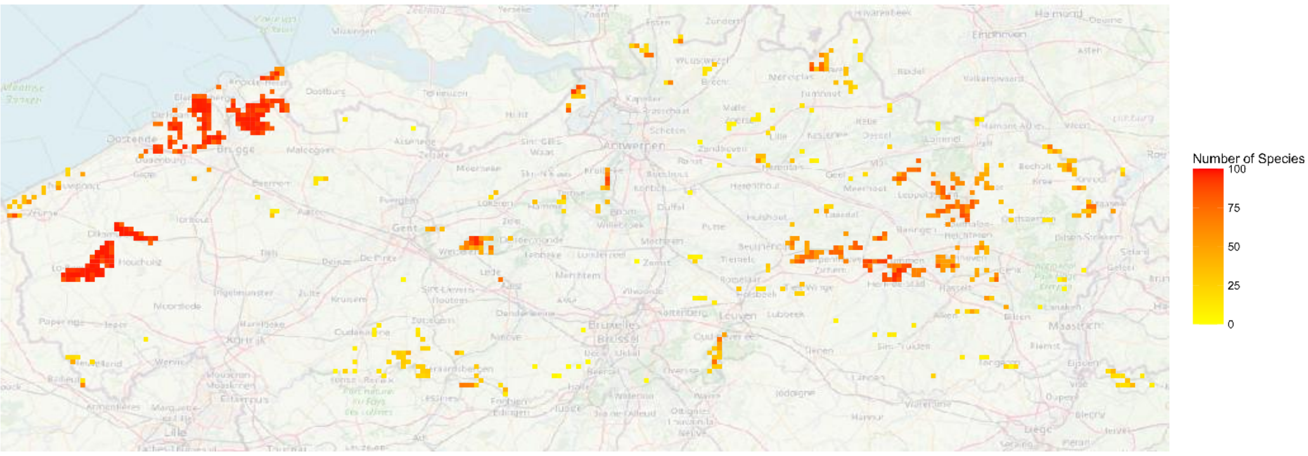
Functional diversity is the last measure of diversity studied. Each life-history trait will be studied separately. The average value for each life-history trait for each cell is calculated, which is dependent on the number of individuals per species present in the cell and is therefore weighted. We also calculate the mean trait value of each landscape by taking the average of all cell means. Next, we determine the coefficient of variation (CV) for each trait in each cell. This allows us to study changes in the average trait value as well as changes in the diversity of traits for the different scenarios. We again calculate a landscape mean for every CV value of each trait by taking the average of all cell-CV-values. For the average trait values and coefficient of variances, the average of the replicates for each cell is calculated to obtain the final results. Heatmaps are again created to show the mean trait values and coefficient of variance for the different scenarios.

Results

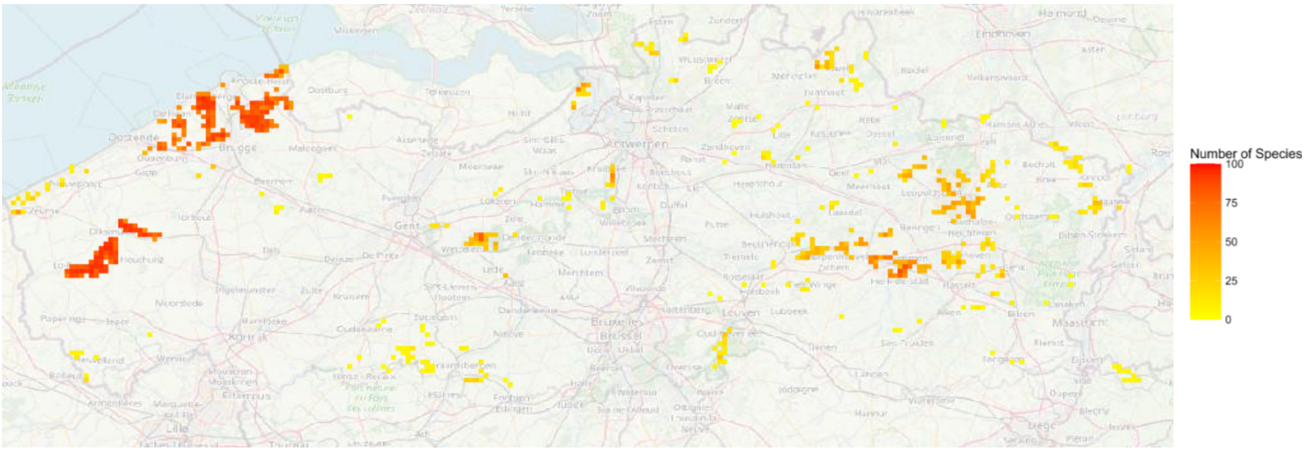
Alpha diversity

Across both landscapes (Figure 8), mean alpha diversity per cell level decreases with rising temperatures. Another trend visible for both landscapes is a higher level of alpha diversity in more connected and/or larger habitats. Since the landscape with all Flanders grasslands has more of these habitats, more cells with high alpha diversity are observed in this landscape.

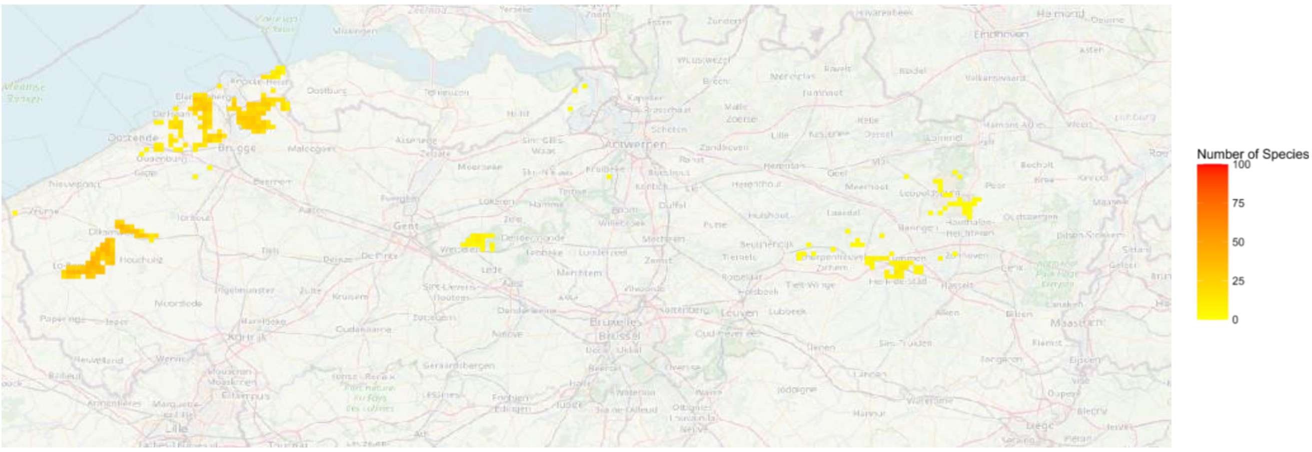
Alpha diversity at cell level for scenario 1



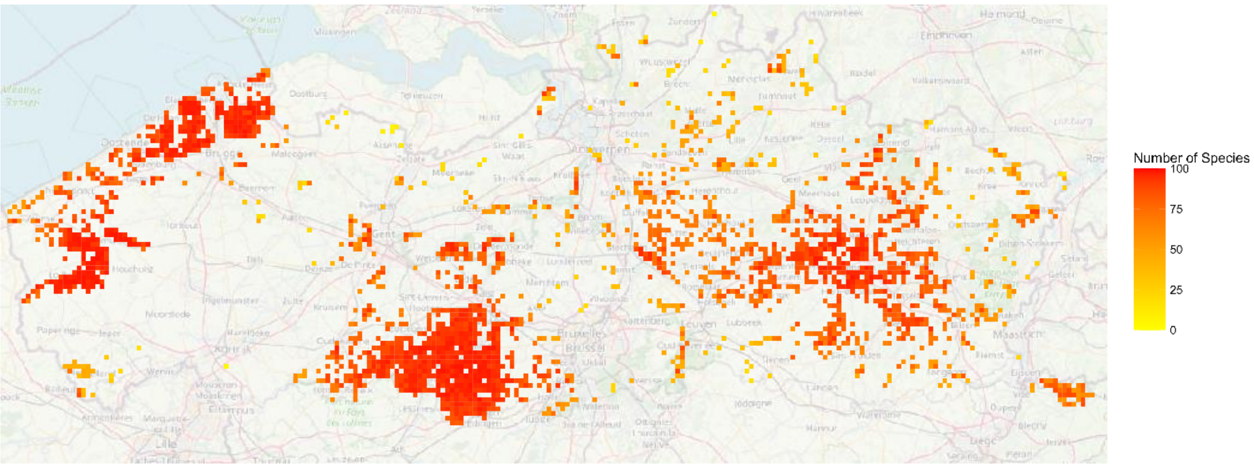
Alpha diversity at cell level for scenario 4



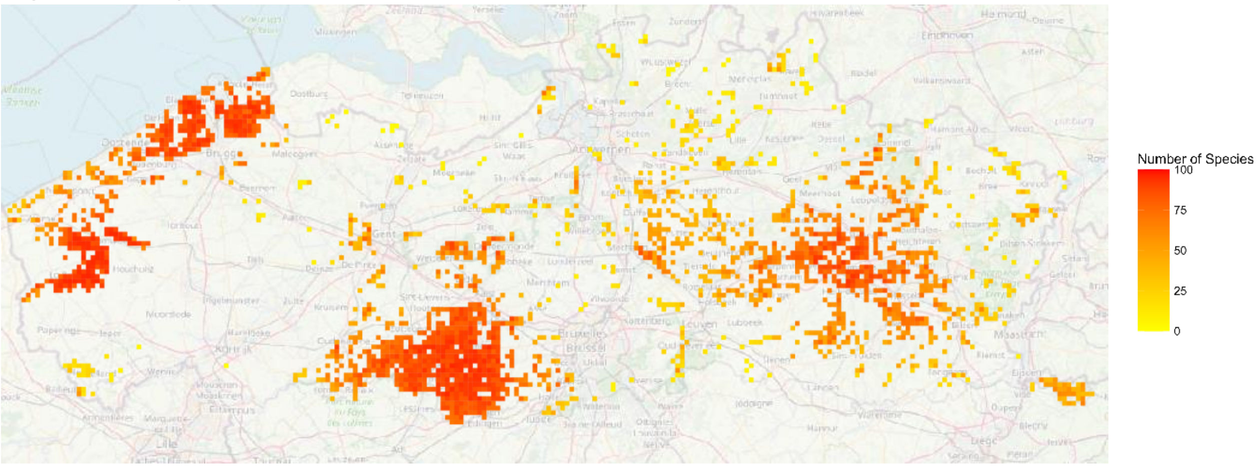
Alpha diversity at cell level for scenario 6



Alpha diversity at cell level for scenario 7



Alpha diversity at cell level for scenario 10



Alpha diversity at cell level for scenario 12

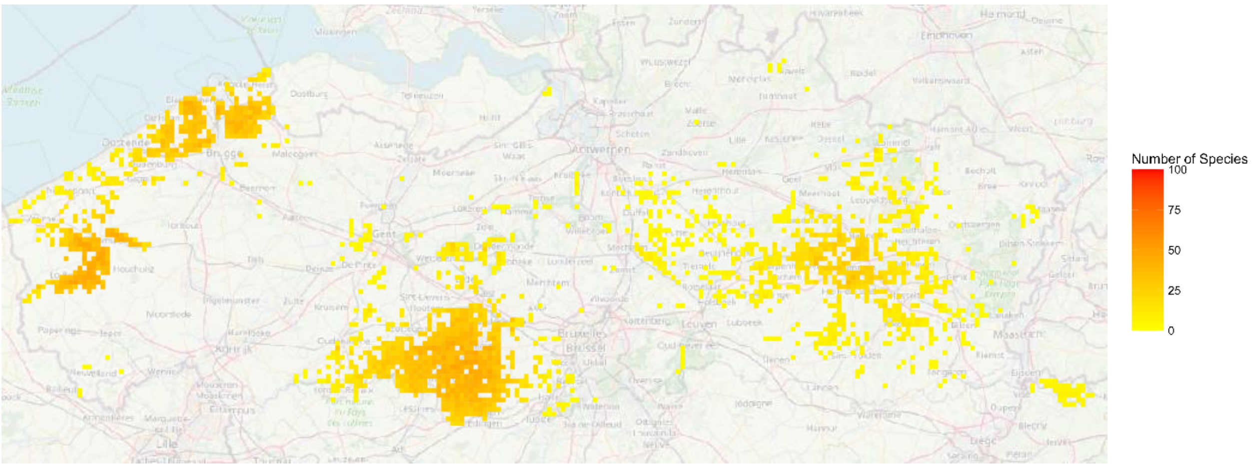


Fig. 8: Heatmaps of scenario 1, 4, 6, 7, 10 and 12 depicting the alpha diversity at cell level. The first three heatmaps are scenarios with only Natura 2000 grasslands while the scenarios of the other three heatmaps use the landscape with all Flanders' suitable grasslands. Scenarios 1 and 7 have an environmental temperature of 12.01°C, scenarios 4 and 10 have a temperature of 13.35°C and finally scenarios 6 and 12 have a temperature of 15.05°C.

The mean alpha diversity for both landscapes decreases with increasing temperatures (Figure 9). Although both landscapes follow the same trend, the landscape including all grasslands always has a higher alpha diversity when comparing scenarios with the same environmental temperature. For the two most extreme heating scenarios, a more pronounced decrease in alpha diversity is observed for the all grassland landscape in comparison to the Natura 2000 landscape. The replicates are very similar with only small standard deviations observed.

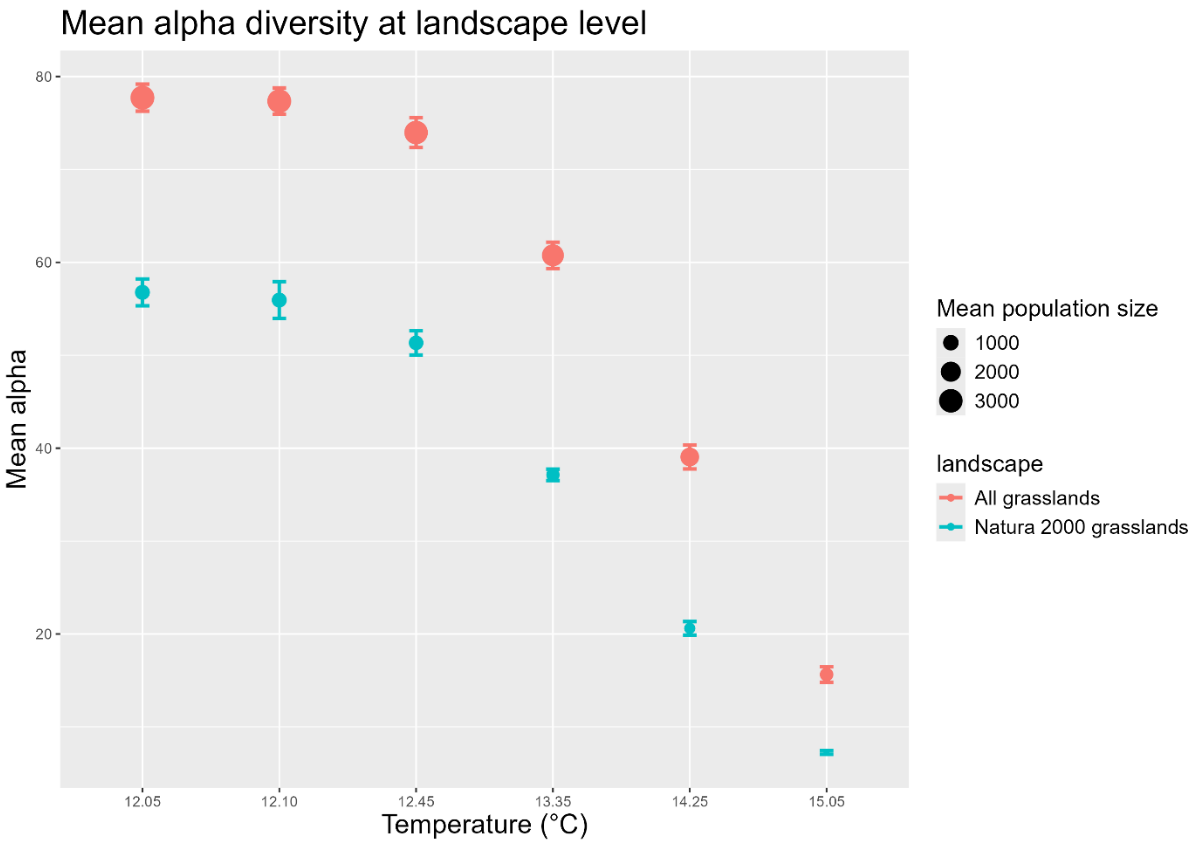


Fig. 9: Mean alpha diversity plotted for all scenarios. Red represents the all grassland landscape and blue represents the landscape with only Natura 2000 grasslands. The dot size represents the mean population size for each scenario. For each scenario, the mean population size is calculated by taking the average of the population sizes at the end of a run for each species present in that scenario. Error bars indicate the standard deviation between replicates.

A decrease in mean population size is observed with increasing temperatures (Figure 9, Figure 10). When comparing scenarios with the same temperature, the Natura 2000 landscape consistently has a lower population size. In addition, we observe more abundant species in the cooler scenarios (Figure 3). The number of rare species increases with increasing temperatures.

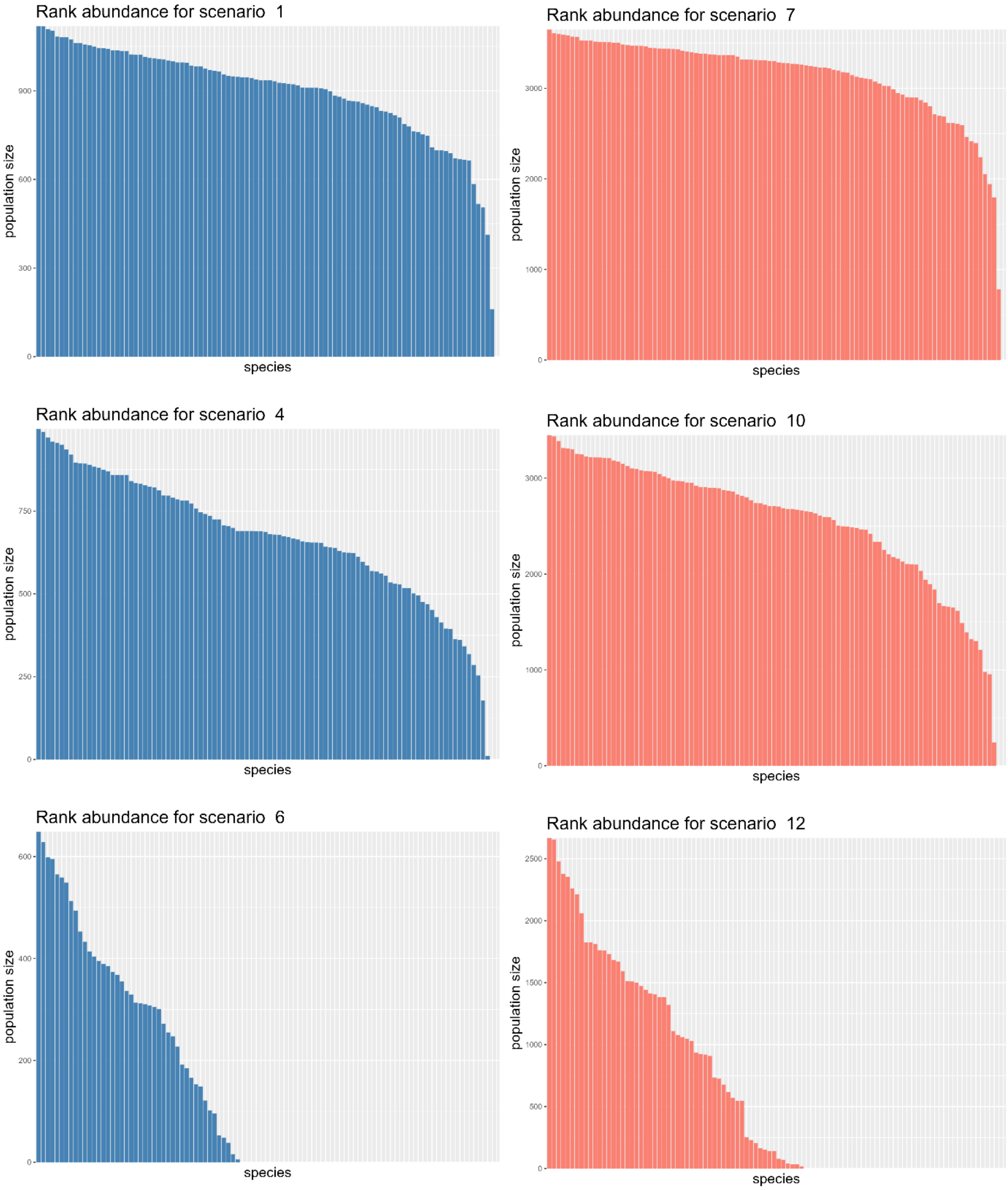


Fig. 10: Rank abundance plots of scenarios 1, 4, 6, 7, 10 and 12. For each scenario, the population size at the end of a species run is plotted for each species present in that scenario, which is subsequently ordered by population size. On the left, scenarios with only Natura 2000 grasslands are plotted, while on the right, scenarios with all suitable grasslands of Flanders are plotted. Scenarios 1 and 7 have an environmental temperature of 12.01°C, scenarios 4 and 10 have a temperature of 13.35°C, and scenarios 6 and 12 have a temperature of 15.05°C. Only one replicate is included in the rank abundance plots.

