The dispersal patterns of a migratory insect are driven by biotic interactions

Insect migration driven by biotic interaction

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Abstract

Aim: *Urania* moths disperse long distances, but the causes of these movements are not clear yet. Previous studies of *Urania* movements were mostly observational or considered environmental connectivity and host plant availability only, ignoring other factors that potentially affect the species distributions. Here, we present simulations of the dispersal patterns of *U. boisduvalii* that incorporate biotic interactions with its host plants and moth dispersal capacity.

Location: Cuba

Taxon: *Urania* and *Omphalea*

Methods: Our approach considers changes in the palatability of plants resulting from foraging by moths, as the novel mechanism driving their dispersal. In our approach, the state of each cell is determined by climate, dispersal, presence of edible food plants, and change in food plant palatability.

Results: *Urania* dispersal occurs among sites with both edible food plants and suitable climates within the dispersal capacity of the moths. The number of isolated clusters of suitable patches decreased with larger dispersal capacities. All simulations where the palatability recovery is faster than palatability loss, lead to periodograms showing an oscillatory pattern of a local nature, while the other ones lead to a steady occupancy or extirpation of the moth species.

Main conclusions: Our results provide theoretical support for the hypothesis that the palatability of food plants drives the pattern of movement of the moths and predict that the relationship between toxic and non-toxic periods is critical to determining steady occupancy, oscillatory occupancy, or extirpation of the moth from the host plant patches. The conceptual framework we used is directly based on classic literature and the methods we used are implemented as an R package. Therefore, our approach is suited to model, in a practical way, invasive species, emerging diseases, or migratory species.

Keywords: Cellular automaton, migration, moths, *Omphalea*, plant defenses

Introduction

"Migration," for the purpose of this work, refers to movements of animals in a direction and distance over which they have control, resulting in change of habitat of residence (Williams, 1957). Migration may be short-distance or long-distance, be completed in a single generation, or may be transgenerational, like that of the Monarch butterfly (Brower, 1995), and be obligate or facultative (Dingle & Drake, 2007). Given such a variety of processes and the conservation challenges for migratory species, migratory and dispersal patterns have been the focus of many studies (Berger, 2004; Gwinner, 2012; May, 2013; Teitelbaum et al., 2015). Insect migrations are driven by environmental, trophic, or reproductive factors (Shaw, 2016). Seasonal changes in weather cause migration of the Monarch (Urquhart, 1966); whereas locust migration has been attributed to changes in environmental conditions and vegetation availability (Dingle, 1996; Shaw, 2016). Despite descriptive reports of their spectacular migrations (Dudley & DeVries, 1990; Murillo-Hiller, 2008; Smith, 1992), movements of diurnal moths of the genus *Urania* (Geometroidea: Uraniidae), have never attracted the same of attention that other insects have.

The three species of *Urania* moths (*U. fulgens*, *U. leilus*, *U. boisduvalii*) are Neotropical, with diurnal habits, and their larvae feed on plants of the genus *Omphalea* exclusively (Lees & Smith, 1991; Nuñez-Penichet & Barro, 2020; Palomeque Morales, 1988; Smith, 1983, 1991, 1992).

Urania's feeding leads to increments of secondary compounds in the plants, as found for other species as well (Karban & Baldwin, 1997), eventually forcing the moths to move to a different host plant population (Smith, 1983). All species of *Urania* have been observed to disperse long distances (Barro & Rodríguez, 2005; Lees & Smith, 1991; Meerman & Boomsma, 1997; Murillo-Hiller, 2008; Smith, 1972, 1983, 1991; Williams, 1937, 1958; Young, 1970), but there is not a detailed characterization of these species' oscillatory movements, and the dispersal routes are poorly understood (Nuñez-Penichet et al., 2019). Using ecological niche modeling tools, we previously estimated potential paths of movements of *U. boisduvalii* in Cuba (Nuñez-Penichet et al., 2019). However, these correlative approaches estimate environmental suitability for the moth and the plants independently, are intrinsically static, and disregard the interactions between the herbivore and its food plant.

The east-west orientation, latitudinal position, and size of the island nation of Cuba suggest that climatic differences are unlikely to be a driving factor for the dispersal of *U. boisduvalii*. On the basis of experiments, it has been hypothesized that *Urania* dispersal is driven by changes in food suitability (Smith, 1983). To explore this hypothesis, we developed a dynamic, process-oriented (Cabral et al., 2017) model of distributional areas. We used the **BAM** scheme (Soberón & Peterson, 2005) which postulates that species' distributions depend on three major factors: biotic interactions (**B**), abiotic conditions that are suitable (**A**), and movement (**M**). In this study, parameters for **B** are scenarios based on biological evidence. Parameters for **A** are obtained from detailed correlative ecological niche modeling. Parameters for **M** comprise different scenarios for dispersal capabilities. We use R software that implements practically this scheme.

