



Landscape structure, dispersal and the evolution of antagonistic plant–herbivore interactions

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Different species have different dispersal capabilities and in the field, species interact with each other within dynamic, heterogeneous and complex landscapes. While plants and certain herbivore species may disperse considerable distances by means of seed dispersal or flight, other herbivores (e.g. root-feeding nematodes or non-winged insect herbivores) are more limited in their dispersal capacities. This difference in dispersal capabilities results in mosaics of plant–herbivore interactions that shift over time and space leading to spatio-temporal variation in both the presence and absence of the species and their interactions. We developed an individual based simulation model in which we examined how multi-species interactions are affected by their mobility within structurally complex landscapes. The main objective was to address the consequences for the arms race between plant defence and herbivore resistance to changes in fundamental landscape and community attributes. We demonstrate that feedbacks between landscape structure, community structure and the specific dispersal rate of the species involved affect the evolutionary dynamics between plants and herbivore antagonists. While three-species interactions result in increased plant defence and herbivore resistance, effects of dispersal have diverse effects depending on the prevailing landscape structure.

The selection that plants exert on herbivores and vice versa are fundamental factors in understanding the functioning of terrestrial communities and, moreover, in determining the co-evolutionary trajectories of plant and insect populations (Marquis 1992, Karban and Agrawal 2002). The continuous arms race between plant defense and herbivore resistance is thought to be the major driver of host plant specialization, speciation and radiation (Ehrlich and Raven 1964). Although this arms race is assumed to be subject to unconstrained reciprocal selection, it must do so within the constraints imposed by trade-offs: because defense strategies are costly, a trade-off evolves between developing mechanisms to cope with herbivores and other traits associated with fitness (de Jong and van der Meijden 2000, Schaefer et al. 2003). Herbivores also pay costs to counter plant defensive strategies (e.g. behavioural, physiological adaptation). In consequence, traits that reduce herbivore damage such as production of deterrents (e.g. alkaloids, glucosinolates), traits that mediate the interaction with natural enemies of herbivores (e.g. extrafloral nectar, allelochemicals), or defensive structures (e.g. hairs, spines) experience a positive directional selection (Maynard Smith 1989, Mayhew 1997).

In plant–herbivore interactions, each species, plant or herbivore, constitutes an ever changing environment to which its opponent has to adapt. Traditionally plant–insect interactions have been considered homogeneous entities in

which spatial considerations played little role. However, this situation has been proved to be rather simplistic and geographic structure is now regarded as an important factor in evolutionary processes (Thompson 2005). Different plant populations may show markedly patterns of distribution of genetic variation for resistance. This leads to selection pressures between plant and herbivores varying spatially (depending on the geographic sites) and contributes to geographic structuring of plant–herbivore interactions. The outcome of the spatial variation in ecological dynamics between plant and herbivores is a geographic mosaic where selection by species on each other might be reciprocal in some places and not in other. Variation in the sign of plant–herbivore interactions, in combination with gene flow produced by migration contributes to maintain ecological diversity within and among populations of species (Thompson 2005, Urban et al. 2008). Although studies addressing geographic structuring in biotic interactions have been subject of numerous studies in recent years (see review by Hoeksema and Forde 2008), the way the properties of landscapes determine the evolutionary pathways in plant–herbivores interactions has not been addressed.

In the field, interactions between plants and herbivores depend on structural aspects beyond the trade-offs between defence/resistance and growth for plant and herbivores. Plant and herbivore species interact within dynamic,

heterogeneous and complex landscapes (Urban et al. 2008), where the capacity of any species to establish and maintain a stable population depends in first instance on the spatial configuration of the landscape, but also on the complexity of the community, in particular the presence of mutualistic or antagonistic species (see detailed review by Tscharrntke and Brandl 2004). Spatial structure combined with community structure will in consequence largely affect eco-evolutionary community dynamics (Dupre and Ehrlén 2002, Porazinska et al. 2003, Eppstein et al. 2006, Stevens and Jones 2006).