Bèta diversity

The slope of the distance decay function increases with increasing temperatures for both landscapes and is most pronounced for the Natura 2000 landscape (Figure 11). The slopes are positive, i.e. an increase in distance between sites leads to an increase in dissimilarity between these sites. The intercept decreases with increasing temperatures for the all grassland landscape. Thus, for this landscape, communities close to each other are more similar at higher temperatures but become increasingly dissimilar as distance increases. Since the intercepts for the all grassland landscape decrease strongly with increasing temperatures and the slopes decline less extreme, an overall decrease in dissimilarity with increasing temperatures is observed. This is not the case for the Natura 2000 landscape, where intercepts vary less and no decreasing trend is found for the two most extreme heating scenarios. For this landscape, dissimilarity is generally highest for the three most extreme heating scenarios. Thus, for the Natura 2000 landscape, communities that are close to each other maintain almost the same level of similarity as temperature increases. However, the increase in dissimilarity between communities with increasing distance becomes more extreme with higher temperatures. However it is important to note that although no overall decrease in dissimilarity is observed for the Natura 2000 landscape, the dissimilarity starts at a lower level in the colder scenarios compared to the all grassland landscape. Therefore, the Natura 2000 landscape has an overall lower level of dissimilarity than the other landscape, there is just no decrease in dissimilarity observed. The replicates are very similar with only small standard deviations observed.

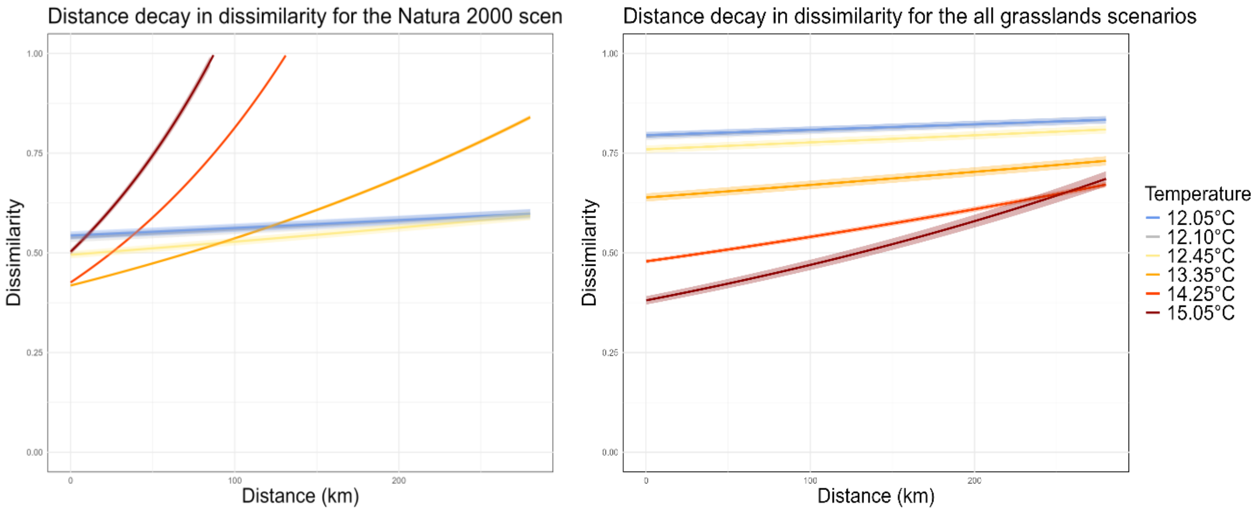


Fig. 11: Distance decay in dissimilarity plotted for the 12 scenarios, with only Natura 2000 scenarios on the left and scenarios including all valuable grasslands on the right. The color of the lines represents the different temperatures. The standard deviation between replicates is also plotted. Since the blue and grey scenarios are very similar only blue is clearly visible.

Gamma diversity

For the three coldest temperatures, the gamma diversity remains constant (Figure 12). A further increase in temperature leads to a decrease in gamma diversity, with a large drop between 14.25°C and 15.05°C. This pattern is observed for both landscapes. When comparing scenarios with the same temperature, the Natura 2000 landscape will always have a lower gamma diversity. This difference increases for the two most extreme heating scenarios. The standard deviation is relatively small, only for scenario 6 we observe a large standard deviation.

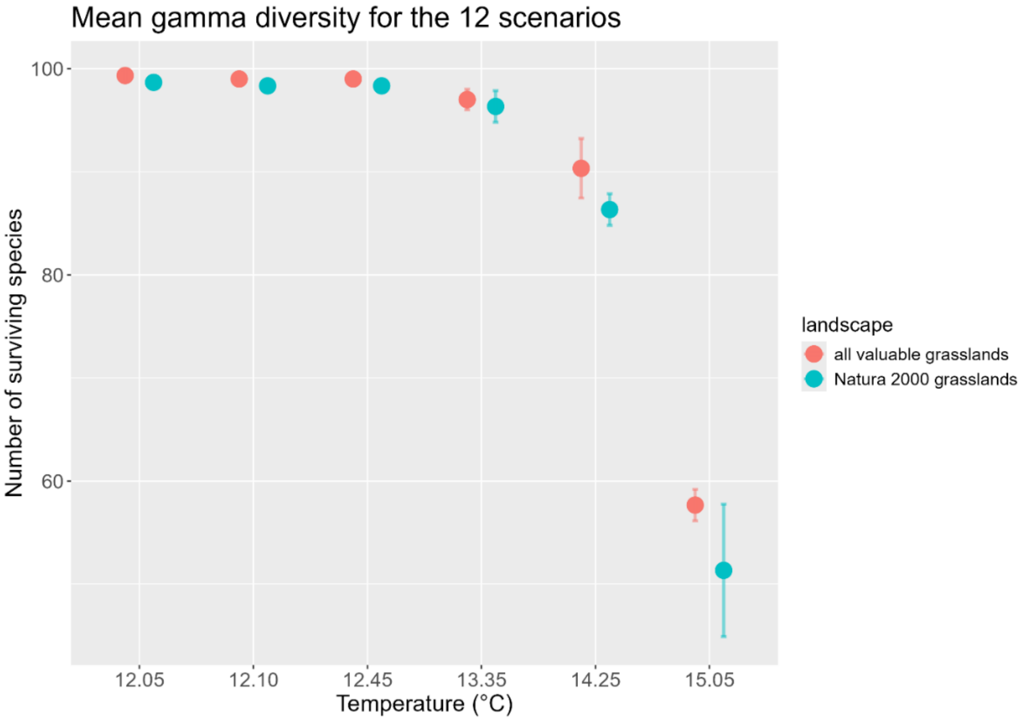


Fig. 12: Mean gamma diversity plotted for all scenarios. Red represents the landscape with all grasslands and blue represents the landscape with only Natura 2000 grasslands. The error bars indicate the standard deviation between the replicates.

Functional diversity

The coefficient of variation (CV) decreases for each life-history trait with increasing temperatures (Figure 13). This means that trait values vary less with higher temperatures. Thus, functional diversity is reduced. Except for dispersal, the CV of the different traits is lower for the Natura 2000 landscape when comparing scenarios with the same environmental temperature. The variance in temperature optimum and breadth is very small, with small CV values between 0.03 and 0.02 and 0.12 and 0.085 respectively, so the observed decrease is also very small. For dispersal, the variance is larger with a CV between 0.40 and 0.44, again with only a small decrease observed. Fecundity is highly variable with a CV above one, with a stronger decrease from 3.50 to 1.50. Finally, size has a CV between 0.80 and 0.55. When considering the CV values for the different traits geographically, there is a general trend towards lower CV values for the more isolated and smaller fragments (Figure 14, Appendix 2.1). Thus functional diversity is lower for the smaller fragments.

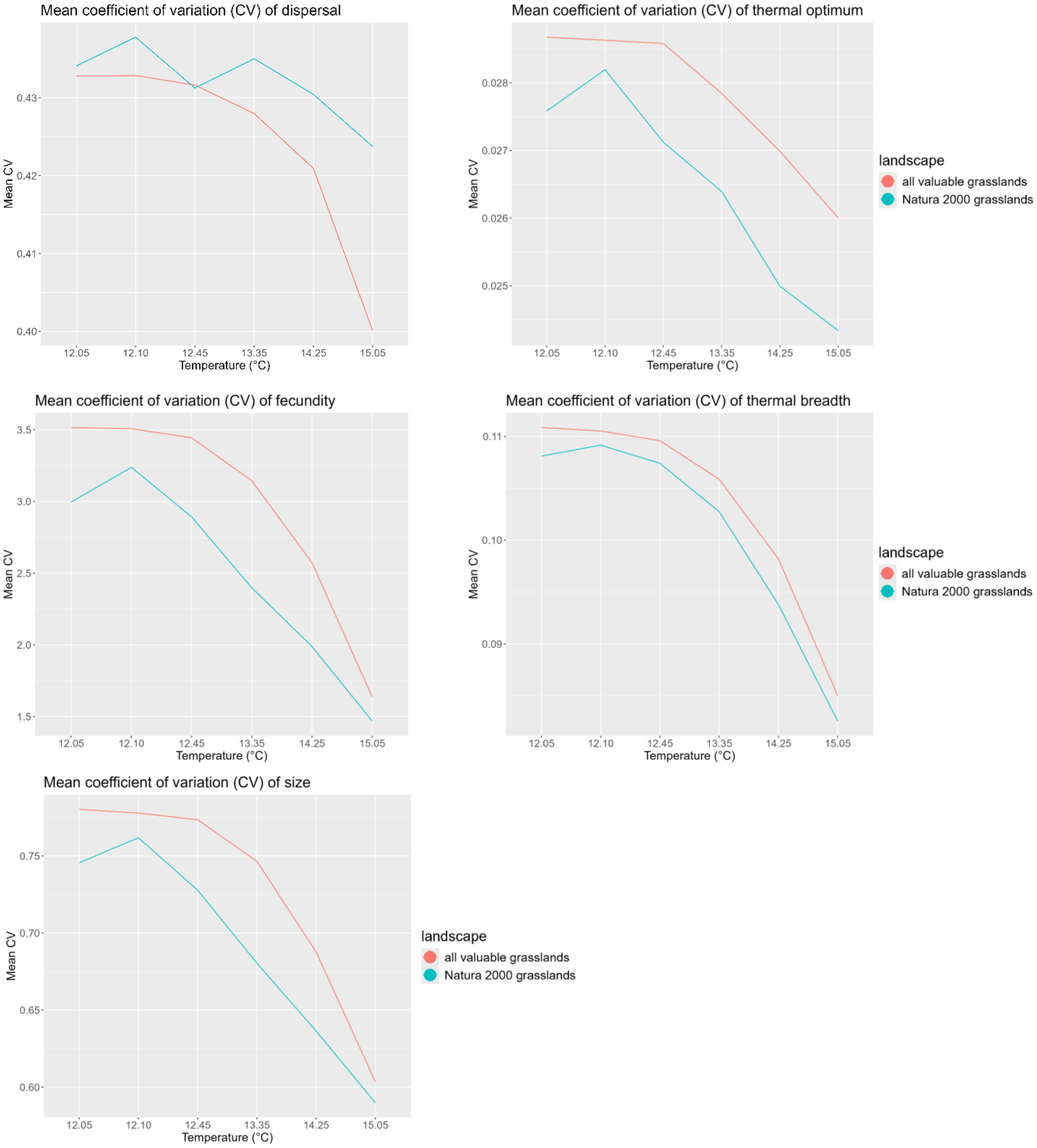
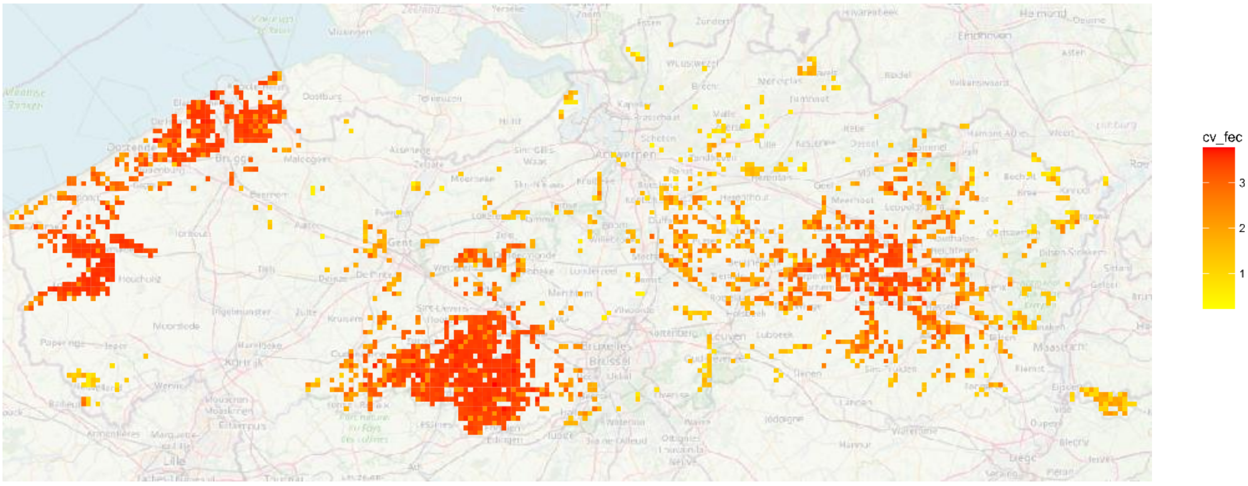


Fig. 13: Mean CV of all life-history traits plotted for the different scenarios. Red represents the landscape with all grasslands and blue represents the landscape with only Natura 2000 grasslands. The mean CV values are calculated only including the cells were at least one individual is present.

CV of fecundity for scenario 11



CV of dispersal for scenario 12

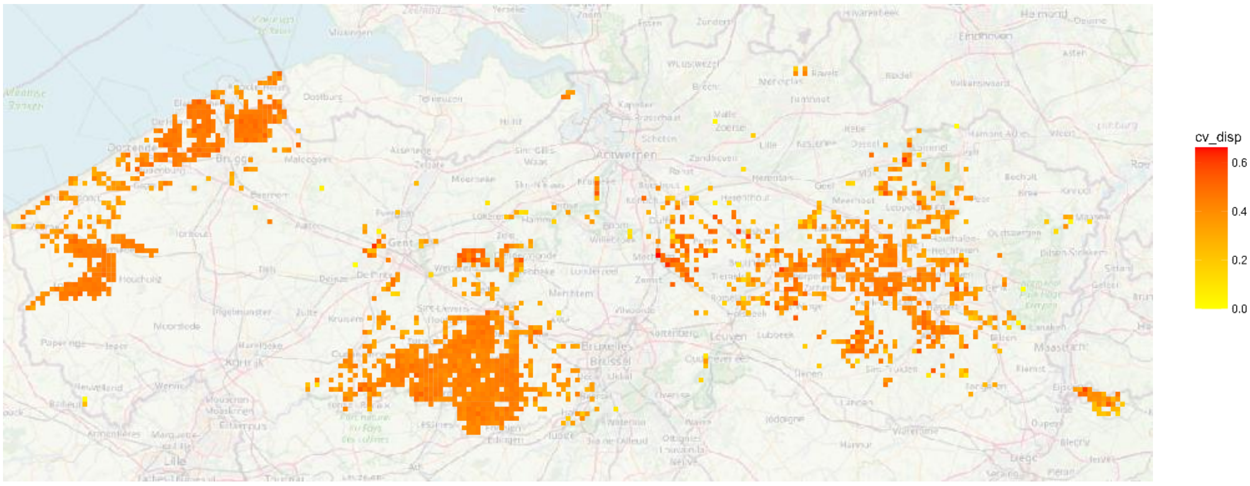
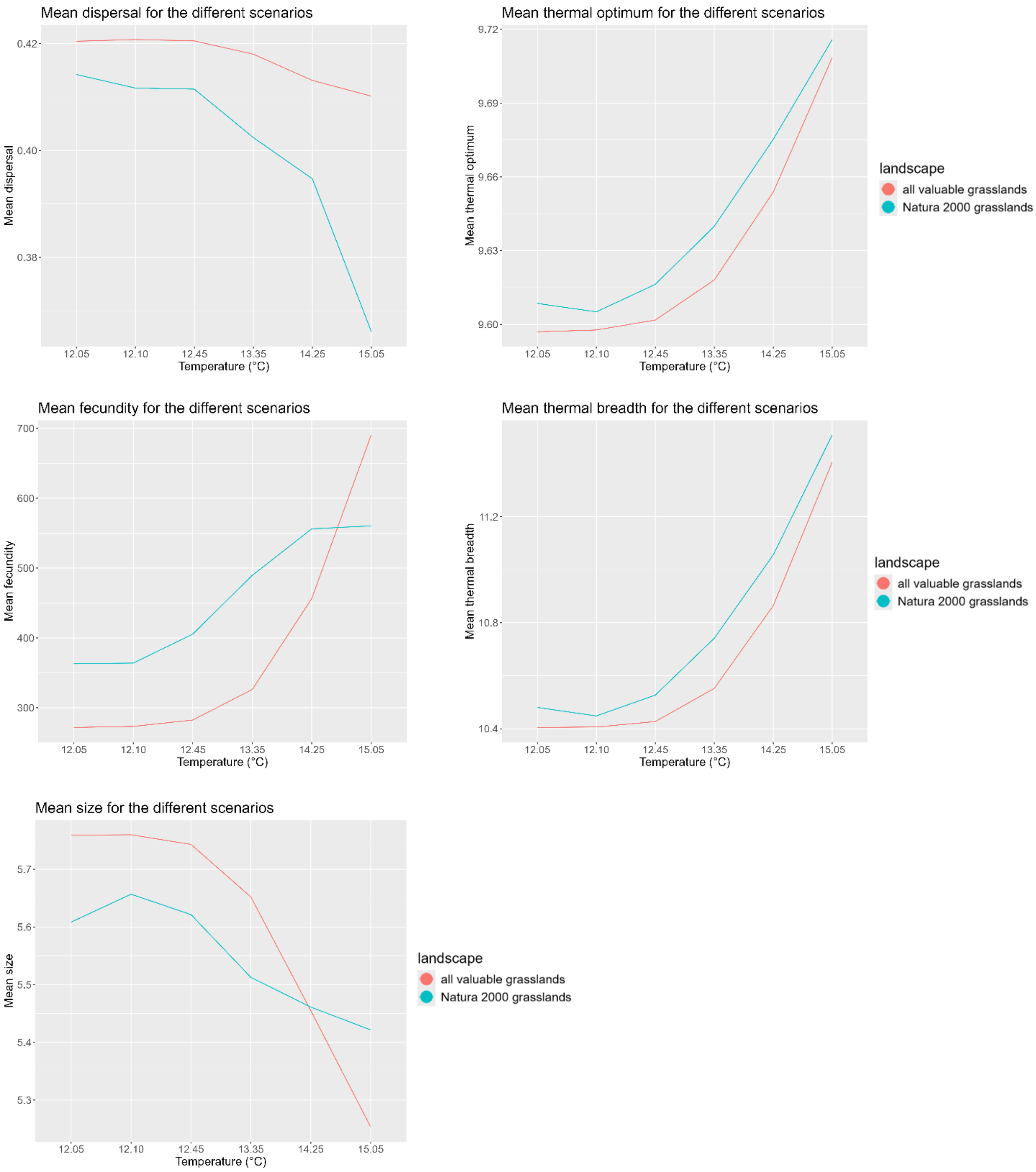


Fig. 14: Heatmaps of the coefficients of variance for fecundity and dispersal for scenarios 11 and 12 respectively. The darker the color of the cell the higher the CV value of the trait is.