Materials and Methods

To model the dispersal dynamics of *U. boisduvalii* we used a cellular automaton implementation of the **BAM** scheme. First, we created a grid of 1 km spatial resolution covering Cuba (136,622 cells). The area occupied by the moth at time t is a vector of cells with a value of 1, while unoccupied cells have values of zero. We use as unit of time the life-span of *U. boisduvalii* (3.5 months, Barro, 2006). The area occupied by the moth is governed by the following equation: $\mathbf{G}(t+1) = \mathbf{B}(t) * \mathbf{A} * \mathrm{M} * \mathbf{G}(t)$, where $\mathbf{G}(t)$ is the vector of 136,622 zeros and ones representing the distribution at time t. The first multiplication, by matrix **M** (assumed constant), determines what cells are accessible from already occupied cells; the second, by matrix **A** (also constant) determines if accessible cells are suitable from a climatic point of view, and the last, by $\mathbf{B}(t)$, whether a cell contains suitable food plants. This last matrix is being updated continuously by the software. The presence of *U. boisduvalii* in patch j at time $t + 1$, therefore, depends on three factors: (1) its interactions with *Omphalea* plants, represented by the diagonal matrix $\mathbf{B}(t)$ with 136,622 diagonal elements. An element in the diagonal has a value of one if the plants in that patch are edible, and a zero otherwise. This value changes over time, depending on whether a grid-cell has been occupied by the moth, and for how long. (2) Climatic suitability represented by a diagonal (i.e., containing zeros everywhere with the exception of the elements in the diagonal that are suitable, and with value of 1) matrix **A** is calculated using conventional ecological niche modeling techniques (see Nuñez-Penichet et al., 2016; Nuñez-Penichet et al., 2019). Finally, (3) the dispersal connectivity between a cell i and the rest of the cells, represented by an adjacency (an adjacency

matrix is a representation of what cells are accessible from other cells) matrix **M** (based on geographic distance, assumed constant through the simulation) (Fig.1).

To parametrize the biotic interaction component (**B**(*t*)) of the models, we used a potential distribution map at 1 km resolution of *Omphalea* plants developed previously (Nuñez-Penichet et al., 2019). We also included two stages in **B** (toxic and edible), as it is known that the plants change their toxicity levels depending on *Urania* larvae herbivory (Smith, 1983). Little is known of the time required for a moth population to make *Omphalea* plants become toxic, or the time needed for the plant to become edible again (but see Smith, 1983). Thus, we hypothesized five different combinations of times (edible/toxic relationships), measured in moth generations: (1) the plants take the same time (three generations) to become toxic and to recover edibility (3/3). (2) The plants will support three generations before becoming toxic, and become edible after the moths are gone, for a time equivalent to two generations (3/2). (3) The plants will support six generations of the moth before becoming toxic and become edible after the moths are gone for three generations (6/3). (4) The plants will support two generations of the moth before becoming toxic and they will be edible after the moths are gone for three generations (2/3). Finally, (5) the plants will support three generations of the moth before becoming toxic and it will be edible after the moths are gone for six generations (3/6). We also explored a scenario in which the host plants are never toxic for the moth to test if this factor is really affecting dispersal patterns.

As the **A** component (suitable abiotic conditions), we used the potential distribution map of *U. boisduvalii* available from Nuñez-Penichet et al. (2019) at 1 km resolution. This map was multiplied by the one used as **B**; the resulting areas (areas potentially suitable for both the moth and its host plant) were the ones considered relevant for our simulations. As the **M** component, due to the lack of information about the dispersal capacities of the moth, we postulated Moore's neighborhoods (Gray et al., 2003) for three dispersal scenarios: (1) short-distance (the moth disperses10 km per unit time), (2) medium-distance (15 km per unit time), and (3) long-distance (20 km per unit time). Each scenario has its own adjacency matrix **M**. The moth left a suitable patch (if accessible) only after it changed from edible to toxic.

For each dispersal scenario, we iterated the model, starting with a hypothesized initial condition, which is a vector of zeroes and ones [**G**(*1*)], as described above. Finally, we computed the possible movement routes *U. boisduvalii* given the dispersal scenarios by analyzing the number of clusters obtained at each dispersal distance. Simulations started from three different places: (1) one of the westernmost occurrences of *U. boisduvalii* in Cuba, (2) the easternmost occurrence of the moth in the archipelago, and (3) in both eastern and western locations (Fig. 2). To show the oscillatory behavior observed in our results, we graphed how the mean longitude of the occupied patch changes with time and displayed a periodogram of the dominant frequency of oscillation, when it occurred. Periodograms were calculated using the functions 'ts' and 'spectrum' from R v. 4.0.2 (R Core Team, 2020) that remove the linear trend in the time series and "smooths" the periodogram by determining how many spikes will be in the graph. We used five as our limit.