Plant–herbivore interactions are not only affected by the landscape structure but also by the intrinsic capacities of the species to move within the landscape (Cousens et al. 2008). Across herbivore species, there is a continuum of movement capabilities, with some species being able to disperse over large geographical distances (e.g. migratory butterflies, locusts), and other species being practically sessile (for instance root-feeding nematodes, root aphids). Empirical and theoretical studies have demonstrated the ecological and evolutionary consequences of dispersal for organisms living in spatially structured populations (Gandon and Michalakis 2002, Kokko and Lopez-Sepulcre 2007, de la Peña et al. 2009). In the same vein, dispersal plays a crucial role in the context of habitat fragmentation by regulating population dynamics in fragmented populations and also, from an evolutionary point of view, it has drastic effects on the patterns in local adaptation and its evolution (Ronce 2007). Paradoxically, the role of dispersal in the evolutionary dynamics of plant–herbivore interactions has received little attention (Sisterson and Averill 2004). Interestingly, in other systems, such as the interaction between parasites and their host species, it has been shown that in simple landscapes the resistance and virulence arms races reached the highest levels and the highest degree of variation when dispersal is high (Sisterson and Averill 2004). Investigations on landscape-level processes, with inherent static or emerging mosaic structures are needed to improve our understanding of evolutionary dynamics in realistic landscapes (Cronin and Reeve 2005, Travis et al. 2005).

In spatially structured systems, we expect shifting mosaics of multispecies interactions in time because of the different dispersal characteristics of the interacting species. Moreover the quality (in terms of possible interactions) also changes as a function of the “evolutionary status” of the species involved (Lankau and Strauss 2008). Nevertheless, it is currently unclear how multi-species interactions are affected by species dispersal rates in complex landscapes and to what extent they feedback on herbivory-related life history traits (e.g. plant toxin production and development of resistance against it by herbivores). Therefore, we developed a stochastic simulation model in which we addressed the effect of two primary components of landscape structure (i.e. habitat availability and its spatial correlation or connectedness) on the evolution of toxin production of a plant and the resistance strategies of one or two herbivores with different dispersal capacities. We tested scenarios in which the habitat for a plant contained one or two herbivore species (either a resident species, a dispersive one, or both). With this system, we expected a collinear dependency of habitat availability and plant/herbivore

dispersal on plant defences, which would ultimately be mirrored in the herbivore resistance strategies. We hypothesized that selection would result in greater levels of defensive traits at multiple species interactions, and when habitat availability and its spatial connectedness is high.

Model

We developed a spatially explicit simulation model (in Delphi environment) in which we studied the combined effect of landscape structure and dispersal on the co-evolution of herbivore resistance to plant defense under a trade-off scenario. Although defense and resistance strategies may be achieved by various mechanisms (Gatehouse 2002), we refer throughout this study to toxin production in the plant and resistance to toxin (detoxifying activity) for the herbivores. Despite the complex nature of defense/resistance strategies, we consciously assumed 1) a system in which herbivores responded to the same defensive trait in the plant, which is compatible with different real systems in which two herbivores respond to the same metabolic pathway (Wolfson and Murdock 1990, Jongsma and Bolter 1997, Gatehouse 2002), and 2) non-induced responses in plant defense to avoid more complex mechanisms related to multiple herbivore movements during their lifespan.

The study system comprised three species: 1) the host plant, 2) a herbivore with low dispersal capacities (hereafter referred to as resident herbivore, RH) and 3) a herbivore with equally or better developed dispersal capacities (hereafter referred to as dispersive herbivore, DH). When the DH’s dispersal capabilities are the same as the RH’s both should be regarded as low dispersive species (see below).

The landscape

We used the program QRULE (Gardner and Urban 2007) to generate spatially structured landscapes. Fractal landscapes provide a tool to tease apart the effects of habitat fragmentation (with high values of H indicating low fragmentation and therefore strong connectedness) from habitat availability (with high values of P indicating high amounts of preserved habitat). The generated landscapes are binary (i.e. only with a distinction between suitable and unsuitable habitat and measured 128×128 grid cells). For details on the landscape generator algorithm we refer to Gardner et al. 1999. To avoid edge effects in the simulations, landscapes were wrapped at the edges into a torus so that edges matched, and consequently could be considered as being infinite but periodic landscapes. In short, we used fractal landscapes that are generated using the mid-point displacement algorithm in which both the fraction (P) and the degree of spatial connectedness (H) can be controlled (With et al. 1997). Schemas in the upper sections of Fig. 1 provide the graphical representation of four landscapes differing in the fraction of suitable habitat (P) and connectedness (H). We performed simulations for landscapes, either consisting of low ($P = 20$) or high ($P = 80$) habitat availability and low ($H = 20$) or