We also observed mean values for body size, dispersal, fecundity, thermal optimum, and thermal breadth (Figure 15). Dispersal and size decreased with increasing temperatures, while the other three life-history traits increased. These responses to temperature increase are observed for both landscapes. When considering the mean values for the different traits geographically, we observe higher mean values for the traits dispersal and thermal breadth in the more isolated and smaller fragments (Figure 16, Appendix 2.2). This means that more species with a high dispersal and or thermal breadth value are present in these fragments in comparison to the rest of the landscape. For the other traits, these trends were absent or less pronounced.



Mean dispersal for the different scenarios

Mean thermal optimum for the different scenarios

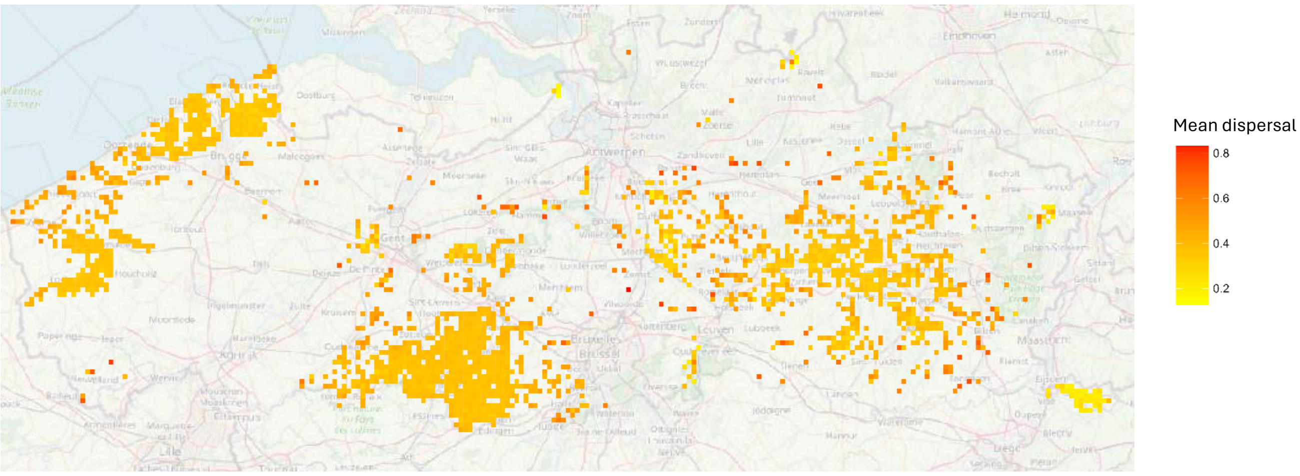
Mean fecundity for the different scenarios

Mean thermal breadth for the different scenarios

Mean size for the different scenarios

Fig. 15: Mean value of all life-history traits plotted for the different scenarios. Red represents the landscape with all grasslands and blue represents the landscape with only Natura 2000 grasslands. The mean values are calculated only including the cells were at least one individual is present.

Mean value for dispersal for scenario 12



Mean value for thermal breadth for scenario 12

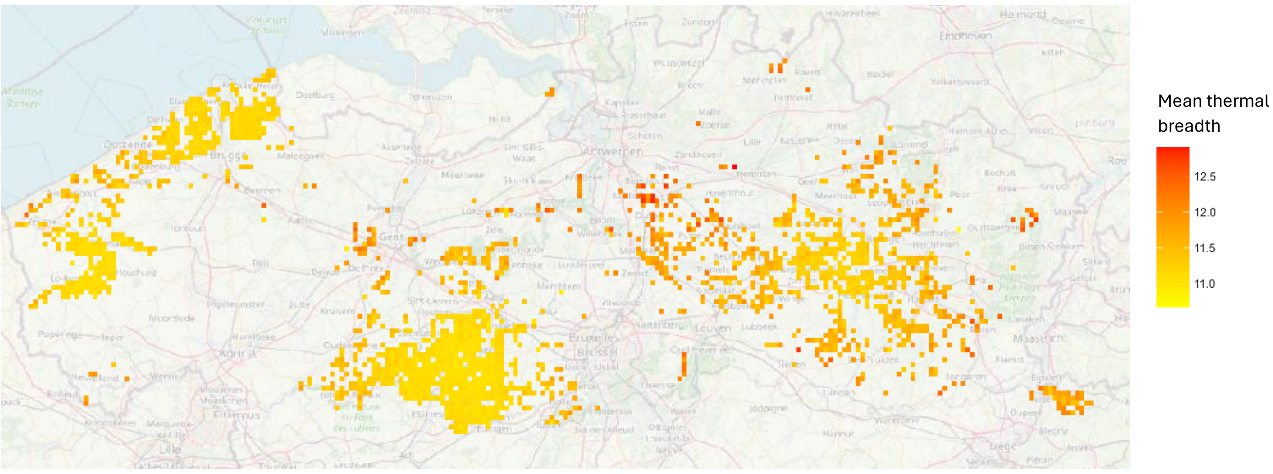


Fig. 16: Heatmaps of the mean trait of dispersal and thermal breadth on the right for scenario 12. The higher the cell color the higher the mean trait value is.

The sensitivity analysis performed on the factors α and *a*, show that changes in these factors do not significantly alter our results (appendix 1). Therefore our insights are robust.

Discussion

We can conclude that an increase in temperature leads to a decrease in diversity, regardless of which landscape we study. This is true for alpha, functional, and gamma diversity, with a direct response of the first two. Gamma diversity decreases only in the more extreme heating scenarios. Bèta diversity is a more complex measure. With increasing temperatures, bèta diversity decreases for the all grassland landscape, indicating homogenization, while no decrease is observed for the Natura 2000 landscape. However, the Natura 2000 landscape starts with a lower beta diversity and therefore still has a lower level of beta diversity compared to the other landscape. The decrease in diversity can be explained by the decrease in the thermal fitness of the virtual beetles. As the mean thermal optimum of all virtual beetles is below the current environmental temperature, species are already experiencing a warmer environment than their optimum, resulting in lower thermal fitness. An increase in temperature will only reduce their thermal fitness further, causing population sizes to decrease and some species to disappear altogether.

Although we see a general effect of temperature on diversity, patterns are not entirely the same between the two landscapes. The most noticeable differences between the two landscapes are the size and number of habitats and the connectivity between them. The landscape with all valuable grasslands consists of larger suitable areas and is more connected. The Natura 2000 landscape on the other hand, has only a few large areas and is generally considered to be very fragmented in terms of beetle dispersal capacity. These differences explain the different responses to temperature increase which we will discuss further.

The more isolated and smaller fragments have lower alpha diversity compared to the other habitats. Thus, smaller fragments contain fewer species. As the Natura 2000 landscape consists of more fragmented areas, a lower mean alpha diversity is observed for this landscape. To explain the species density distribution, we consider the equilibrium theory of island biogeography and related metapopulation dynamics (MacArthur & Wilson, 2001). This theory explains species density on isolated fragments through colonization and extinction. Smaller fragments support smaller populations that are more susceptible to the effects of demographic stochasticity and thus extinction (Melbourne & Hastings, 2008). In contrast, larger fragments can support larger populations that are less vulnerable to extinction. These larger habitats can act as sources of colonization for the smaller habitats, neutralizing the increased extinction rate. This phenomenon is known as the rescue effect (Brown & Kodric-Brown, 1977). However, smaller fragments are also often isolated, leading to the combination of less colonization and more extinction, which explains the lower number of species in these fragments. The landscape containing all grasslands has many small habitats but differs from the Natura 2000 landscape in that these fragments are more connected to source habitats, resulting in a higher number of species within smaller fragments compared to the Natura 2000 landscape as colonizing chance increases with increasing connectivity.

The equilibrium theory of island biogeography is further supported when examining the variance in life-history traits. We observe a higher trait value for dispersal in the smaller fragments. Thus as expected, the more dispersive species can more easily colonize and maintain populations in these isolated habitats. Overall, trait variation is lower in these fragments because species with certain traits, such as high dispersal and fecundity, are more likely to establish populations in these isolated fragments. In addition, the lower number of species present in these areas further reduces trait variation. This decrease in trait variation indicates a decrease in functional diversity. A reduction in functional diversity linked to the isolation of a fragment has also been demonstrated in plant, bird, and insect communities (Arellano-Rivas et al., 2016; Matuoka et al., 2020; Tu et al., 2019). Because functional diversity is a key determinant of ecosystem functioning, it is an important metric on which to focus conservation planning (Gagic et al., 2015).

Mean alpha diversity decreases with temperature increase. Consequently, the mean number of species present in a cell is declining, indicating that many species ranges are shrinking. A decline in distribution range is mainly due to loss of species in the smaller, more isolated patches, which can be again explained by island biogeography (MacArthur & Wilson, 2001). As population sizes decline, the probability of an individual reaching an isolated area also decreases. The loss of individuals in some fragments will further reduce landscape connectivity, thus reducing the probability of colonization to the smaller patches. Furthermore, the probability of extinction in a small fragment is further increased as a consequence of the reduced fitness of the virtual species following an increase in temperature. This explains why even more species are lost in smaller isolated fragments during temperature increase leading to a decline in range distribution. Range contraction due to climate change and habitat loss has been observed in multiple species, including insects (Pacifici et al., 2020; Sánchez-Bayo & Wyckhuys, 2019). However, insects are also known to shift their range during climate change (Rubenstein et al., 2023). This phenomenon is described as tracking of the climatic niche which is not possible in our model due to the temperature being constant over the whole landscape, and the individuals' inability to move beyond the boundaries of Flanders. Therefore we can only conclude that some species will experience a contraction of their Flemish distribution. To determine whether this is accompanied by range shift further studies are needed.

The mean number of species per cell decreases in a similar trend for both landscapes for the four coldest temperatures. However, for the two warmest scenarios, the species density decreases faster for the all grassland landscape. We hypothesize that this is related to the decrease in population size. As mentioned above, smaller populations are more sensitive to the effects of demographic stochasticity. The Natura 2000 landscape has smaller population sizes to begin with and is therefore already more susceptible to the effects of demographic stochasticity. We assume that around the scenario with an environmental temperature of 14.25°C, the all grassland landscape crosses a threshold where demographic stochasticity noticeably changes the species density, which was already the case for the Natura 2000 landscape. Nevertheless, alpha diversity is always higher for the all grassland landscape than for the Natura 2000 landscape when comparing the same temperature scenarios.

When dissimilarity between communities decreases we talk about homogenization (Baeten et al., 2012). An increase in homogenization is observed for the all grassland landscape with an increase in temperature meaning there is a decrease in beta diversity. It is, however, important to note that while no increase in homogenization is observed for the Natura 2000 landscape, the landscape in general has a higher level of homogenization compared with the all grassland landscape. Homogenization is a widespread phenomenon with recent studies showing it destabilizes ecosystem functioning (Petsch, 2016; Wang et al., 2021; Wang & Loreau, 2016). Therefore this phenomenon must be included in conservation plans. The homogenization of a landscape can be attributed to the loss of rare species and/or an increase in species present over the entire landscape (Socolar et al., 2016). Given that only certain species can persist in isolated fragments under higher temperatures, the observed homogenization can be attributed to the loss of rare species. However, the extinction of rare species is observed for both landscapes. We assume nestedness is the reason for the obstruction of homogenization for the Natura 2000 landscape.

Nestedness refers to the difference in community composition between sites due to species loss. This results in a nested pattern in which smaller and/or isolated habitats are inhabited by smaller subgroups of the total beetle community (Ulrich &

Almeida-Neto, 2012). We therefore expect an overall increase in nestedness with increasing temperatures for both landscapes due to loss of connectivity. We know that landscape connectivity and population size decrease significantly with increasing temperatures in both landscapes. This significant decrease will inhibit the rescue effect in smaller and more isolated habitats. Therefore, species will go extinct in the isolated patches, resulting in communities that differ from each other due to species loss. As the loss of connectivity is more extreme for the Natura 2000 landscape, we predict that the increase in nestedness will also be more pronounced compared to the all grassland landscape, ultimately preventing homogenization. However, this is not a positive phenomenon in terms of diversity, as it simply means that the Natura 2000 landscape loses more species compared to the all grassland landscape. We also observe that the increase in dissimilarity with distance becomes more extreme for both landscapes. We assume that this reflects the increase in nestedness with increasing temperatures. Together with nestedness, turnover provides a complete picture of community differences (Baselga, 2009). Turnover describes the change in community composition between sites due to species replacement. A decrease in this measure leads to homogenization (Baeten et al., 2012). Thus, we expect turnover to decrease for both landscapes, but the effects of this decline are offset by the increase in nestedness for the Natura 2000 landscape.

Next, we take a closer look at functional diversity. We observe a decrease in the variance of all life-history traits for both landscapes, indicating a decrease in functional diversity. The Natura 2000 landscape has the lowest functional diversity value for all life-history traits except dispersal. This decrease in trait variation means that certain trait values make a species more vulnerable to temperature decrease, ultimately leading to the loss of these types of traits. These correlations have been the subject of recent studies showing that they are useful for conservation plans, but difficult to generalize as they are species-dependent (Dawson et al., 2011; Pacifici et al., 2017). Of all traits, we observe the largest relative decrease in variation for fecundity (approximately 57%), which is consistent with studies showing a correlation between fecundity and climate change (Advani, 2023; Dawson et al., 2011). This decrease in variation is due to an increase in individuals with high fecundity values. A higher fecundity value directly affects the fitness of a species; if an individual has more offspring, the chance of an offspring finding a suitable area increases, which in turn increases fitness. Thermal breadth, optimum, and body size also decrease in variation, although the relative decrease is smaller (about 30%). Other studies have also found that these traits are associated with vulnerability to climate change (Dewenter et al., 2024; Jiguet et al., 2006; Lehmann et al., 2020). Of these traits, body size decreases with increasing temperatures, a trend already observed in other species (Sheridan & Bickford, 2011). Since body size in our model is only related to other life-history traits, the correlation between these traits and the change they undergo due to temperature increase determines the decrease in body size. The mean of the other traits, thermal optimum and breadth, increases with warmer temperatures. This implies that individuals with a higher thermal optimum and a larger thermal breadth are less vulnerable to temperature increases, as would be expected. Since thermal optimum and breadth are used to determine the thermal niche in our model, the decline of species with lower thermal optimum and breadth during temperature increase can be directly linked to a decrease in thermal fitness. In summary, species with a low fecundity value, a low thermal optimum, a low thermal breadth, and a large body size are more vulnerable to climate change.

The trait dispersal is also studied. This is the only trait where the variance is lower in the all grassland landscape compared to the Natura 2000 landscape. We assume that this is a consequence of the method used to calculate the trait variation. We only include cells with at least one individual when calculating the different variation values. As mentioned above, the Natura 2000 landscape loses species faster in the isolated fragments than in the all grassland landscape. Thus, fewer of these fragments are used to calculate dispersal variation for the Natura 2000 landscape, which ultimately leads to a smaller decrease in dispersal variation. This effect is only observed for dispersal, as this trait plays an important role in determining whether a species reaches a more isolated fragment. A decrease in dispersive individuals is the reason for the decrease in variance. Although this could mean that dispersive species are more vulnerable to temperature increases, the most likely reason is the method used to calculate mean dispersal. A mean dispersal value is calculated for each cell. The average of all these cell means is taken to calculate the overall mean. Only the more dispersive species can reach the isolated cells, these cells will increase the mean dispersal value. As the temperature increases, fewer of these isolated cells will be inhabited and thus not included in the mean trait calculation. This is most likely the reason for the observed decrease in mean dispersal. Thus, dispersive species are not necessarily more vulnerable, they are just unable to reach the more isolated habitats anymore due to the general population decline. However, they do experience a decline in range distribution. Which we already observed for some species determined via mean alpha diversity. To further investigate the effects of climate change on dispersal we should look at the mean dispersal of the population instead of on a landscape level. Informed dispersal decision is also not included in our model which could also alter the results to benefit more dispersive species during climate change since in our model species have a high possibility of moving to a non-suitable cell (Mortier et al., 2018). This could again be the subject of further research.

As mentioned above, gamma diversity decreases only in the two most extreme heating scenarios. This is related to the fitness of a species. As the temperature rises, the fitness of most species starts to decrease, so their chance of dying increases. Species become less abundant. However, only at the 13.35°C scenarios, fitness crosses a threshold where the detrimental effects of demographic stochasticity become visible. Since the Natura 2000 landscape contains smaller populations, these stochasticity effects are even more pronounced for this landscape, resulting in a greater decrease in gamma diversity.

It is important to note that our predictions of biodiversity decline are optimistic because we do not include biotic interactions in our model. The loss of ecological interactions often occurs long before species go extinct (Valiente-Banuet et al., 2014). Therefore, even in the cooler scenarios with minimal diversity loss, we can expect many losses of ecological interactions. These losses will not only negatively affect the functioning of an ecosystem, but will also accelerate the extinction rate through secondary extinctions (Sandor et al., 2022). Therefore, the loss of biodiversity observed in our model without biotic interactions is an optimistic representation of reality.

Another factor that leads to an overestimation of the effectiveness of landscapes in protecting beetles from extinction is the absence of genetics in our model. We have already mentioned the sensitivity of small populations to the effects of demographic stochasticity. These effects are partly present in our model through randomizing survival, dispersal direction and number of offspring. However, there is also an important genetic aspect to the vulnerability of small populations that we were not able to include in our model. Small populations experience an increase in inbreeding and genetic drift, leading to an increase in homozygosity and ultimately a loss of genetic diversity (Blomqvist et al., 2010). The loss of genetic diversity makes a species vulnerable to a variety of factors. The combination of low genetic diversity and vulnerability to the effects of demographic stochasticity increases the likelihood that a species will enter a downward spiral in which the population becomes smaller and smaller until the species disappears completely. This is the so-called extinction vortex (Gilpin and Soulé 1986). Thus, even though we only see a decline in gamma diversity in the most extreme heating scenarios, some species will already be at the tipping point of extinction in the cooler scenarios, where population sizes have already started to decline.

Finally, the inability of the Natura 2000 area to cover an important grassland area should also be noted. Looking at the heatmaps of the landscape including all the valuable grasslands, we can observe three important source areas where many species survive in the warmest scenarios. Even though none of these areas are well covered by the Natura 2000 network, one has almost no coverage, the area in the south of Flanders. It is important to protect these source areas as they keep the populations in the neighboring smaller cells alive. Thus, in addition to the low connectivity of the Natura 2000 network, it also lacks the protection of important areas for beetles to survive climate change.

The Natura 2000 network is currently not effective in protecting beetles from climate change. Therefore, the current management plans need to be modified. To improve beetle conservation in Flanders, management should focus on increasing the number of protected areas with valuable grasslands that are currently not part of the Natura 2000 network, thereby increasing the carrying capacity and to some degree connectivity of the protected valuable grasslands. This will lead to larger populations and more diversity in all aspects, making the beetle community in Flanders less sensitive to climate change. As valuable grasslands in Flanders are still fragmented, additional measures are needed to further increase connectivity. Restoration of non-valuable grasslands will help with this. As beetles play an important role in ecosystem functioning, special attention should be paid to increasing functional diversity. Therefore, especially species with traits leading to an increased vulnerability to climate change should be considered in conservation plans. These species include beetles with one or more of the following traits: low thermal optimum, thermal range, fecundity, and/or large body size. Despite these efforts, beetle diversity will still decline with extinctions in the most extreme heating scenarios. This is another indication that we need to limit climate change as soon as possible to prevent further extinctions.

Conclusion

Currently, the Natura 2000 network in Flanders is not effective in protecting beetles from climate change, as an overall decline in biodiversity and population size is observed with warmer temperatures. This decline can be attributed to the small amount of valuable grasslands within the Natura 2000 network and the low connectivity between these areas. Therefore, an adapted management plan focusing on increasing the amount of habitat and improving the connectivity of protected areas is needed. In addition, management plans should prioritize more vulnerable species, using life-history traits to aid in the selection process. Although this approach will result in more resilient beetle populations, beetle diversity will still decline. This is yet another reminder that we need to limit climate change to mitigate species extinction. Although our results already indicate significant problems, our results are optimistic because we did not consider genetics and biotic interactions in our model. This could be the focus of further studies, as these factors are likely to further accelerate beetle population declines, making management issues even more urgent. In addition, more research is needed to determine the effects of increasing temperatures on beetle dispersal traits, which could further inform conservation strategies.