All the simulations were performed in R, using the bamm package (Soberón & Osorio-Olvera, 2022). The R code needed to replicate these analyses is available at https://github.com/claununez/Dispersal_Urania, and all data needed are available at https://doi.org/10.6084/m9.figshare.19217592 (Nuñez-Penichet et al., 2022). The simulations are strictly deterministic, though we are in the process of developing a stochastic version.

Results

In our simulations, dispersal occurs among sites with both edible food plants and suitable climates within the dispersal capacity of the moths. The number of isolated clusters of suitable patches decreased with larger dispersal capacities (Fig. 3). Isla de La Juventud resulted in an isolated cluster in all simulations. When the moth was experimentally allowed to move 10 km per generation (unit time), Cuba (the main island) was predicted to split into three major clusters of distributional areas for the moth. The first comprised all western provinces including Matanzas (west); the second one (central) included patches in Villa Clara, Cienfuegos, Sancti Spíritus, and Ciego de Ávila; and the last included the most suitable areas for the moth in eastern Cuba (east; Fig. 3). Allowing 15 km/generation dispersal, we obtained only two clusters (west, and center + east). Finally, with a dispersal potential of 20 km/generation, a single large system of connected regions emerged (Fig. 3). However, to go beyond these static results, we endeavored on performing simulations.

All our simulations predicted a pattern of spread, sometimes with a strong oscillatory component. Starting in a single point at the westernmost or easternmost points of the island (Fig. 4), dispersal patterns of *U. boisduvalii* were highly dependent on the periods over which host plant patches were edible, versus toxic. Considering the five edible/toxic time relationships analyzed (2/3, 3/2, 3/3, 3/6, 6/3) and the scenario where the plant was not toxic, we obtained three distinct dispersal patterns. First, when *Omphalea* plants did not become toxic, all potentially suitable areas for the moth (considering their dispersal capacities) were occupied and reached a steady state of occupancy (Fig. 4, SI Appendix 1). In contrast, if the plants were edible for a shorter time than they were toxic (edible/toxic, 2/3, 3/6), we obtained a wave of movement but with no return (i.e., extirpation at the end of the wave). In this scenario, occupied patches shifted forward, and the patches behind them changed to unoccupied and were not used by the moth again (Fig. 4, SI Appendix 2). Finally, assuming time-edible equal to or larger than time-toxic (3/3, 3/2, 6/3) we obtained an oscillation on the occupancy of *Omphalea* patches (SI Appendix 3, SI Appendix 4). These oscillations were present both among and within patches, and the proportion of grid-cells occupied/unoccupied was determined by the size of the patch (Fig. 4).

The periods for global oscillations seem to be affected by the ratio of edible/toxic times, and the amplitude of the oscillation by the dispersal capacity (several examples in SI Appendix 5). Figure 4 displays a map of the dispersal pattern, the mean longitude of the occupied region revealing the position of the dispersal pattern, and a periodogram to show possible oscillations. All simulations where the palatability recovery is faster than palatability loss, lead to periodograms showing an oscillatory pattern of a local nature.

Discussion

Species in the genus *Urania* have been reported as undergoing migrations (Lees & Smith, 1991; Meerman & Boomsma, 1997; Smith, 1991; Williams, 1937; Young, 1970), but without the detailed documentation available for Monarch butterflies (Oberhauser & Solensky, 2004; Zhan et

al., 2011). The case of *U. boisduvalii* is particularly intriguing because of the apparent lack of climatic patterns likely to drive movements. Our simulation results strongly suggest that, as long as the plant remains edible for a longer period of time than the plant is unpalatable, changes in the herbivore-produced edibility of the food plant may drive oscillatory movements of the moth. Since anecdotal evidence supports the idea of such oscillations, we predict that *Omphalea* remains edible for longer periods of time that it is toxic, a prediction to be tested experimentally and under field conditions.

Cellular automata (CA) are often used to model spatially-explicit ecological systems or phenomena (Molofsky & Bever, 2004), like vegetation dynamics (Balzter et al., 1998), predator-prey systems (Cattaneo et al., 2006), invasion dynamics (Nuñez-Penichet et al., 2021), species distributional dynamics (Machado-Stredel et al., 2021), among others. Dispersal modeled using CA is a "contagion" process, rather than population dynamics *sensu stricto*. Cells change state (occupied, unoccupied) depending on their intrinsic properties and the state of neighbors. A major advantage of CA is that, although capable of generating complex spatial dynamics, their conceptual structure is easy to understand (Breckling et al., 2011). Moreover, due to its simplicity, the number of parameters to be provided is much smaller than those in other approaches like reaction-diffusion models, that to be treatable require an assumption of spatio-temporal homogeneity of their parameters (Holmes et al., 1994). However, CA simplify biology drastically, by mostly ignoring details of demography, dispersal, and biotic interactions and producing coarse-grained outputs. The deterministic nature of the simulation also determines some very regular patterns, like the regular bands in figure 4. These are simple artifacts of the method.

It is doubtful that a single modeling approach will be useful in every case. We suspect that CA can be better suited to questions related to large geographic extents and low spatial resolution, and demographic models, like reaction-diffusion models, better suited to smaller spatial scales where local processes and biological details matter. A typical reaction-diffusion model (or the discrete counterparts based on metapopulation schemes) represent reality much better, but they can be impossibly demanding in terms of the data required to produce parameters, since often they require dozens of spatially and temporally-dependent life-history parameters (see Keith et al., 2008). In view of the above and until more work is done on the biology of both the host plants and the moth, a CA approach seems to be an acceptable compromise between a fully-detailed simulation and simple verbal arguments.

In particular, our approach is a deterministic model of a scheme for the dynamics of the area of distribution (Soberón & Peterson, 2005). By feeding on *Omphalea* plants, the moths reduce their palatability (Smith, 1983). When feeding stops due to unpalatability, the plant eventually reverts from toxic to edible. This is a variation on host-parasite dynamics. Previous work on such dynamics, modeled using cellular automata, also predicts local oscillations (Cattaneo et al., 2006). Our approach strongly suggests that the details of this cycle may determine the form of the dispersal of the moth: situations in which palatability recovery is faster than palatability loss creates a local oscillatory behavior in the simulations, but when the toxic period exceeds the edible period, oscillations do not happen.

Oscillations would be "local" in the sense that they take place over regions of ~100 km. It is an open question whether a more realistic model (perhaps with random elements affecting dispersal and the edible-toxic dynamics) will create a global wave over the entire island. The local oscillation

pattern emerges when the initial spread starts at either, or both ends of the island, suggesting that oscillations do not depend on initial conditions (SI Appendix 4, SI Appendix 6, SI Appendix 7).

Our simulations showed a three generations cycle of movements (Fig. 4), which concurs with previous, lab-derived results for *U. fulgens* (Smith, 1983). However, the number of moth generations that the plants will be able to support may depend on the number of larvae feeding on them, the size of the host plant patch, as well as the plants' densities in those patches as it has been described for other herbivore insects (Bach, 1988; Masters, 1995). These factors are not considered in our simulations (these data are not currently available), therefore, more precise results may be obtained in the future if these factors are considered. Also, it is worth mentioning that in our simulations, we only included potential geographic dispersal barriers (i.e., elevations > 600 m) as part of the abiotic suitability layer and not as a cost matrix layer, which could be the ideal scenario. The possibility of adding a cost matrix in the simulation is not yet implemented in the algorithm used. However, we consider that in our case, this is not a big inconvenience as *Urania boisduvalii* has not been reported in high areas of Cuba, and the areas with high elevations in the Cuban archipelago are restricted to a few localities (Fig. 2).

The different dispersal distances considered did not affect the movements patterns obtained (steady, extirpation, or oscillation) but were crucial to identifying the patches of *Omphalea* that can be reached by the moth (SI Appendix 4, SI Appendix 8, SI Appendix 9). Dependency on connectivity could help to elucidate why neither the moth nor its host plant has been reported from localities in central Cuba (Aborrezco, 1995; Barro, 2006; Barro & Rodríguez, 2005, 2006; Capote et al., 1988; Claro & Rodríguez, 1989; González-Torres et al., 2016; Lees & Smith, 1991; Fig. 4), despite the presence of suitable climatic conditions in that area (Nuñez-Penichet et al., 2016; Nuñez-Penichet et al., 2019). This can be tested by a population genetic analysis of the moth.

A simple model based on (i) a substantial amount of data and (ii) scenarios for parameter combinations, yield predictions of unpalatability-driven oscillatory patterns of patch occupation. These results are strong predictions that can be tested in the field, and we are in the process of doing it.

To define species distribution and movements, we considered not only the abiotic climatic conditions but also the dispersal capabilities and a biotic interaction. These factors have a strong conceptual framework behind it (Soberón & Peterson, 2005). Computational and ecological knowledge limitations may have prevented testing this framework, however, our results provide theoretical support for the hypothesis that the palatability of food plants drives the pattern of movement of *Urania* moths. Ours results also predict that the relationship between toxic and non-toxic periods is critical to determining steady occupancy, oscillatory occupancy, or extirpation of the moth from the host plant patches. Our approach, based on cellular automata, allows its application, in a practical way, to model invasive species, emerging diseases, or migratory species.