Acknowledgements

I would like to thank Prof. Dr. Dries Bonte, Dr. Femke Batsleer and Drs. Garben Logghe for their assistance and guidance throughout this study. I also would like to thank Siebe van Wunnik, Pauline Blerot and Lennert Beele for their support during this period.

References

Advani, N. K. (2023). Assessing species vulnerability to climate change, and implementing practical solutions. *Biological Conservation*, *286*, 110284. https://doi.org/10.1016/j.biocon.2023.110284

Amarasekare, P. (2024). Temperature-dependent dispersal and ectotherm species' distributions in a warming world. *Journal Of Animal Ecology*, *93*(4), 428–446. https://doi.org/10.1111/1365-2656.14054

Arellano-Rivas, A., De-Nova, J. A., & Munguía-Rosas, M. A. (2016). Patch isolation and shape predict plant functional diversity in a naturally fragmented forest. *Journal Of Plant Ecology*, rtw119. https://doi.org/10.1093/jpe/rtw119

Baeten, L., Vangansbeke, P., Hermy, M., Peterken, G., Vanhuyse, K., & Verheyen, K. (2012). Distinguishing between turnover and nestedness in the quantification of biotic homogenization. *Biodiversity And Conservation*, *21*(6), 1399–1409. https://doi.org/10.1007/s10531-012-0251-0

Baselga, A. (2009). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology And Biogeography*, *19*(1), 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Blomqvist, D., Pauliny, A., Larsson, M., & Flodin, L. (2010). Trapped in the extinction vortex? Strong genetic effects in a declining vertebrate population. *BMC Evolutionary Biology*, *10*(1), 33. https://doi.org/10.1186/1471-2148-10-33

Bonte, D., Hovestadt, T., & Poethke, H. (2010). Evolution of dispersal polymorphism and local adaptation of dispersal distance in spatially structured landscapes. *Oikos*, *119*(3), 560–566. https://doi.org/10.1111/j.1600-0706.2009.17943.x

Brodie, J. F., Giordano, A. J., Dickson, B., Hebblewhite, M., Bernard, H., Mohd-Azlan, J., Anderson, J., & Ambu, L. (2014). Evaluating multispecies landscape connectivity in a threatened tropical mammal community. *Conservation Biology*, *29*(1), 122–132. https://doi.org/10.1111/cobi.12337

Brown, A. M., Warton, D. I., Andrew, N. R., Binns, M., Cassis, G., & Gibb, H. (2014). The fourth-corner solution – using predictive models to understand how species traits interact with the environment. *Methods in Ecology And Evolution*, *5*(4), 344–352. https://doi.org/10.1111/2041-210x.12163

Brown, J. H., & Kodric-Brown, A. (1977). Turnover Rates in Insular Biogeography: Effect of Immigration on Extinction. *Ecology*, *58*(2), 445–449. https://doi.org/10.2307/1935620

Buckley, L. B., Huey, R. B., & Kingsolver, J. G. (2022). Asymmetry of thermal sensitivity and the thermal risk of climate change. *Global Ecology And Biogeography*, *31*(11), 2231–2244. https://doi.org/10.1111/geb.13570

Cardoso, P., Barton, P. S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T., Fukushima, C. S., Gaigher, R., Habel, J. C., Hallmann, C. A., Hill, M. J., Hochkirch, A., Kwak, M. L., Mammola, S., Noriega, J. A., Orfinger, A. B., Pedraza, F., Pryke, J. S., Roque, F. O., . . . Samways, M. J. (2020). Scientists' warning to humanity on insect extinctions. *Biological Conservation*, *242*, 108426. https://doi.org/10.1016/j.biocon.2020.108426

Chen, I., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science*, *333*(6045), 1024–1026. https://doi.org/10.1126/science.1206432

Cheptou, P., Hargreaves, A. L., Bonte, D., & Jacquemyn, H. (2017). Adaptation to fragmentation: evolutionary dynamics driven by human influences. *Philosophical Transactions - Royal Society. Biological Sciences*, *372*(1712), 20160037. https://doi.org/10.1098/rstb.2016.0037

Clobert, J., Ims, R. A., & Rousset, F. (2004). Causes, Mechanisms and Consequences of Dispersal. In *Elsevier eBooks* (pp. 307–335). https://doi.org/10.1016/b978-012323448-3/50015-5

Comte, L., Bertrand, R., Diamond, S., Lancaster, L. T., Pinsky, M. L., Scheffers, B. R., Baecher, J. A., Bandara, R. M. W. J., Chen, I., Lawlor, J. A., Moore, N. A., Oliveira, B. F., Murienne, J., Rolland, J., Rubenstein, M. A., Sunday, J., Thompson, L. M., Villalobos, F., Weiskopf, S. R., & Lenoir, J. (2024). Bringing traits back into the equation: A roadmap to understand species redistribution. *Global Change Biology*, *30*(4). https://doi.org/10.1111/gcb.17271

D'Amen, M., Bombi, P., Campanaro, A., Zapponi, L., Bologna, M.A., Franco, M. (2013). Protected areas and insect conservation: questioning the effectiveness of Natura 2000 network for saproxylic beetles in Italy. *Animal Conservation 16*(4), 370-378, https://doi.org/10.1111/acv.12016

De Vega, C., Arista, M., Ortiz, P. L., Herrera, C. M., & Talavera, S. (2011). Endozoochory by beetles: a novel seed dispersal mechanism. *Annals Of Botany*, *107*(4), 629–637. https://doi.org/10.1093/aob/mcr013

DeAngelis, D. L., & Grimm, V. (2014). Individual-based models in ecology after four decades. *F1000 Prime Reports*, *6*. https://doi.org/10.12703/p6-39

Dewenter, B. S., Shah, A. A., Hughes, J., Poff, N. L., Thompson, R., & Kefford, B. J. (2024). The thermal breadth of temperate and tropical freshwater insects supports the climate variability hypothesis. *Ecology And Evolution*, *14*(2). https://doi.org/10.1002/ece3.10937

Eisenhauer, N., Bonn, A., & Guerra, C. A. (2019). Recognizing the quiet extinction of invertebrates. *Nature Communications*, *10*(1). https://doi.org/10.1038/s41467-018-07916-1

Eiserhardt, W. L., Svenning, J., Baker, W. J., Couvreur, T. L. P., & Balslev, H. (2013). Dispersal and niche evolution jointly shape the geographic turnover of phylogenetic clades across continents. *Scientific Reports*, *3*(1). https://doi.org/10.1038/srep01164

Elek, Z., Drag, L., Pokluda, P., Čížek, L., & Bérces, S. (2014). Dispersal of individuals of the flightless grassland ground beetle, Carabus hungaricus (Coleoptera: Carabidae), in three populations and what they tell us about mobility estimates based on mark-recapture. *European Journal Of Entomology*, *111*(5), 663–668. https://doi.org/10.14411/eje.2014.080

Fahrig, L. (2017). Ecological Responses to Habitat Fragmentation Per Se. *Annual Review Of Ecology, Evolution, And Systematics*, *48*(1), 1–23. https://doi.org/10.1146/annurev-ecolsys-110316-022612

Fahrig, L., Arroyo-Rodríguez, V., Bennett, J. R., Boucher-Lalonde, V., Cazetta, E., Currie, D. J., Eigenbrod, F., Ford, A. T., Harrison, S. P., Jaeger, J. A., Koper, N., Martin, A. E., Martin, J., Metzger, J. P., Morrison, P., Rhodes, J. R., Saunders, D. A., Simberloff, D., Smith, A. C., . . . Watling, J. I. (2019). Is habitat fragmentation bad for biodiversity? *Biological Conservation*, *230*, 179–186. https://doi.org/10.1016/j.biocon.2018.12.026

Fletcher, R. J., Didham, R. K., Banks-Leite, C., Barlow, J., Ewers, R. M., Rosindell, J., Holt, R. D., Gonzalez, A., Pardini, R., Damschen, E. I., Melo, F. P., Ries, L., Prevedello, J. A., Tscharntke, T., Laurance, W. F., Lovejoy, T., & Haddad, N. M. (2018). Is habitat fragmentation good for biodiversity? *Biological Conservation*, *226*, 9–15. https://doi.org/10.1016/j.biocon.2018.07.022

Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., Slade, E. M., Steffan-Dewenter, I., Emmerson, M., Potts, S. G., Tscharntke, T., Weisser, W., & Bommarco, R. (2015). Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proceedings - Royal Society. Biological Sciences/Proceedings - Royal Society. Biological Sciences*, *282*(1801), 20142620. https://doi.org/10.1098/rspb.2014.2620

García, C., & Borda-de-Água, L. (2016). Extended dispersal kernels in a changing world: insights from statistics of extremes. *Journal Of Ecology*, *105*(1), 63–74. https://doi.org/10.1111/1365-2745.12685

Gilpin, M. E., and M. E. Soulé. (1986). Minimum viable populations: processes of species extinction. Pages 19-34 *in* M. E. Soulé, editor. *Conservation biology: the science of scarcity and diversity.* Sinauer Associates, Sunderland, Massachusetts, USA.

Graco-Roza, C., Aarnio, S., Abrego, N., Acosta, A. T. R., Alahuhta, J., Altman, J., Angiolini, C., Aroviita, J., Attorre, F., Baastrup-Spohr, L., Barrera-Alba, J. J., Belmaker, J., Biurrun, I., Bonari, G., Bruelheide, H., Burrascano, S., Carboni, M., Cardoso, P., Carvalho, J. C., . . . Soininen, J. (2022). Distance decay 2.0 – A global synthesis of taxonomic and functional turnover in ecological communities. *Global Ecology And Biogeography*, *31*(7), 1399–1421. https://doi.org/10.1111/geb.13513

Green, S. J., Brookson, C. B., Hardy, N. A., & Crowder, L. B. (2022). Trait-based approaches to global change ecology: moving from description to prediction. *Proceedings - Royal Society. Biological Sciences/Proceedings - Royal Society. Biological Sciences*, *289*(1971). https://doi.org/10.1098/rspb.2022.0071

Grimm, V., Ayllón, D., & Railsback, S. F. (2016). Next-Generation Individual-Based Models Integrate Biodiversity and Ecosystems: Yes We Can, and Yes We Must. *Ecosystems*, *20*(2), 229–236. https://doi.org/10.1007/s10021-016-0071-2

Hernández-manrique, O. L., Numa, C., Verdú, J. R., Galante, E., & Lobo, J. M. (2012). Current protected sites do not allow the representation of endangered invertebrates: the Spanish case. *Insect Conservation And Diversity*, *5*(6), 414–421. https://doi.org/10.1111/j.1752-4598.2011.00175.x

Honěk, A. (1993). Intraspecific Variation in Body Size and Fecundity in Insects: A General Relationship. *Oikos*, *66*(3), 483. https://doi.org/10.2307/3544943

Jeffries, D. L., Chapman, J., Roy, H. E., Humphries, S., Harrington, R., Brown, P. M. J., & Handley, L. L. (2013). Characteristics and Drivers of High-Altitude Ladybird Flight: Insights from Vertical-Looking Entomological Radar. *PloS One*, *8*(12), e82278. https://doi.org/10.1371/journal.pone.0082278

Jenkins, D. G., Brescacin, C. R., Duxbury, C. V., Elliott, J. A., Evans, J. A., Grablow, K. R., Hillegass, M., Lyon, B. N., Metzger, G. A., Olandese, M. L., Pepe, D., Silvers, G. A., Suresch, H. N., Thompson, T. N., Trexler, C. M., Williams, G. E., Williams, N. C., & Williams, S. E. (2007). Does size matter for dispersal distance? *Global Ecology And Biogeography*, *16*(4), 415–425. https://doi.org/10.1111/j.1466-8238.2007.00312.x

Jiguet, F., Julliard, R., Thomas, C. D., Dehorter, O., Newson, S. E., & Couvet, D. (2006). Thermal range predicts bird population resilience to extreme high temperatures. *Ecology Letters*, *9*(12), 1321–1330. https://doi.org/10.1111/j.1461-0248.2006.00986.x

Klok, C. J., & Harrison, J. F. (2013). The Temperature Size Rule in Arthropods: Independent of Macro-Environmental Variables but Size Dependent. *Integrative And Comparative Biology*, *53*(4), 557–570. https://doi.org/10.1093/icb/ict075

Koch, M., Bowes, G., Ross, C., & Zhang, X. (2012). Climate change and ocean acidification effects on seagrasses and marine macroalgae. *Global Change Biology*, *19*(1), 103–132. https://doi.org/10.1111/j.1365-2486.2012.02791.x

La Sorte, F. A., & Jetz, W. (2012). Tracking of climatic niche boundaries under recent climate change. *Journal Of Animal Ecology*, *81*(4), 914–925. https://doi.org/10.1111/j.1365-2656.2012.01958.x

Lande, R., Engen, S., Sæther, B., & Saether, B. (1998). Extinction Times in Finite Metapopulation Models with Stochastic Local Dynamics. *Oikos*, *83*(2), 383. https://doi.org/10.2307/3546853

Lehmann, P., Ammunét, T., Barton, M., Battisti, A., Eigenbrode, S.D., Jepsen, J.U., Kalinkat, G., Neuvonen, S., Niemelä, P., Terblanche, J.S., Økland, B., Björkman, C. (2020). Complex responses of global insect pests to climate warming, *Frontiers in Ecology and the Environment 18*(3), 141-150, https://doi.org/10.1002/fee.2160

Louette G., De Knijf G., Anselin A., Devos K., Vermeersch G., Pollet M., Van Hove M. & Paelinckx D(2015). Actualisatie van de Europese standaardgegevensformulieren voor Vlaanderen in uitvoering van de Europese Habitat- en Vogelrichtlijn. Rapporten van het Instituut voor Natuur- en Bosonderzoek 2015 (INBO.R.2015.7125262). Instituut voor Natuur- en Bosonderzoek, Brussel.

MacArthur, R. H., & Wilson, E. O. (2001). The Theory of Island Biogeography. In Princeton University Press eBooks. https://doi.org/10.1515/9781400881376

Martín-Devasa, R., Jiménez-Valverde, A., Leprieur, F., Baselga, A., & Gómez-Rodríguez, C. (2024). Dispersal limitation shapes distance-decay patterns of European spiders at the continental scale. *Global Ecology And Biogeography*. https://doi.org/10.1111/geb.13810

Matuoka, M. A., Benchimol, M., De Almeida-Rocha, J. M., & Morante-Filho, J. C. (2020). Effects of anthropogenic disturbances on bird functional diversity: A global meta-analysis. *Ecological Indicators*, *116*, 106471. https://doi.org/10.1016/j.ecolind.2020.106471

McKenna, D. D., Shin, S., Ahrens, D., Balke, M., Beza-Beza, C., Clarke, D. J., Donath, A., Escalona, H. E., Friedrich, F., Letsch, H., Liu, S., Maddison, D., Mayer, C., Misof, B., Murin, P. J., Niehuis, O., Peters, R. S., Podsiadlowski, L., Pohl, H., . . . Beutel, R. G. (2019). The evolution and genomic basis of beetle diversity. *Proceedings Of The National Academy Of Sciences Of The United States Of America*, *116*(49), 24729–24737. https://doi.org/10.1073/pnas.1909655116

Melbourne, B. A., & Hastings, A. (2008). Extinction risk depends strongly on factors contributing to stochasticity. *Nature*, *454*(7200), 100–103. https://doi.org/10.1038/nature06922

Morlon, H., Chuyong, G. B., Condit, R. S., Hubbell, S. P., Kenfack, D., Thomas, D. W., Valencia, R., & Green, J. L. (2008). A general framework for the distance–decay of similarity in ecological communities. *Ecology Letters*, *11*(9), 904–917. https://doi.org/10.1111/j.1461-0248.2008.01202.x

Mortier, F., Bafort, Q., Milosavljevic, S., Kauai, F., Boxoen, L. P., van de Peer, Y. and Bonte, D. (2024). Understanding polyploid establishment: temporary persistence or stable coexistence? *Oikos, 2024 (5)*. https://doi.org/10.1111/oik.09929

Newbold, T. (2018). Future effects of climate and land-use change on terrestrial vertebrate community diversity under different scenarios. *Proceedings - Royal Society. Biological Sciences/Proceedings - Royal Society. Biological Sciences*, *285*(1881), 20180792. https://doi.org/10.1098/rspb.2018.0792

Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S., & Favila, M. (2008). Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation*, *141*(6), 1461–1474. https://doi.org/10.1016/j.biocon.2008.04.011

Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, *120*(3), 321–326. https://doi.org/10.1111/j.1600-0706.2010.18644.x

Pacifici, M., Rondinini, C., Rhodes, J. R., Burbidge, A. A., Cristiano, A., Watson, J. E. M., Woinarski, J. C. Z., & Di Marco, M. (2020). Global correlates of range contractions and expansions in terrestrial mammals. *Nature Communications*, *11*(1). https://doi.org/10.1038/s41467-020-16684-w

Pacifici, M., Visconti, P., Butchart, S. H. M., Watson, J. E. M., Cassola, F. M., & Rondinini, C. (2017). Species' traits influenced their response to recent climate change. *Nature Climate Change*, *7*(3), 205–208. https://doi.org/10.1038/nclimate3223

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*(6918), 37–42. https://doi.org/10.1038/nature01286

Petsch, D. K. (2016). Causes and consequences of biotic homogenization in freshwater ecosystems. *International Review Of Hydrobiology*, *101*(3–4), 113–122. https://doi.org/10.1002/iroh.201601850

Qiao, H., Peterson, A. T., Campbell, L. P., Soberón, J., Ji, L., & Escobar, L. E. (2016). NicheA: creating virtual species and ecological niches in multivariate environmental scenarios. *Ecography*, *39*(8), 805–813. https://doi.org/10.1111/ecog.01961

Richards, C., Cooke, R. S. C., & Bates, A. E. (2021). Biological traits of seabirds predict extinction risk and vulnerability to anthropogenic threats. *Global Ecology And Biogeography*, *30*(5), 973–986. https://doi.org/10.1111/geb.13279

Roitberg, B. D., & Mangel, M. (2016). Cold snaps, heatwaves, and arthropod growth. *Ecological Entomology*, *41*(6), 653–659. https://doi.org/10.1111/een.12324

Rubenstein, M. A., Weiskopf, S. R., Bertrand, R., Carter, S. L., Comte, L., Eaton, M. J., Johnson, C. G., Lenoir, J., Lynch, A. J., Miller, B. W., Morelli, T. L., Rodriguez, M. A., Terando, A., & Thompson, L. M. (2023). Climate change and the global redistribution of biodiversity: substantial variation in empirical support for expected range shifts. *Environmental Evidence*, *12*(1). https://doi.org/10.1186/s13750-023-00296-0

Ruel, J. J., & Ayres, M. P. (1999). Jensen's inequality predicts effects of environmental variation. *Trends in Ecology & Evolution*, *14*(9), 361–366. https://doi.org/10.1016/s0169-5347(99)01664-x

Sanchey-Bayo, F., Wyckhuys, K. (2019). Worldwide decline of the entomofauna. *Biological Conservation 232*, 8-27, https://doi.org/10.1016/j.biocon.2019.01.020

Sandor, M. E., Elphick, C. S., & Tingley, M. W. (2022). Extinction of biotic interactions due to habitat loss could accelerate the current biodiversity crisis. *Ecological Applications*, *32*(6). https://doi.org/10.1002/eap.2608

Santini, L., Cornulier, T., Bullock, J. M., Palmer, S. C. F., White, S. M., Hodgson, J. A., Bocedi, G., & Travis, J. M. J. (2016). A trait-based approach for predicting species responses to environmental change from sparse data: how well might terrestrial mammals track climate change? *Global Change Biology*, *22*(7), 2415–2424. https://doi.org/10.1111/gcb.13271

Saura, S., Bodin, Ö., & Fortin, M. (2013). EDITOR'S CHOICE: Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. *Journal Of Applied Ecology*, *51*(1), 171–182. https://doi.org/10.1111/1365-2664.12179