Data Availability Statement

All data needed to replicate this study and all simulations performed are available at https://doi.org/10.6084/m9.figshare.19217592. The R code used in this research is available at https://github.com/claununez/Dispersal_Urania.

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Biosketches

Claudia Nuñez -Penichet is an entomology interested in understanding species distributional patterns. She uses computational and molecular tools for answering questions about dispersal ecology, insect-host plant interaction, and population ecology.

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Author contributions

CNP and JS designed the study and wrote the manuscript. LOO wrote the software. All authors performed the analyses, created the figures, and reviewed and approved the final version of the manuscript.

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Figure legends

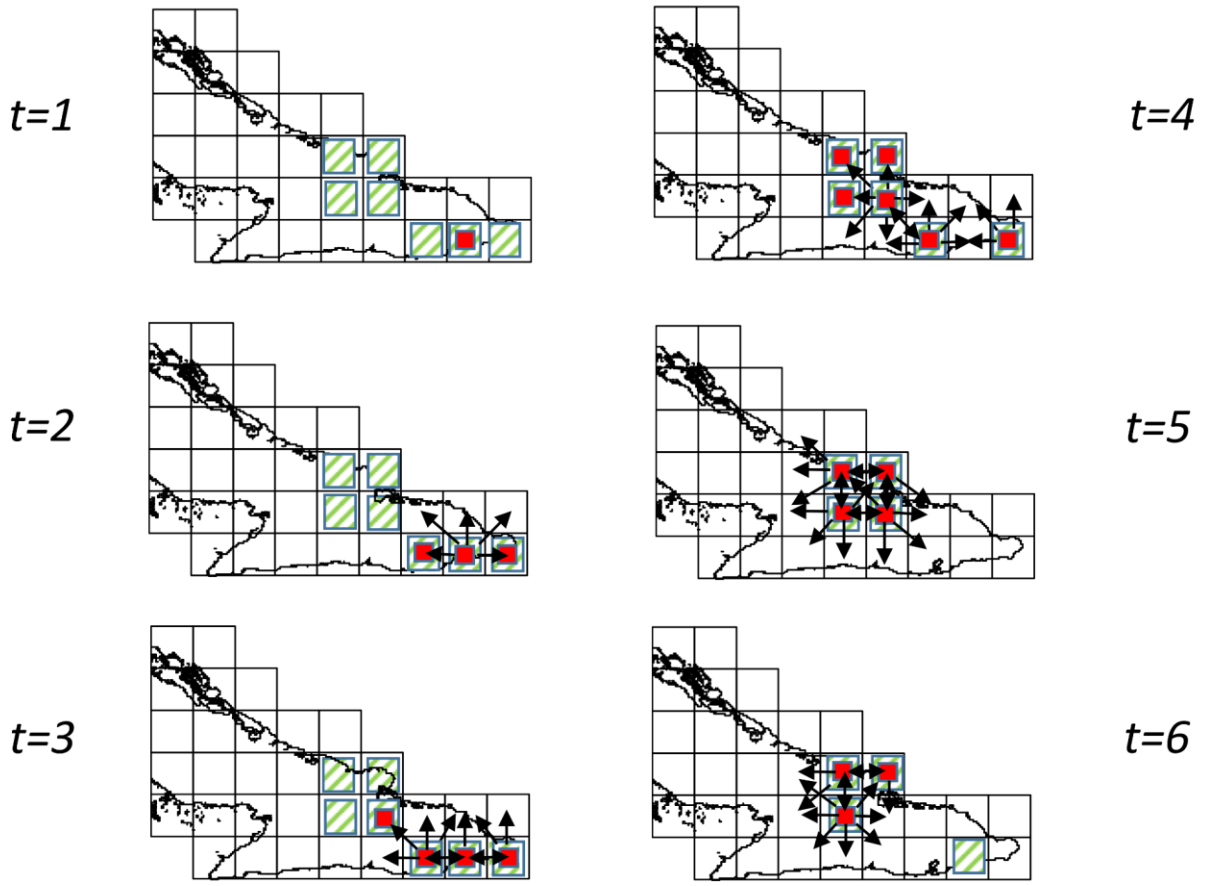
Figure 1. Diagram of the algorithm used. A region (eastern Cuba) is partitioned by a grid of given resolution. The cells in green represent cells with edible food plants at a given time. Color red represents the presence of the moth. Dispersal is assumed only to contiguous cells, represented by the arrows in black. Empty cells lack plants, or the plants are not edible due to herbivory sustained for more than a certain amount of moth generations. In the example this number is three, meaning that after three time units (generations) with presence of the moth, the plants will become toxic (and after two without moth, edible again). At time t=1 one cell is assumed to be occupied by the moth. This cell "infects" neighboring cells in t=2. The process is repeated in t=3. In t=4 dispersal still occurs, but now the original cell becomes unsuitable due to herbivory causing food plants to become inedible. At t=5 the entire bottom row of cells has inedible food plants and by t=6 the central cell in the lower row reverted to edible. The bamm software keeps track of movements, state of suitability of plants, if present, and changes of state (occupied to unoccupied). [double column]