Schlaepfer, D. R., Braschler, B., Rusterholz, H., & Baur, B. (2018). Genetic effects of anthropogenic habitat fragmentation on remnant animal and plant populations: a meta-analysis. *Ecosphere*, *9*(10). https://doi.org/10.1002/ecs2.2488

Seibold, S., Gossner, M. M., Simons, N. K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J. C., Linsenmair, K. E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E., Vogt, J., Wöllauer, S., & Weisser, W. W. (2019). Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature*, *574*(7780), 671–674. https://doi.org/10.1038/s41586-019-1684-3

Shelomi, M. (2012). Where are we now? Bergmann's rule sensu lato in insects. ˜ *The œAmerican Naturalist*, *180*(4), 511–519. https://doi.org/10.1086/667595

Sheridan, J. A., & Bickford, D. (2011). Shrinking body size as an ecological response to climate change. *Nature Climate Change*, *1*(8), 401–406. https://doi.org/10.1038/nclimate1259

Short, F. T., Kosten, S., Morgan, P. A., Malone, S., & Moore, G. E. (2016). Impacts of climate change on submerged and emergent wetland plants. *Aquatic Botany*, *135*, 3–17. https://doi.org/10.1016/j.aquabot.2016.06.006

Socolar, J. B., Gilroy, J. J., Kunin, W. E., & Edwards, D. P. (2016). How should Beta-Diversity inform biodiversity conservation? *Trends in Ecology & Evolution*, *31*(1), 67–80. https://doi.org/10.1016/j.tree.2015.11.005

Stevens, V. M., Trochet, A., Blanchet, S., Moulherat, S., Clobert, J., & Baguette, M. (2013a). Dispersal syndromes and the use of life-histories to predict dispersal. *Evolutionary Applications*, *6*(4), 630–642. https://doi.org/10.1111/eva.12049

Terlau, J. F., Brose, U., Boy, T., Pawar, S., Pinsky, M., & Hirt, M. R. (2023). Predicting movement speed of beetles from body size and temperature. *Movement Ecology*, *11*(1). https://doi.org/10.1186/s40462-023-00389-y

Terry, J. C. D., O'Sullivan, J. D., & Rossberg, A. G. (2024). Schrödinger's Range-Shifting Cat: How Skewed Temperature Dependence Impacts Persistence with Climate Change. ˜ *The œAmerican Naturalist*, *203*(2), 161–173. https://doi.org/10.1086/728002

The IUCN Red List of Threatened Species. (n.d.). IUCN Red List of Threatened Species. https://www.iucnredlist.org/

Travis, J. M. J., Delgado, M., Bocedi, G., Baguette, M., Bartoń, K., Bonte, D., Boulangeat, I., Hodgson, J. A., Kubisch, A., Penteriani, V., Saastamoinen, M., Stevens, V. M., & Bullock, J. M. (2013). Dispersal and species' responses to climate change. *Oikos*, *122*(11), 1532–1540. https://doi.org/10.1111/j.1600-0706.2013.00399.x

De Knijf G., Adams Y. & D. Paelinckx. (2010). Biologische Waarderingskaart, versie 2. Toelichting bij de kaartbladen 30-38 (Rapport en digitaal bestand).. Rapporten van het Instituut voor Natuur- en Bosonderzoek 2010, (INBO.R.2010.6). Instituut voor Natuur- en Bosonderzoek, Brussel.

Vriens, L., Bosch, H., De Knijf, G., De Saeger, S., Guelinckx, R., Oosterlynck, P., Van Hove, M., Paelinckx, D. (2011). De Biologische Waarderingskaart. Biotopen en hun verspreiding in Vlaanderen en het Brussels Hoofdstedelijk Gewest. Research Institute of Nature and Forest.

De Saeger S., Dhaluin P., Erens R., Guelinckx G., Hennebel D., Jacobs I., Kumpen M., Van Oost F., Spanhove T., Leyssen A., Oosterlynck P., Van Dam G., Van Hove M., Wils C. (red.) (2023). Biologische Waarderingskaart en Natura 2000 Habitatkaart, uitgave 2023. Rapporten van het Instituut voor Natuur- en Bosonderzoek 2023 (31). Instituut voor Natuur- en Bosonderzoek, Brussel. DOI: doi.org/10.21436/inbor.96375305

IPCC, 2022: Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [H.-O. Pörtner, D.C. Roberts, M. Tignor, E.S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, B. Rama (eds.)]. Cambridge University Press. Cambridge University Press, Cambridge, UK and New York, NY, USA, 3056 pp., doi:10.1017/9781009325844.

Wickham H (2016). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. ISBN 978-3-319-24277-4, https://ggplot2.tidyverse.org.

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Wickham H, François R, Henry L, Müller K, Vaughan D (2023). dplyr: A Grammar of Data Manipulation. R package version 1.1.4, https://CRAN.R-project.org/package=dplyr.

Wickham H (2023). forcats: Tools for Working with Categorical Variables (Factors). R package version 1.0.0, https://CRAN.R-project.org/package=forcats.

Baselga A, Orme D, Villeger S, De Bortoli J, Leprieur F, Logez M, Martinez-Santalla S, Martin-Devasa R, Gomez-Rodriguez C, Crujeiras R (2023). betapart: Partitioning Beta Diversity into Turnover and Nestedness Components. R package version 1.6, https://CRAN.R-project.org/package=betapart.

Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill M, Lahti L, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A, Ter Braak C, Weedon J (2022). vegan: Community Ecology Package. R package version 2.6-4, https://CRAN.R-project.org/package=vegan.

Trotter, R. T., Ryan, J. K., Chandler, J. L., & Pfister, S. (2023). Tracking the push towards extinction: combining dispersal and management data to monitor Asian longhorned beetle eradication in the U.S. Frontiers in Insect Science, 3. https://doi.org/10.3389/finsc.2023.1286935

Troudet, J., Grandcolas, P., Blin, A., Vignes-Lebbe, R., & Legendre, F. (2017). Taxonomic bias in biodiversity data and societal preferences. *Scientific Reports*, *7*(1). https://doi.org/10.1038/s41598-017-09084-6

Ulrich, W., & Almeida-Neto, M. (2012). On the meanings of nestedness: back to the basics. *Ecography*, *35*(10), 865–871. https://doi.org/10.1111/j.1600-0587.2012.07671.x

Valiente-Banuet, A., Aizen, M. A., Alcántara, J. M., Arroyo, J., Cocucci, A., Galetti, M., García, M. B., García, D., Gómez, J. M., Jordano, P., Medel, R., Navarro, L., Obeso, J. R., Oviedo, R., Ramírez, N., Rey, P. J., Traveset, A., Verdú, M., & Zamora, R. (2014). Beyond species loss: the extinction of ecological interactions in a changing world. *Functional Ecology*, *29*(3), 299–307. https://doi.org/10.1111/1365-2435.12356

Wagner, D. L., Grames, E. M., Forister, M. L., Berenbaum, M. R., & Stopak, D. (2021). Insect decline in the Anthropocene: Death by a thousand cuts. *Proceedings Of The National Academy Of Sciences Of The United States Of America*, *118*(2). https://doi.org/10.1073/pnas.2023989118

Wang, S., & Loreau, M. (2016). Biodiversity and ecosystem stability across scales in metacommunities. *Ecology Letters*, *19*(5), 510–518. https://doi.org/10.1111/ele.12582

Wang, S., Loreau, M., De Mazancourt, C., Isbell, F., Beierkuhnlein, C., Connolly, J., Deutschman, D. H., Doležal, J., Eisenhauer, N., Hector, A., Jentsch, A., Kreyling, J., Lanta, V., Lepš, J., Polley, H. W., Reich, P. B., Van Ruijven, J., Schmid, B., Tilman, D., . . . Craven, D. (2021). Biotic homogenization destabilizes ecosystem functioning by decreasing spatial asynchrony. *Ecology*, *102*(6). https://doi.org/10.1002/ecy.3332

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J., Olesen, J., Valido, A., & Warren, P. (2005). Body size in ecological networks. *Trends in Ecology & Evolution*, *20*(7), 402–409. https://doi.org/10.1016/j.tree.2005.04.005

Yang, L. H., & Gratton, C. (2014). Insects as drivers of ecosystem processes. *Current Opinion in Insect Science*, *2*, 26–32. https://doi.org/10.1016/j.cois.2014.06.004

Zhang, Z. (2011). Animal biodiversity: An introduction to higher-level classification and taxonomic richness. *Zootaxa*, *3148*(1), 7. https://doi.org/10.11646/zootaxa.3148.1.3

Appendix

1. Sensitivity analysis

Methods

We conducted a sensitivity analysis on two parameters. The first parameter is a, which determines the tail of the dispersal curve and was set to 2 in our model. The second parameter is α, which determines the asymmetry of the fitness curve and was set to 0.1. To test the effect of these parameters on our results, we ran our model for -25%, -10%, +10%, and +25% of these values. This resulted in a total of eight runs with a equal to 1.5, 1.8, 2.2, and 2.5 and α equal to 0.075, 0.090, 0.110, and 0.125.

We specifically tested the effects of these parameters on mean alpha diversity, mean population size, and gamma diversity. These variables were calculated for the different values of *a* and α in the same way as described above and plotted for each scenario. We also calculated the relative variance for each result. Thus, we subtract the result (alpha diversity, mean population or gamma diversity for a given scenario) obtained with one of the newly chosen values for a and α from the corresponding result obtained with the base model and finally divide this by the result obtained with the base model.

Results

We observe similar trends even though the values for *a* change meaning the Natura 2000 landscape always has lower values in comparison with the all grassland landscape (Figure 1 – 3). The most variance is observed for the most extreme heating scenarios. But overall there is no large variance between the results.

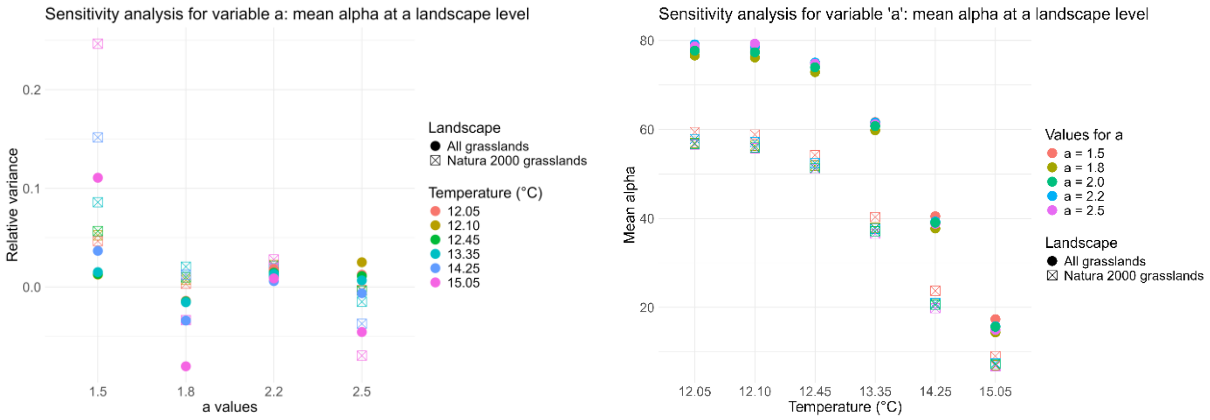


Fig. 1: Sensitivity analysis for the variable a for mean alpha diversity. On the left, the relative variance for each run and scenario is plotted. On the right are the mean alpha values for every scenario plotted.

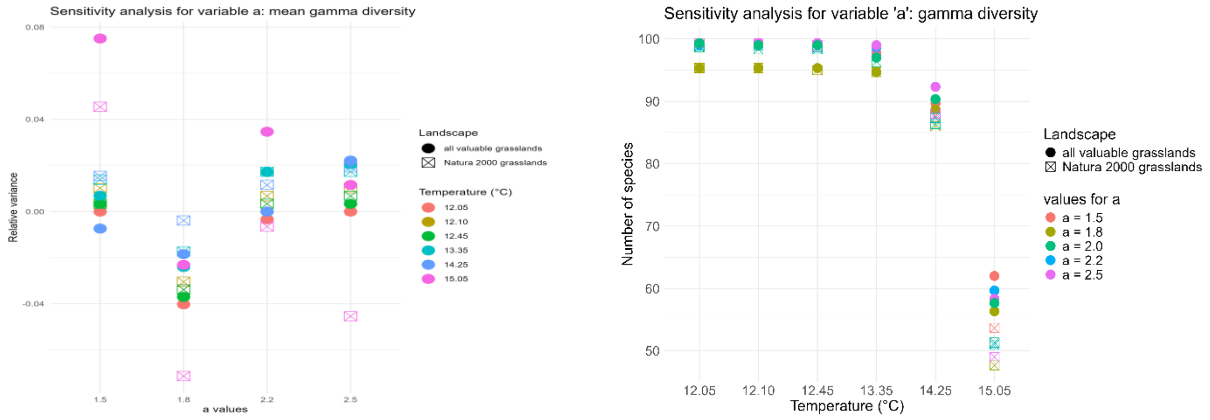


Fig. 2: Sensitivity analysis for the variable a for mean gamma diversity. On the left, the relative variance for each run and scenario is plotted. On the right are the mean gamma values for every scenario plotted.

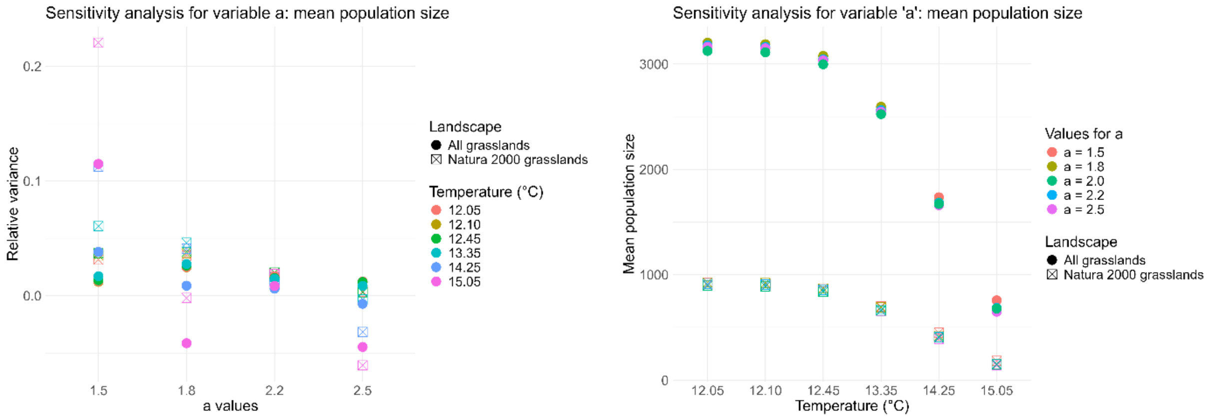


Fig. 3: Sensitivity analysis for the variable a for mean population size. On the left, the relative variance for each run and scenario is plotted. On the right are the mean population sizes for every scenario plotted.

We observe similar trends even though the values for α change meaning the Natura 2000 landscape always has lower values in comparison with the all grassland landscape (Figure 4 – 6). The most variance is observed for the most extreme heating scenarios. There is some variance but this does not change the patterns observed in the main model.

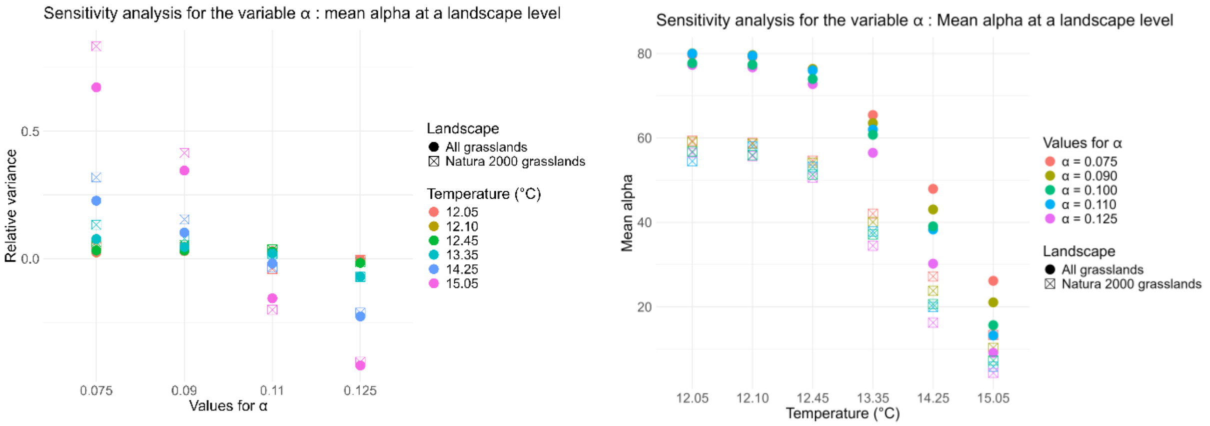


Fig. 4: Sensitivity analysis for the variable α for mean alpha diversity. On the left, the relative variance for each run and scenario is plotted. On the right are the mean alpha values for every scenario plotted.

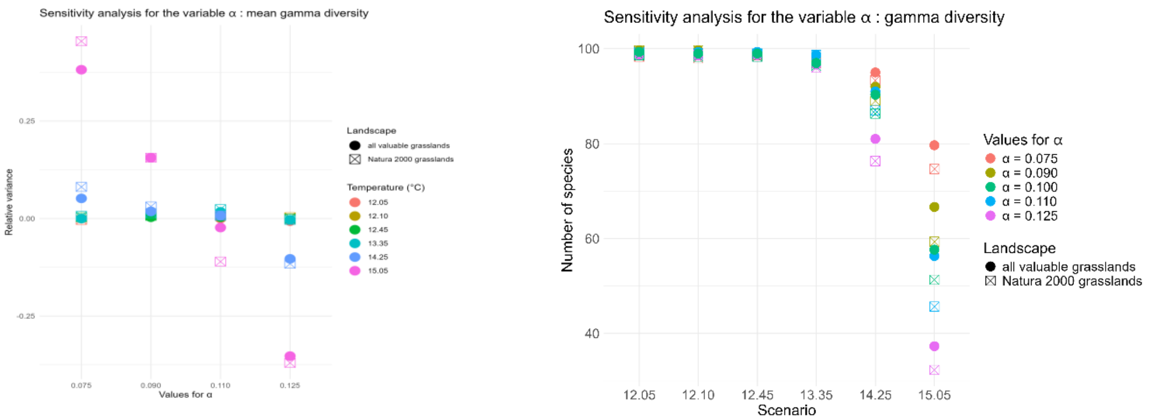


Fig. 5: Sensitivity analysis for the variable α for mean gamma diversity. On the left, the relative variance for each run and scenario is plotted. On the right are the mean gamma values for every scenario plotted.

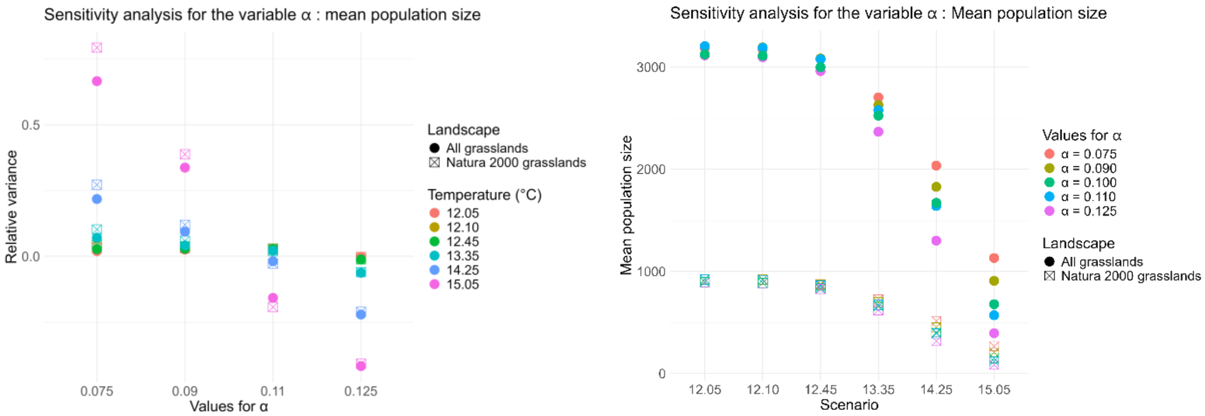


Fig. 6: Sensitivity analysis for the variable α for mean population size. On the left, the relative variance for each run and scenario is plotted. On the right are the mean population sizes for every scenario plotted.