Figure 2. Known occurrences of *Urania boisduvalii* across the Cuban archipelago. The red dots represent the localities used to start the simulations. [double column]

Figure 3. Number of clusters of *Omphalea* host plants obtained with different potential dispersal distances of the moth *Urania boisduvalii,* and geographic representation of the patches reached by the moth with 3 km, 10 km, 15 km, and 20 km dispersal capacities. In the maps, the colors are

representing the clusters. The line on the northeast side of Cuba represents 10 km, 15 km, and 20 km, respectively. [double column]

Figure 4. Dispersal pattern for three edible/toxic ratio scenarios (represented on the columns), and dispersal of 20 km/3.5 months. The top panels show a geographic depiction of the pattern, for three different times in the simulation. The middle panel is a time series of the mean longitude of occupied cells over time (generations) and the bottom panel shows the corresponding periodograms. In the periodogram, the x-axis is the reciprocal of the "period," or number of time units (generations, about 3.5 months) that will produce a full cycle (thus 0.5 means seven months are required to produce a full cycle). The y axis, or "Spectral density" is a measure of how likely is for the time series to be composed of frequencies in the x scale. The first two columns represent cases with no or very long periods. The third column displays a very apparent cycle every three generations. [double column]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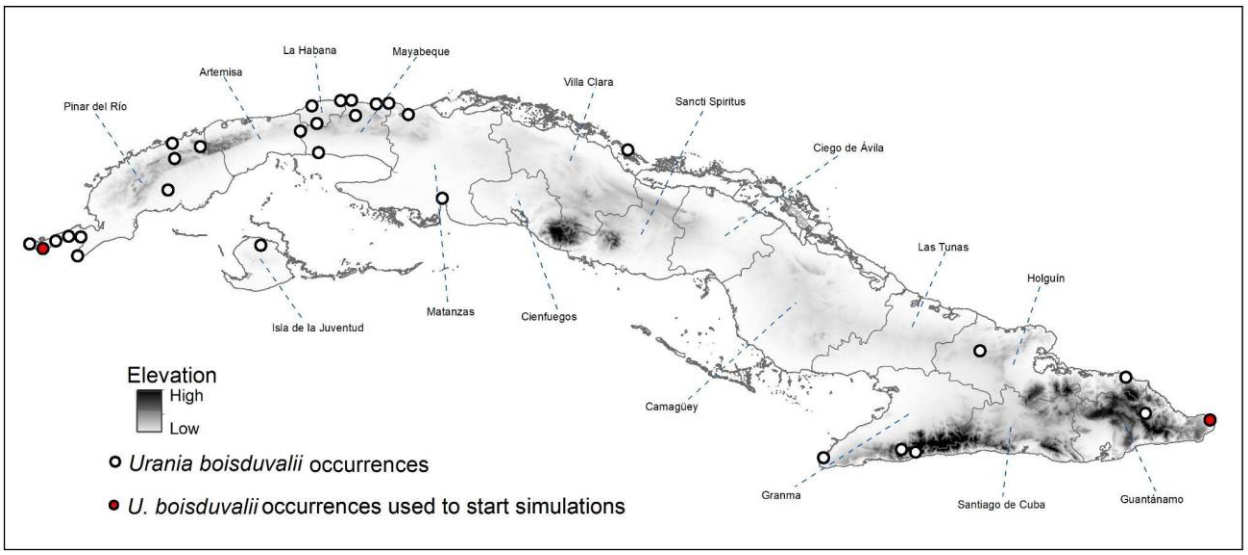
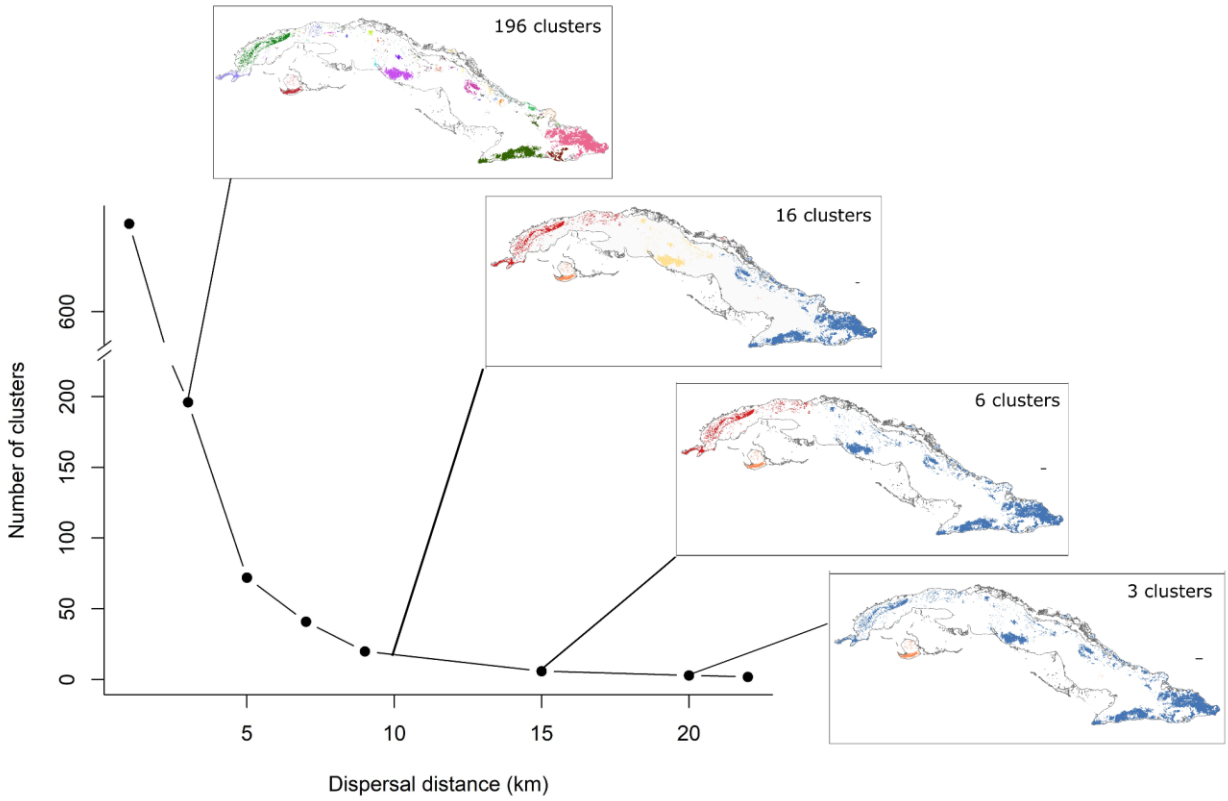
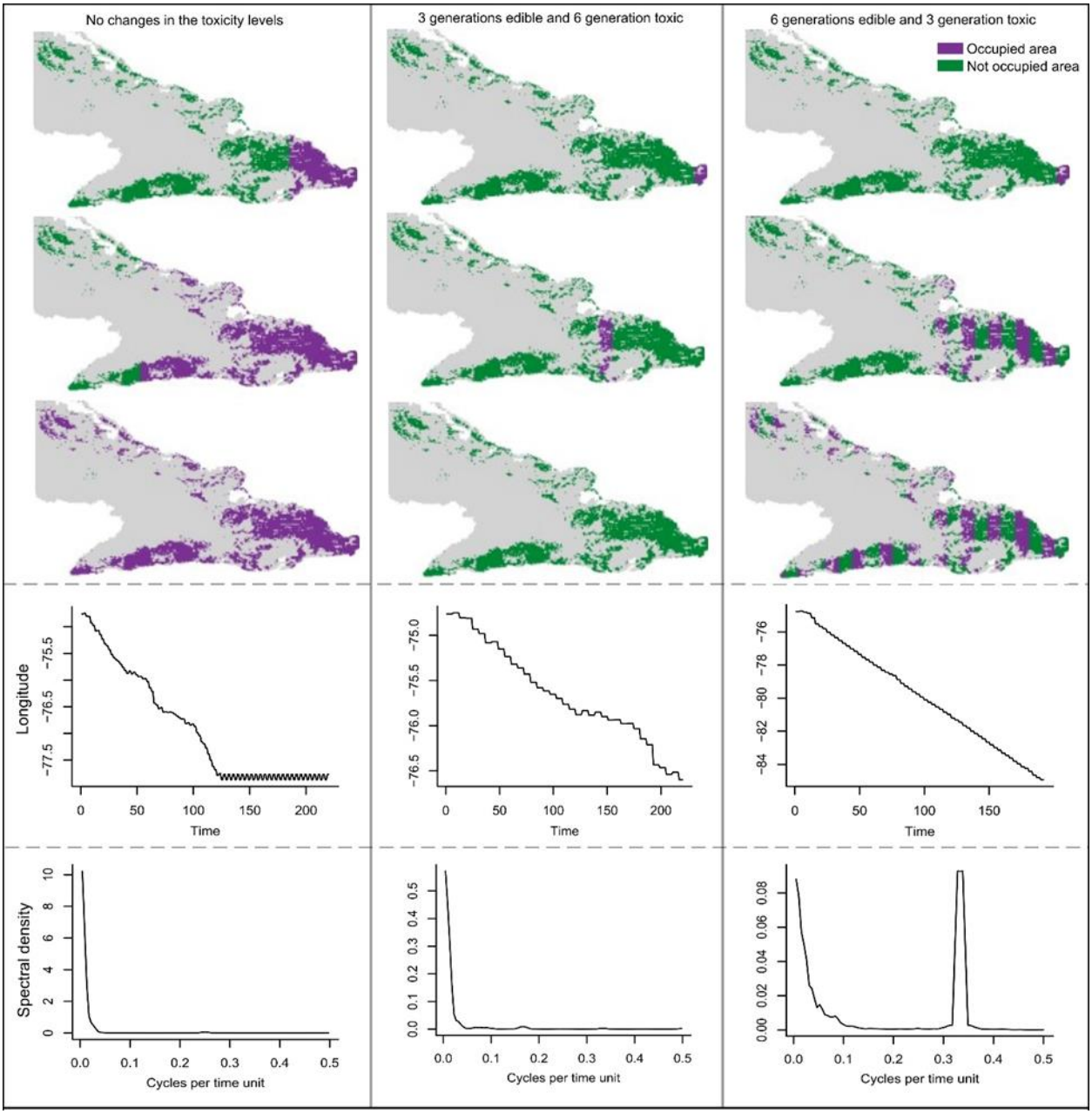
t=6