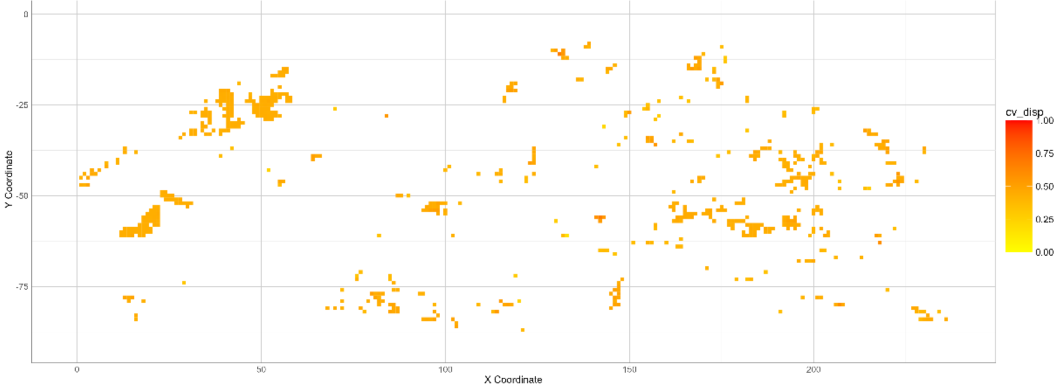
Conclusion

The sensitivity analysis performed on the factors α and a shows that changes in these factors do not significantly alter our results. Therefore, our results are robust. A more complete sensitivity analysis would include other results such as functional diversity. However, this was not possible due to the time frame of the thesis. Nevertheless, we do not expect significant deviations from our current findings if we included these outcomes as well.

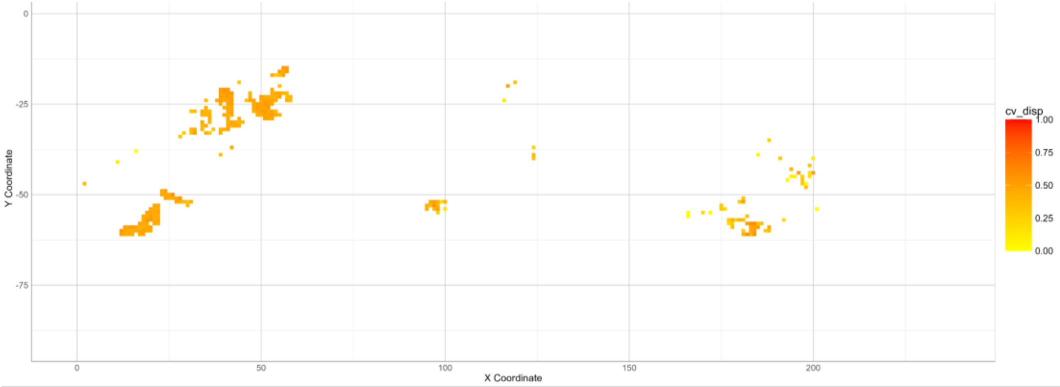
2. Functional diversity

2.1 Coefficient of variation

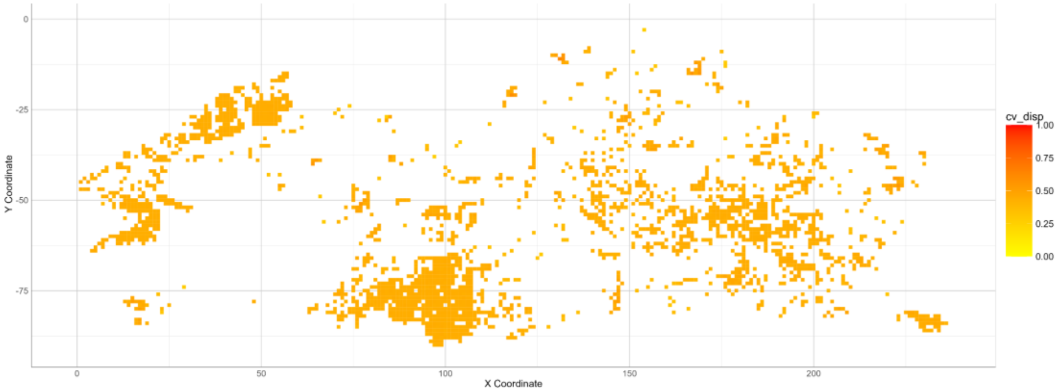
Heatmap of CV of dispersal for scenario 1



Heatmap of CV of dispersal for scenario 6



Heatmap of CV of dispersal for scenario 7



Heatmap of CV of dispersal for scenario 12

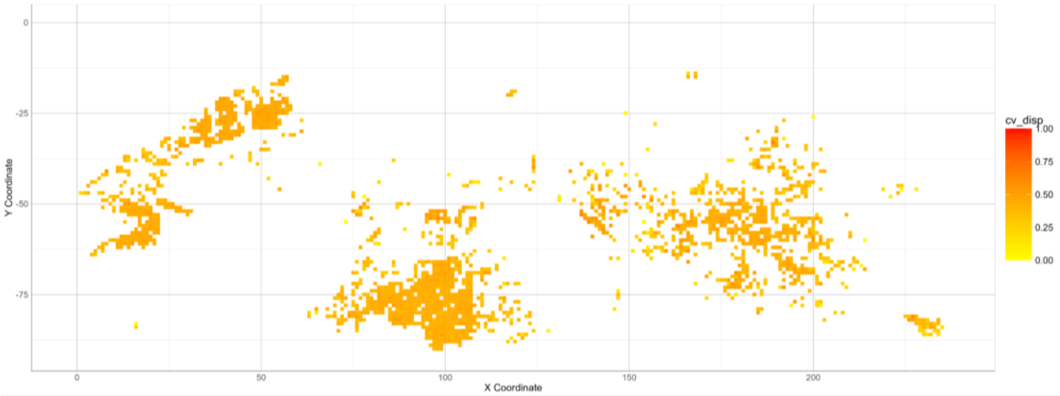
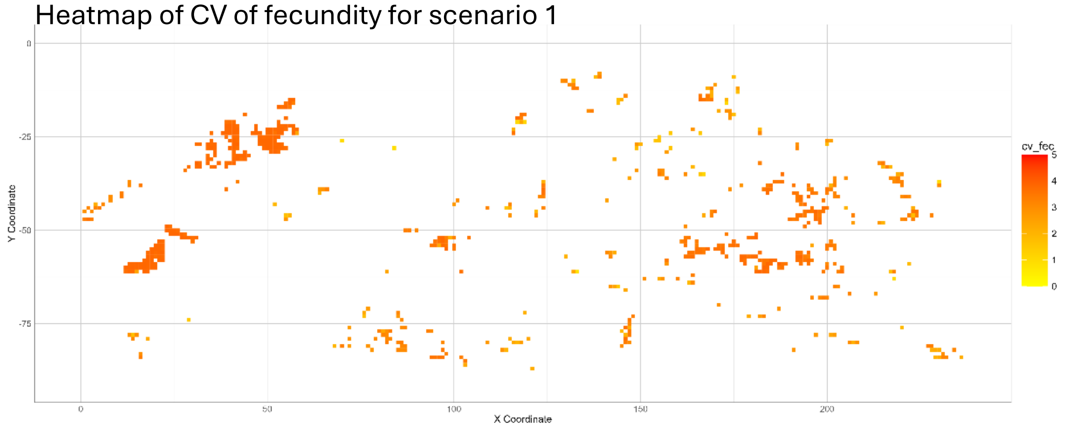
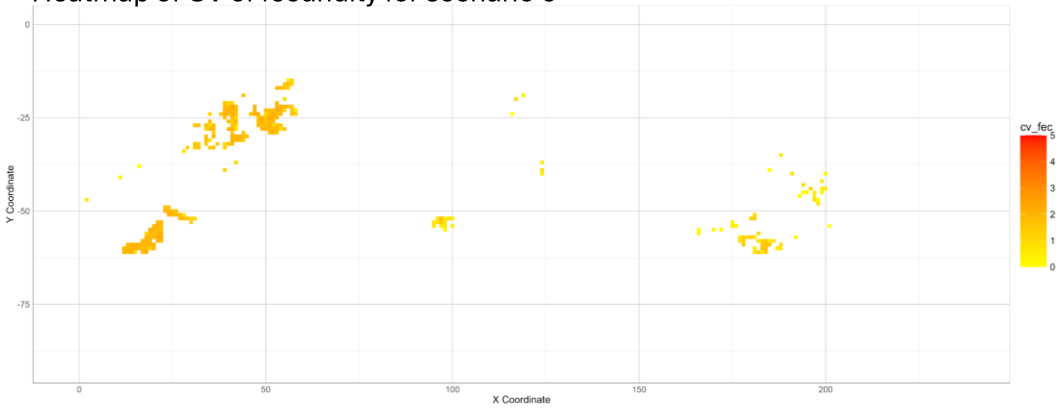


Fig. 7: Heatmaps of the CV of dispersal for scenarios 1, 6, 7 and 12. The darker the color the larger the diversity in dispersal is.

Heatmap of CV of fecundity for scenario 1



Heatmap of CV of fecundity for scenario 6



Heatmap of CV of fecundity for scenario 7

Heatmap of CV of fecundity for scenario 12

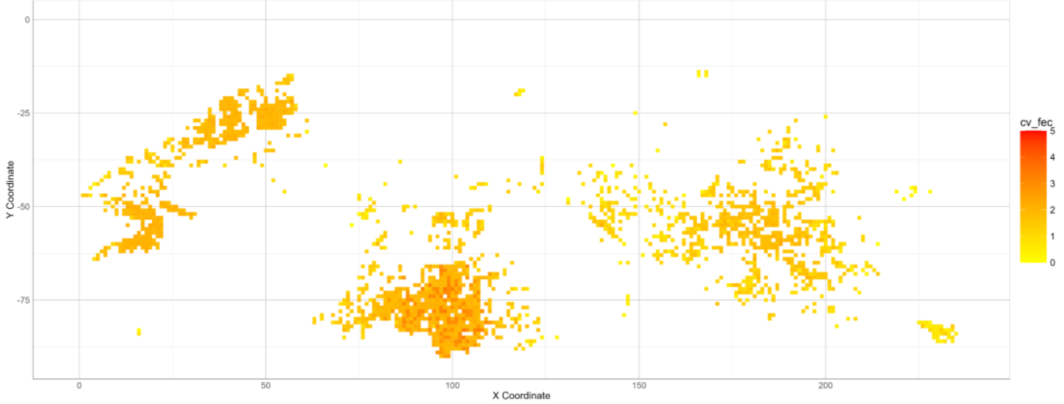


Fig. 8: Heatmaps of the CV of fecundity for scenarios 1, 6, 7 and 12. The darker the color the larger the diversity in fecundity is.

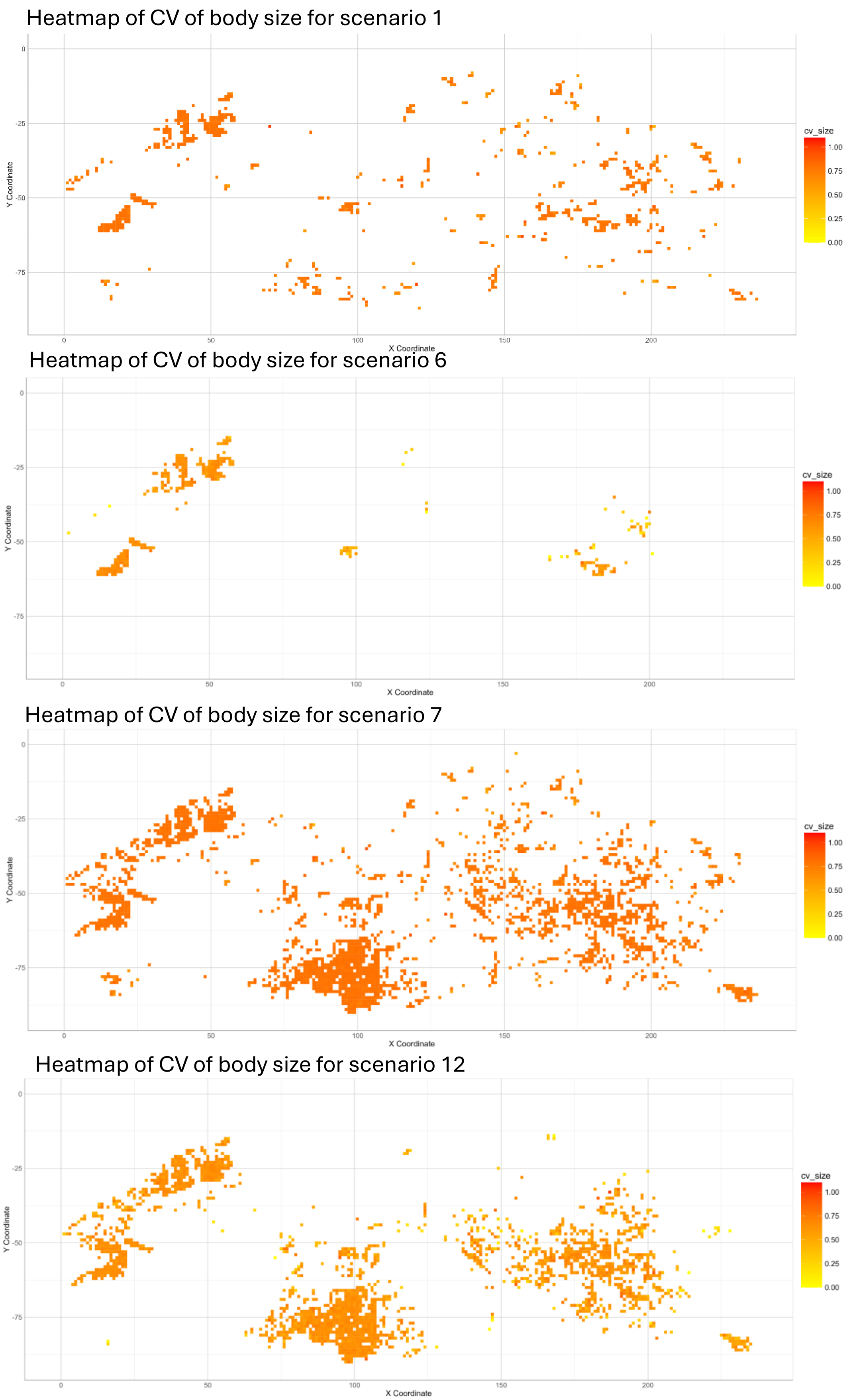
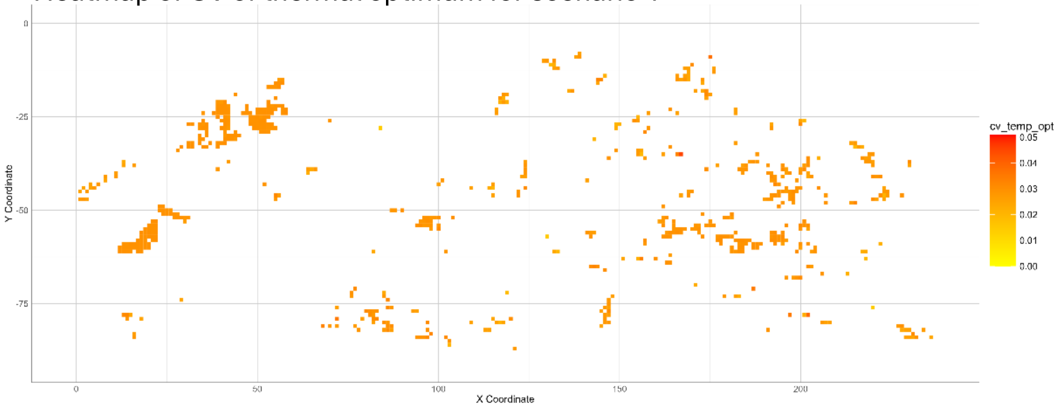
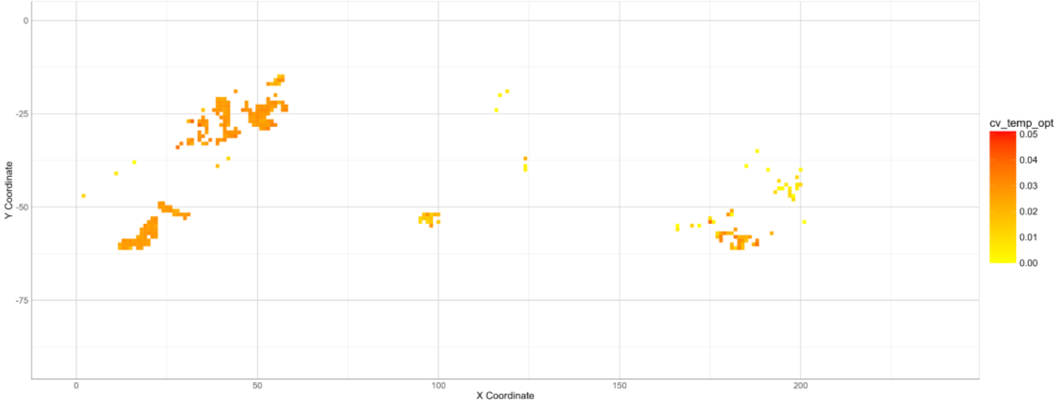


Fig. 9: Heatmaps of the CV of body size for scenarios 1, 6, 7 and 12. The darker the color the larger the diversity in body size is.

Heatmap of CV of thermal optimum for scenario 1



Heatmap of CV of thermal optimum for scenario 6



Heatmap of CV of thermal optimum for scenario 7

Heatmap of CV of thermal optimum for scenario 12

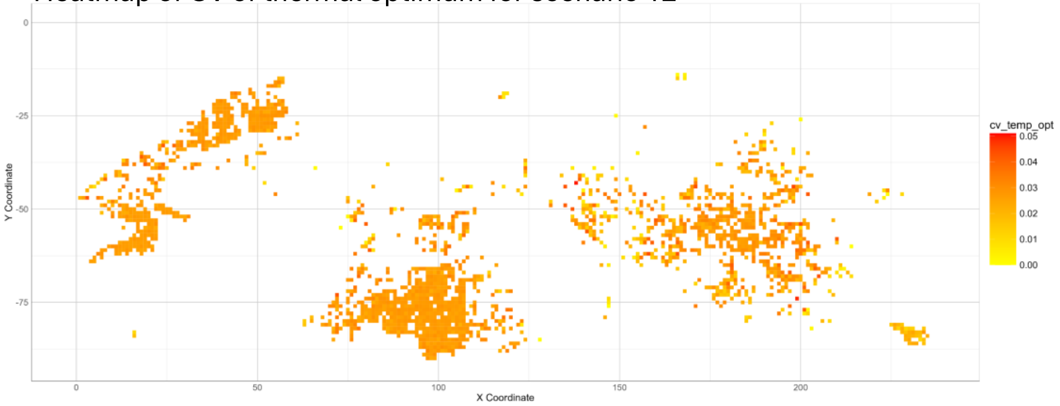
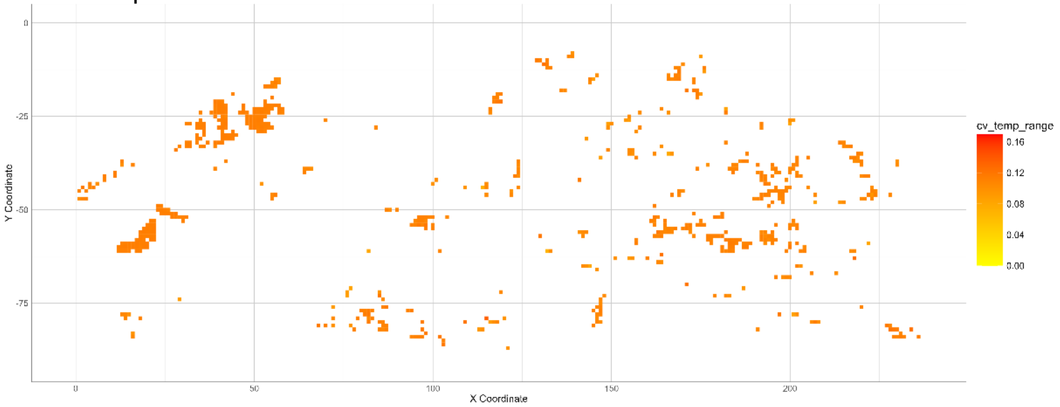
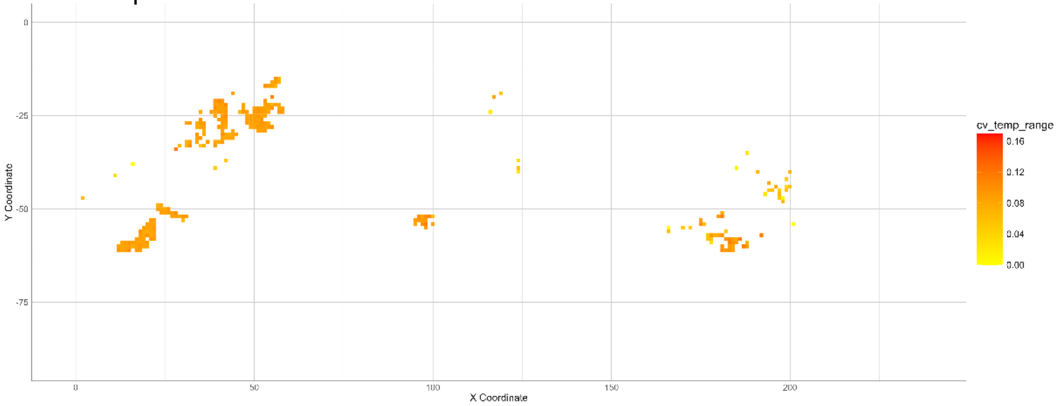


Fig. 10: Heatmaps of the CV of thermal optimum for scenarios 1, 6, 7 and 12. The darker the color the larger the diversity in thermal optimum is.

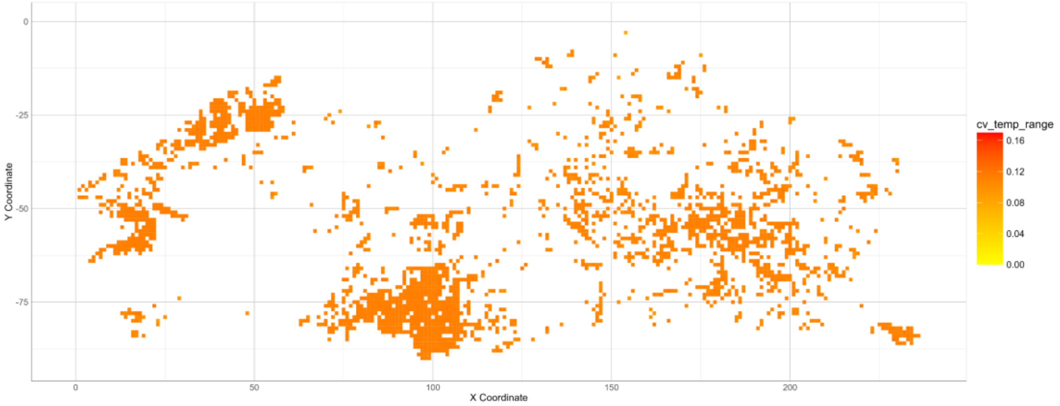
Heatmap of CV of thermal breadth for scenario 1



Heatmap of CV of thermal breadth for scenario 6



Heatmap of CV of thermal breadth for scenario 7

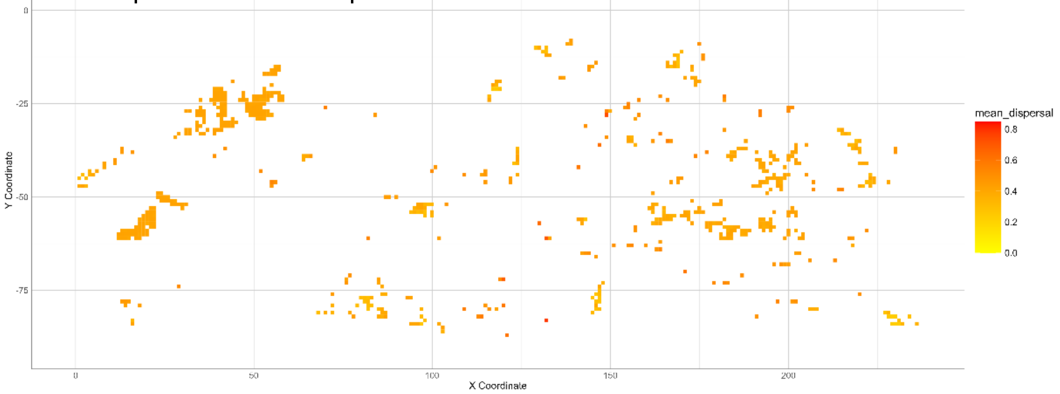


Heatmap of CV of thermal breadth for scenario 12

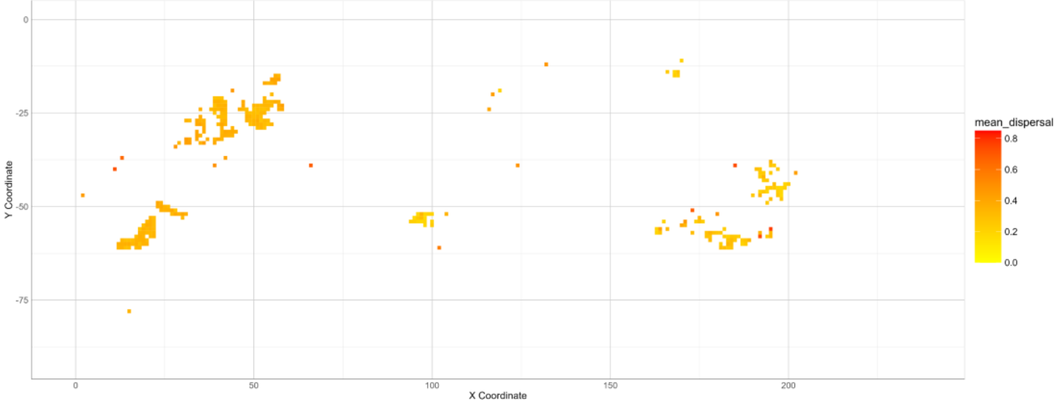
Fig. 11: Heatmaps of the CV of thermal breadth for scenarios 1, 6, 7 and 12. The darker the color the larger the diversity in thermal breadth is.

2.2 Mean of life-history traits

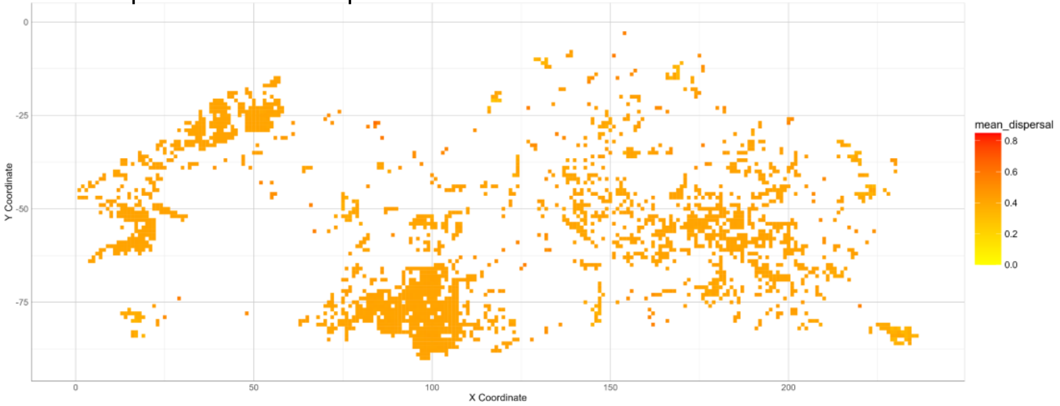
Heatmap of the mean dispersal for scenario 1



Heatmap of the mean dispersal for scenario 6



Heatmap of the mean dispersal for scenario 7



Heatmap of the mean dispersal for scenario 12

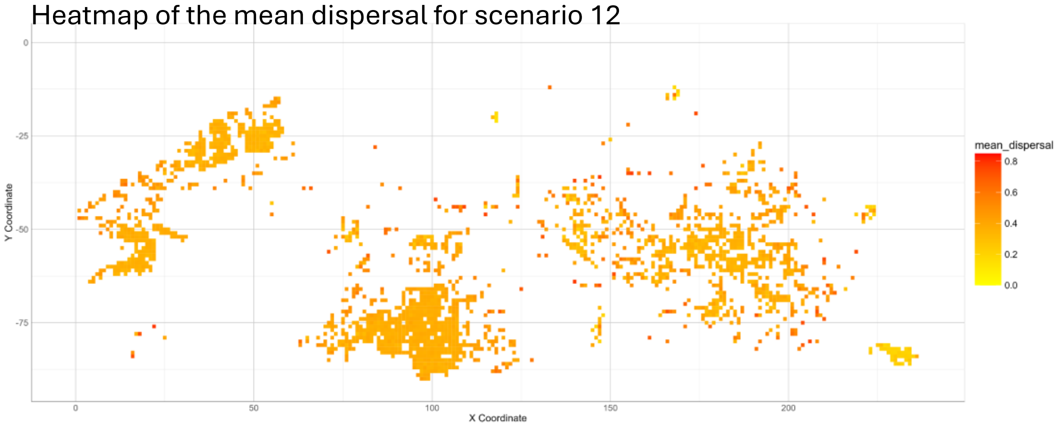
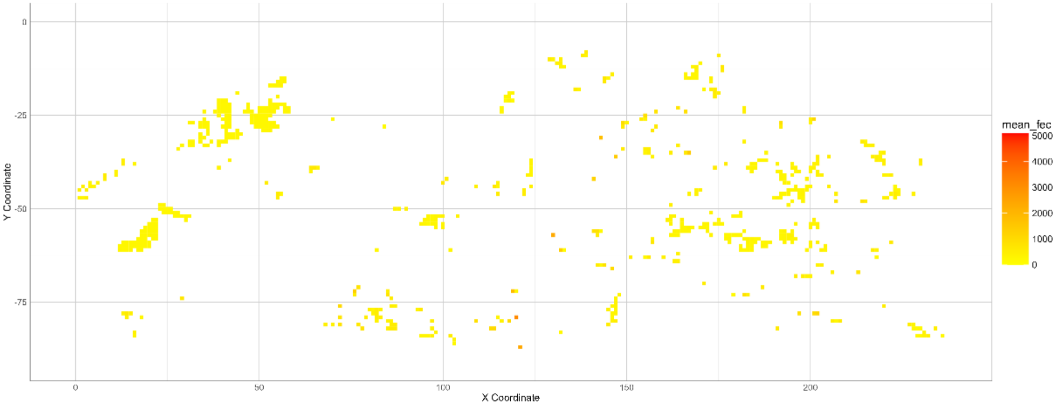
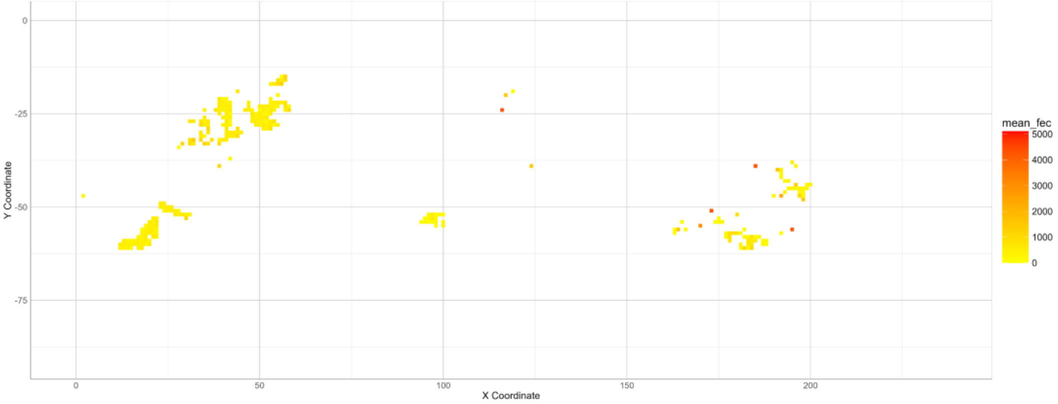


Fig. 12: Heatmaps of the mean dispersal for scenarios 1, 6, 7 and 12.

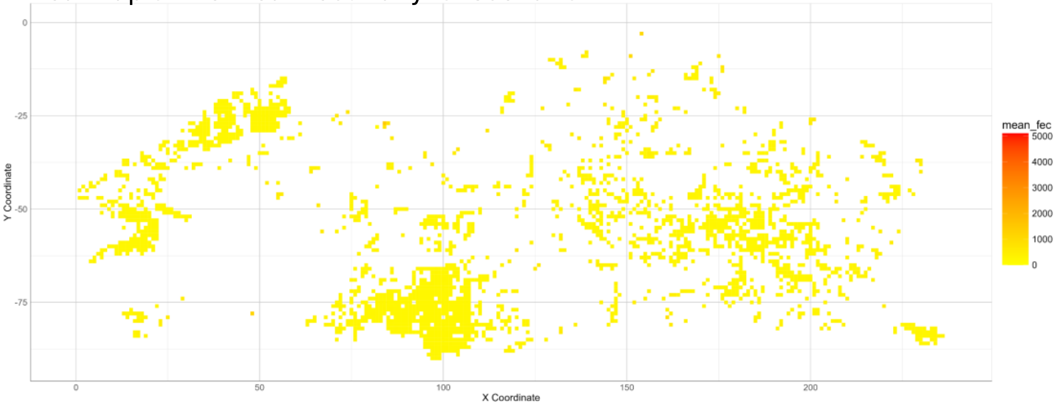
Heatmap of the mean fecundity for scenario 1



Heatmap of the mean fecundity for scenario 6



Heatmap of the mean fecundity for scenario 7



Heatmap of the mean fecundity for scenario 12

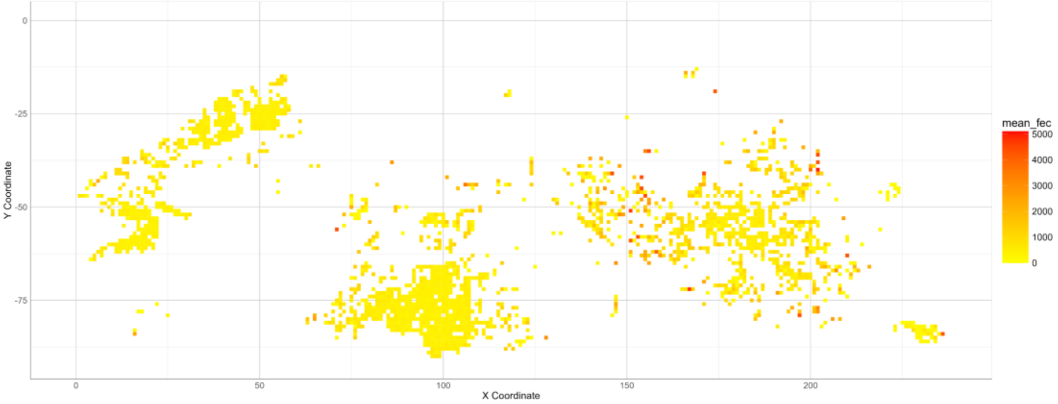
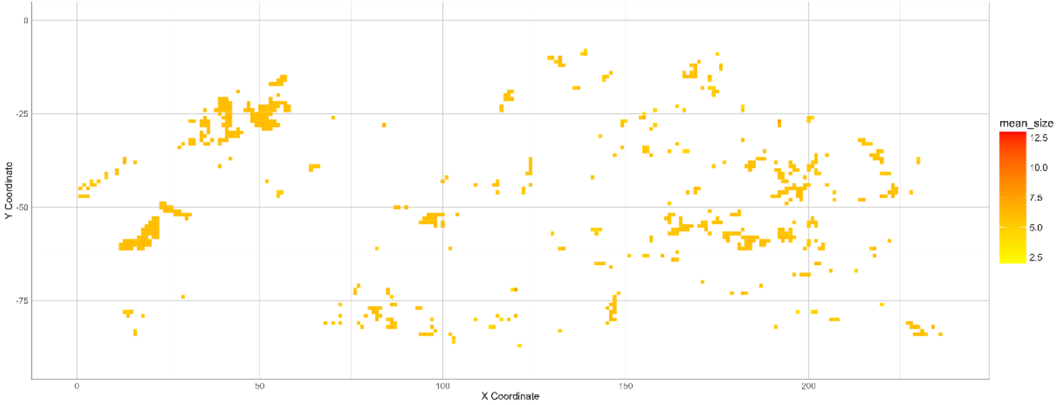
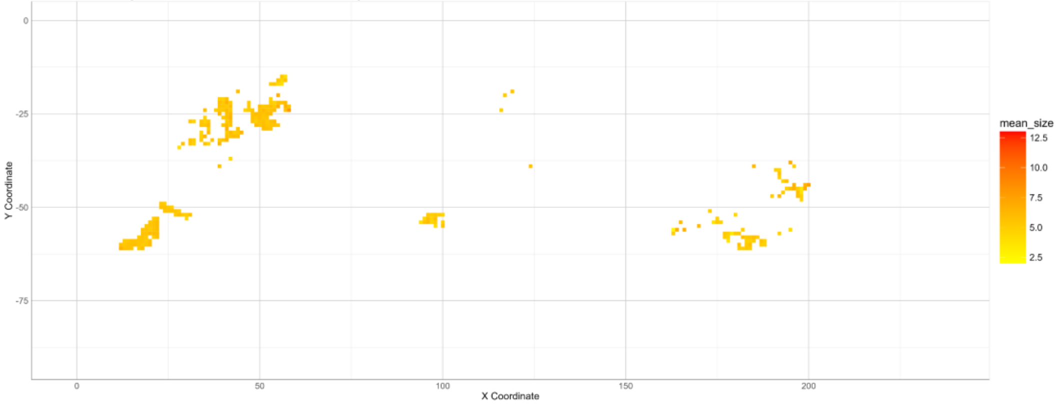


Fig. 13: Heatmaps of the mean fecundity for scenarios 1, 6, 7 and 12.

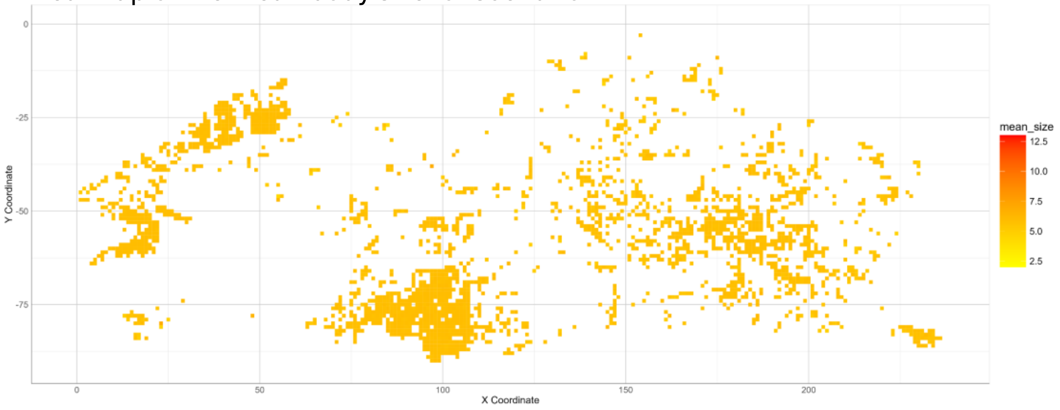
Heatmap of the mean body size for scenario 1



Heatmap of the mean body size for scenario 6



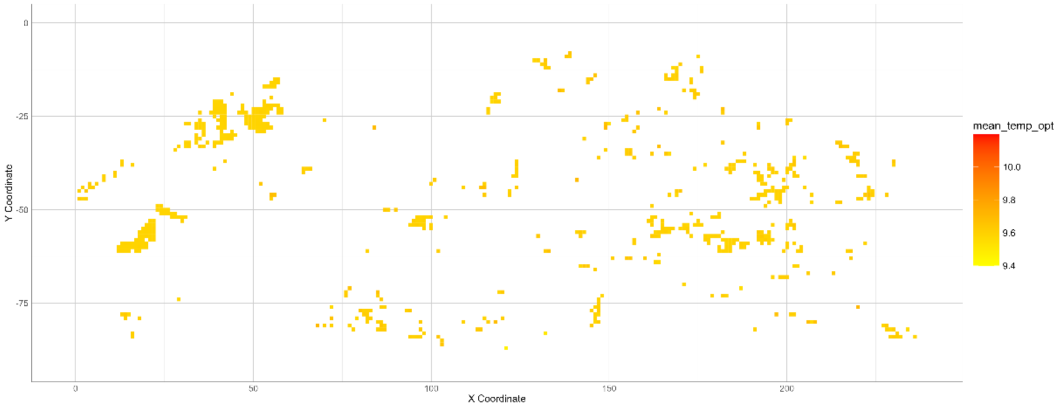
Heatmap of the mean body size for scenario 7



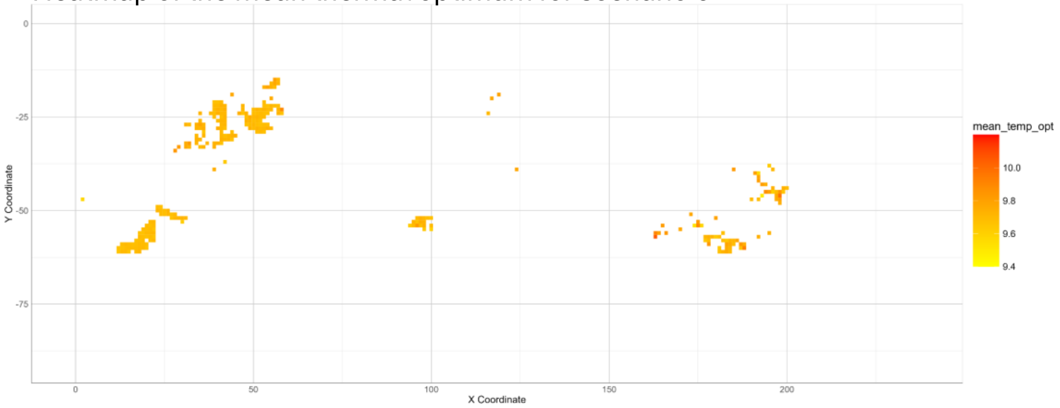
Heatmap of the mean body size for scenario 12

Fig. 14: Heatmaps of the mean body size for scenarios 1, 6, 7 and 12.