La Habana
Mayabeque
Artemisa
Pinar del Río
Villa Clara
Sancti Spiritus
Ciego de Ávila
Las Tunas
Holguín
Isla de la Juventud
Matanzas
Cienfuegos
Camagüey
Granma
Santiago de Cuba
Guantánamo
Elevation
High
Low
Urania boisduvalii occurrences
U. boisduvalii occurrences used to start simulations


196 clusters
16 clusters
6 clusters
3 clusters
Number of clusters
0
50
100
150
200
600
5
10
15
20
Dispersal distance (km)


No changes in the toxicity levels
3 generations edible and 6 generation toxic
6 generations edible and 3 generation toxic
Occupied area
Not occupied area
Longitude
Time
Spectral density
Cycles per time unit

Supplementary information captions

SI Appendix 1: Simulation of dispersal pattern of *Urania boisduvalii* when *Omphalea* plants do not become toxic. The moth disperses 20 km/time unit, and the simulation starts in the easternmost locality of the moth in Cuba.

SI Appendix 2: Simulation of dispersal pattern of *Urania boisduvalii* when *Omphalea* plants are edible for 3 generations of the moth and are toxic for 6 generations. The moth disperses 20 km/time unit, and the simulation starts in the easternmost locality of the moth in Cuba.

SI Appendix 3: Simulation of dispersal pattern of *Urania boisduvalii* when *Omphalea* plants are edible for 3 generations of the moth and are toxic for 3 generations. The moth disperses 20 km/time unit, and the simulation starts in the easternmost locality of the moth in Cuba.

SI Appendix 4: Simulation of dispersal pattern of *Urania boisduvalii* when *Omphalea* plants are edible for 6 generations of the moth and are toxic for 3 generations. The moth disperses 20 km/time unit, and the simulation starts in the easternmost locality of the moth in Cuba.

SI Appendix 5. Illustration that when the time were the plant is toxic < time were the plant isas edible, oscillations take place. When the opposite is true, or when the two times are the same, there are no oscillations. There are nine instances of the first case, and eighteen of the second. The presence, or lack of oscillations is apparent from the figures. Start: area of Cuba where the simulation started; dispersal is represented in km; time is represented in moth's generations; Tx: time that the plants were toxic; St: time that the plants were edible.

SI Appendix 6: Simulation of dispersal pattern of *Urania boisduvalii* when *Omphalea* plants are edible for 6 generations of the moth and are toxic for 3 generations. The moth disperses 20 km/time unit, and the simulation starts in the westernmost locality of the moth in Cuba.

SI Appendix 7: Simulation of dispersal pattern of *Urania boisduvalii* when *Omphalea* plants are edible for 6 generations of the moth and are toxic for 3 generations. The moth disperses 20 km/time unit, and the simulation starts in both the westernmost and easternmost localities of the moth in Cuba.

SI Appendix 8: Simulation of dispersal pattern of *Urania boisduvalii* when *Omphalea* plants are edible for 6 generations of the moth and are toxic for 3 generations. The moth disperses 15 km/time unit, and the simulation starts in the easternmost locality of the moth in Cuba.

SI Appendix 9: Simulation of dispersal pattern of *Urania boisduvalii* when *Omphalea* plants are edible for 6 generations of the moth and are toxic for 3 generations. The moth disperses 10 km/time unit, and the simulation starts in the easternmost locality of the moth in Cuba.