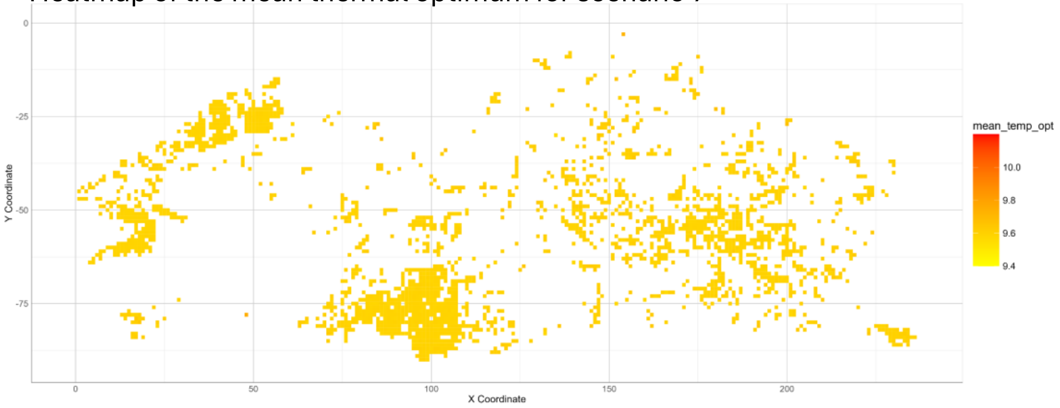
Heatmap of the mean thermal optimum for scenario 1



Heatmap of the mean thermal optimum for scenario 6



Heatmap of the mean thermal optimum for scenario 7



Heatmap of the mean thermal optimum for scenario 12

Fig. 15: Heatmaps of the mean thermal optimum for scenarios 1, 6, 7 and 12.

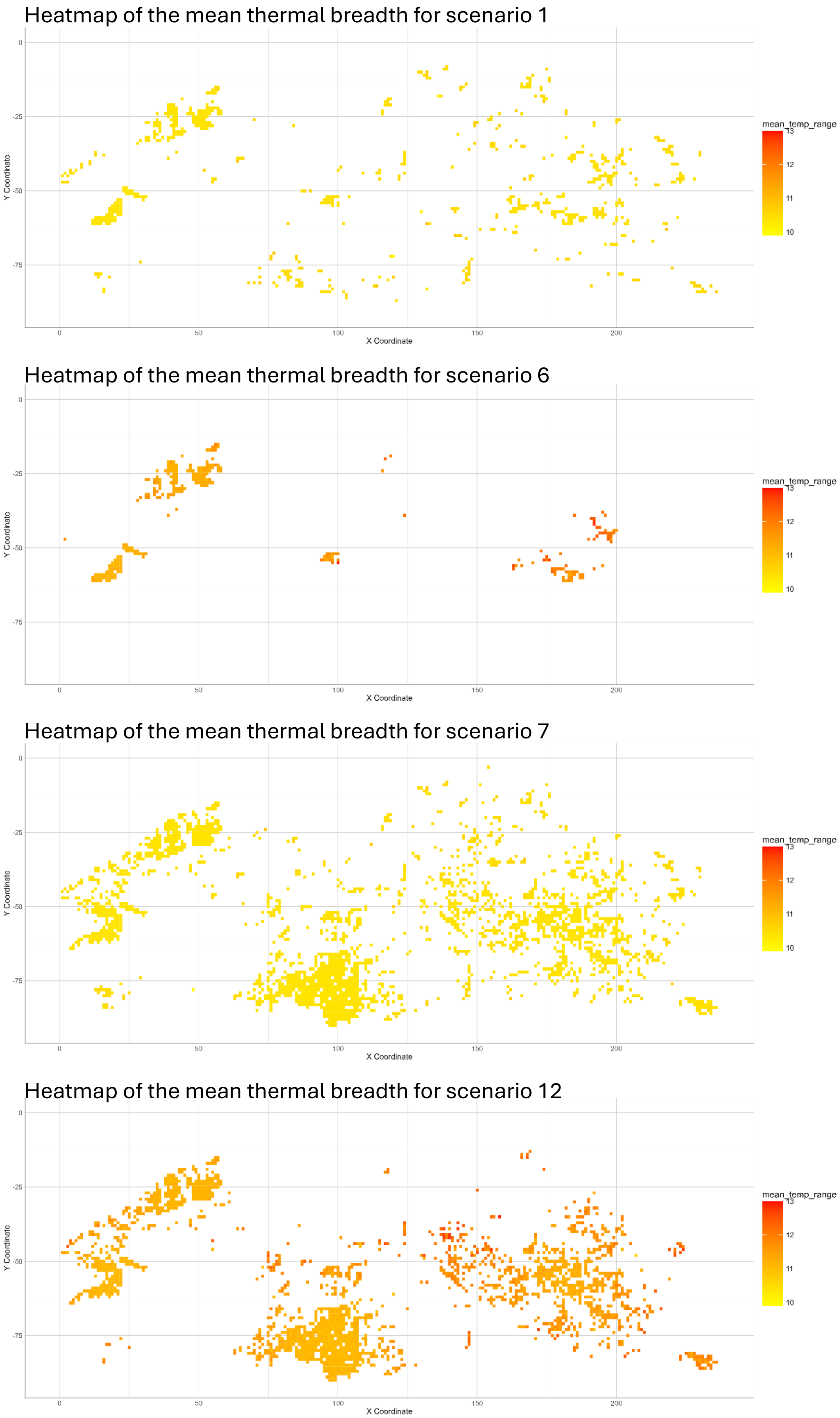


Fig. 16: Heatmaps of the mean thermal breadth for scenarios 1, 6, 7 and 12.

ODD protocol

1. Purpose

The purpose of this model is to predict the survival of beetle populations in Flanders under climate change. Another objective is determining the correlations between different life-history traits of the species and survival rates. The last goal is determining the effect of different amounts of habitat and habitat connectivity on the survival rate of beetle populations.

2. Entities, state variables, and scales

Types of entities and their state variables

The first type of entity in this model is individuals. Individuals can be grouped into different species. Each individual has three state variables. The first two describe their position in the landscape using an X and Y value. The other state variable is size, which is used to calculate the life-history traits of different species. The second type of entity is the spatial unit. In this model, they represent rectangular grid cells. Each grid cell contains two different state variables. The first is the list of individuals present in the grid cell. The second variable is the percentage of habitat cover for that cell. This percentage depends on the landscape being modeled. The last type of entity is the environment. This entity acts on all spatial units and is homogeneous. The only state variable here is temperature. Each species goes through six different environmental temperatures. These temperatures do not change gradually but are constant for each scenario run.

Scale and extent

Each time step represents one generation. For each scenario, 100 generations per species are modeled. In reality, one grid cell represents a square of 1 km × 1 km. The total extent of the landscape is 91 × 237 km, which is 21.567 km^2 (approximately equal to the size of Flanders).

3. Process overview and scheduling Design concepts

```
Setup
    Create all the documents needed and clear them.
    Create the two different landscapes. A landscape with only Natura 2000 grasslands and
    a landscape with all Flanders' grasslands included.

Start loop for the different species (This will be done 100 times)
    Initialize the species by assigning life-history traits
    Start loop to go through all the scenarios (12 in total with 6 different temperatures and 2
    different landscapes)

    Generational loop (This will be done 100 times)
            Initialize population, here coordinates are assigned to all individuals
            Shuffle the population list
```

```
                Determine which individuals will survive according to the environment
                temperature
                Individuals get offspring
                All the individuals of the old generation die
                The offspring list gets shuffled
                Random offspring above the carrying capacity of their cell move
                List of offspring get shuffled
                Random offspring above the carrying capacity of their cell die

        The end position of each individual is saved.
        The population size of each scenario is saved.

The life-history traits of the species are saved.
```

Time is modeled in discrete steps.

4. Design concepts

Basic principles

Many studies have documented the generality of left-tailed skewed thermal niches (Ruel & Ayres 1999; Roitberg & Mangel 2016). Thereby, the performance of an individual decreases faster when the environmental temperature is above its optimum than when the environmental temperature is below its optimum. We include this observed asymmetry into the calculation of an individual's fitness to make the model more realistic.

Furthermore, density-dependent dispersal is included in the model. Only when local populations exceed the carrying capacity of their cell, will individuals disperse. Individuals will continue to disperse away from the cell until the carrying capacity in that particular cell is reached again. Which individuals move out of the cell is completely random.

Many studies have shown that the life-history traits of species are closely correlated with their body size (Honěk 1993; Jenkins et al., 2007; Klok & Harrison, 2013; Shelomi, 2012). Therefore, we use body size to determine the other life-history traits of a species.

Emergence

One of the emerging results of this model is the population dynamics, which is mostly observed by the population sizes of the different species. In addition, the distribution of species in the landscape is also an emerging result.

Adaptation

When the carrying capacity of a cell is satisfied, individuals move to other cells. This is adaptive behavior. However, which individuals will move is random. In addition, the direction of dispersal is also random; thus, there is no guarantee that an individual will move to a cell under its carrying capacity.

Objectives

The objective of this adaptive behavior is to increase the fitness of an individual. Moving away from a cell above its carrying capacity increases the chance of survival by finding less densely populated cells. Since all individuals above the carrying capacity will die, the selection process of which individuals will die is random.

Learning
There is no aspect of learning in the model.

Prediction
Individuals cannot make predictions about the cells they move to.

Sensing
Individuals can sense the number of individuals in a grid cell thus if the carrying capacity is met. This triggers the movement of an individual.

Interaction
There are indirect interactions in the model. Some individuals are forced to move if the carrying capacity of a cell is satisfied. No communication accompanies these interactions.

Stochasticity
One form of stochasticity in the model is the position of an individual within a cell at timestamp zero. Scenarios with the same landscape always start with the same number of individuals in each cell. However, the positions of individuals within these cells are random.

The survival chance of an individual leads to stochasticity, as it is only partly influenced by their fitness value. Randomization is performed by generating a random number between one and zero for each individual. If this number is lower than the individual's fitness, the individual is removed from the model. Thus, the higher an individual’s fitness, the higher its chance of survival will be.

Demographic stochasticity is also added via the number of offspring an individual has. Stochasticity is added by taking a Poisson distribution of the individual's fecundity value to determine the number of offspring per individual.

For each species, a dispersal curve is formed using the Pareto distribution. Since individuals of the same species will have the same dispersal curve, we include the random value U in the dispersal curve equation. U represents a random value between one and zero and is used to add stochasticity to the model; thus, individuals of the same species will not disperse the same distance. The direction of dispersal is also random.

Some individuals will move when the carrying capacity of a cell is reached. However, which individuals move is randomized. This is done by shuffling the population list before selecting the moving individuals. After all individuals have dispersed, the carrying capacity is checked again. Since the dispersing individuals could have reached a full cell again. All individuals above carrying capacity die, the selection process of these individuals is again randomized by shuffling the population list.

Finally, stochasticity is added to the creation of the virtual species. For each species, a random body size is selected from a list of realistic body sizes. The other life-history traits, dispersal capacity, fecundity, temperature optimum, and temperature range, are calculated using this random body size. For each trait, we have a list of different intercepts and slopes describing the relationship between body size and that particular trait. To obtain these values real trait data was used. A random intercept and slope are selected for each trait. These values and body sizes are then used to determine the life-history traits of the virtual species.

Stochasticity is used to include variability in processes for which it is unimportant to model the actual causes of variability.

Collectives

Individuals can be grouped into species. Individuals of a species differ in their x and y values, but their life-history traits are the same. Sharing life-history traits means that fitness and the dispersal curve are the same as these variables are determined by life-history traits. Therefore, individuals of the same species are expected to behave more similarly than individuals of different species. However, this collective is more a definition we give than a real collective created by individuals flocking together as a result of individual behavior since species are never modeled in the same simulation.

Observation

Each species runs through twelve different scenarios. For each species, the population size and positions at the end of a scenario run are collected. Additionally, all life-history traits generated for each species are collected at the end of each species loop. However, since the life-history traits do not change during the run for each species, the timing is not important here.

5. Initialization

For each new virtual species, new life-history traits are created. These traits are not completely random, but based on values obtained in the field. Next, the landscape is added. There are two different landscapes, one containing all the valuable grasslands in Flanders and the other containing only the grasslands present in the Natura 2000 networka of Flanders. Depending on the scenario, one of the two landscapes is selected. Next, an environmental temperature is assigned, also depending on which scenario is run. There are six different temperatures; these are based on the IPCC report and reflect the expected temperature increase in Flanders by 2100 based on the Shared Socioeconomic Pathways (SSPs).

At time zero, all cells of the landscape are filled with individuals until their carrying capacity is reached. The carrying capacity of each cell depends on the landscape used. This means that scenarios with the same landscape always start with the same initial population size, even if different species are modeled. However, the location of individuals within the cell is random and therefore not constant between the same scenarios.

6. Input data

Input data is used to create the life-history traits of each species. There is one dataset for each trait. The body size dataset contains only one column with realistic beetle sizes. The other datasets contain one column of intercepts and a second column of correlated slopes. These intercepts and slopes describe the relationship between size and that particular life-history trait. In addition, external data is used to create the landscapes. One tiff file is used per landscape. The tiff files are created using the Natura 2000 and BWK habitat maps from INBO and are modified in QGis.

7. Submodels

Creating the two different landscapes

Two different tiff files are used for the two different landscapes. The tiff files contain a raster where each cell contains a value. These values represent the percentage of grassland cover in each cell. The Natura 2000 and BWK habitat maps from INBO are used to calculate these coverage percentages using qgis. The percentages are used to calculate the carrying capacity for each cell by multiplying this number by 10, this final number is rounded down. Thus, the maximum carrying capacity of a cell is ten individuals per species. The array function of numpy is used to return a grid of values from the tiff files, which can then be implemented as the landscape of the model.

Species initialization

The initialization of a species starts by selecting a random body size from the body size dataset. Next, for each trait, a random slope and intercept are selected from the corresponding data sets. Using the randomly selected body size, slope, and intercept, the trait values can be determined using Equation 1. This creates a virtual beetle with five unique life-history traits.

$$Trait\ value = intercept + \log(size) * slope \quad (1)$$

The traits fecundity and dispersal need different back transformations. The back transformation for fecundity will be: $e^{\text{trait value}}$. The back transformation for dispersal capacity will look like this: $e^{\text{trait value}}$ / 1 + $e^{\text{trait value}}$.

Population initialization

At the end of the population initialization, the landscape must be filled with individuals up to its carrying capacity. To achieve this, we loop through each cell of the landscape. When a cell has a carrying capacity of at least one, an individual is assigned to that cell by generating coordinates for that individual that falls within that cell. Where in the cell these coordinates fall is completely random. We repeat this until the cell reaches its carrying capacity. All this is done for each cell, resulting in the landscape being filled to its carrying capacity.

Determine which individuals will survive according to the environment temperature

As mentioned above, survival is partly determined by fitness. Fitness is linked to the life-history traits temperature optimum and temperature range and the environmental temperature. Each individual receives a fitness that ranges from one to zero. We used a Morse potential function to calculate this fitness as we wanted to include asymmetry in the fitness calculation (Equation 2).

$$G_{Mor}(E) = R_{max}\left(1 - \frac{\left(1 - e^{a(E-\phi)}\right)^2}{a^2W^2}\right) \quad (2)$$

The value a determines the asymmetry of the niche and is set to 0.1. *RMax* describes the local intrinsic growth rate of an individual at its temperature optimum. In the model, *RMax* is equal to one. *E* is the parameter for the individual's temperature optimum, whereas *W* describes the thermal range of the individual.

A random value between one and zero is generated for each species. If this number is higher than the fitness value of the individual, the species will die. Thus, the higher the fitness of an individual, the higher its chance of survival.

Individuals get offspring

The number of offspring, depends on the life-history trait fecundity. We take the base ten logarithm of the fecundity value of the individual and add one. The number of offspring per individual of the same virtual species is constant. Thus, demographic stochasticity is added by taking a Poisson distribution to determine the final number of offspring per individual. Offspring inherit the life-history traits and position of the parent. In a later step, the offspring will be able to disperse.

Dispersal

When the carrying capacity of a cell is reached, any individuals above the carrying capacity will disperse. Which individuals disperse is random. As mentioned above, each species has its dispersal curve. This curve is created using the Pareto distribution (Equation 3).

$$Y = \frac{\frac{\alpha-1}{\alpha} * X\_mean}{U^{\frac{1}{\alpha}}} \qquad (3)$$

X_mean represents the average distance traveled by a virtual species and is calculated by adding 18 to an individual's dispersal trait value. 18 is added because this is a known mean dispersal distance for the highly dispersal beetle species in Flanders. *α* determines the tail of the curve. We want a heavy fixed tail, so this value was set to two. This type of tail results in the inclusion of rare long-distance dispersal events in our model. Since individuals of the same species will receive the same dispersal curve, we include the random value *U* in the equation. *U* represents a random value between one and zero and is used to add stochasticity to the model.

A random value of *U* is chosen for each individual. Adding this value to Equation 3 determines the distance the individual will travel. The direction of dispersal is completely random.

8. References

Honěk, A. (1993). Intraspecific Variation in Body Size and Fecundity in Insects: A General Relationship. *Oikos*, *66*(3), 483. https://doi.org/10.2307/3544943

Jenkins, D. G., Brescacin, C. R., Duxbury, C. V., Elliott, J. A., Evans, J. A., Grablow, K. R., Hillegass, M., Lyon, B. N., Metzger, G. A., Olandese, M. L., Pepe, D., Silvers, G. A., Suresch, H. N., Thompson, T. N., Trexler, C. M., Williams, G. E., Williams, N. C., & Williams, S. E. (2007). Does size matter for dispersal distance? *Global Ecology And Biogeography*, *16*(4), 415–425. https://doi.org/10.1111/j.1466-8238.2007.00312.x

Klok, C. J., & Harrison, J. F. (2013). The Temperature Size Rule in Arthropods: Independent of Macro-Environmental Variables but Size Dependent. *Integrative And Comparative Biology*, *53*(4), 557–570. https://doi.org/10.1093/icb/ict075

Roitberg, B. D., & Mangel, M. (2016). Cold snaps, heatwaves, and arthropod growth. *Ecological Entomology*, *41*(6), 653–659. https://doi.org/10.1111/een.12324

Ruel, J. J., & Ayres, M. P. (1999). Jensen's inequality predicts effects of environmental variation. *Trends in Ecology & Evolution*, *14*(9), 361–366. https://doi.org/10.1016/s0169-5347(99)01664-x