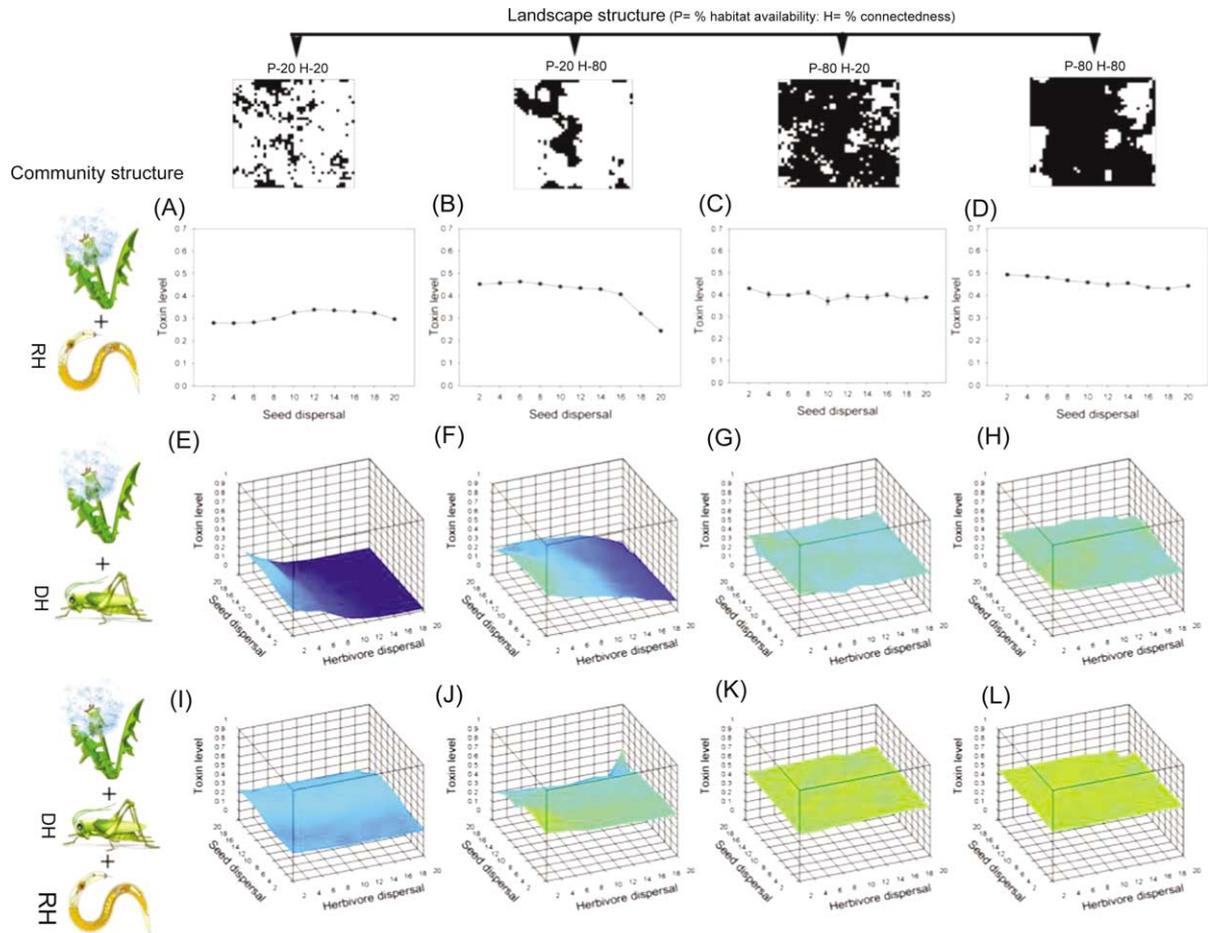


Figure 1. Mean toxin production in planta as a function of types of species interaction, landscape structure and dispersal capacities of the species involved. Schematic representation of landscapes with different levels of habitat availability (P) and connectedness (H) are represented in black and white in the top part of the figure and black cells represent habitat available for plant establishment. Types of interactions are explained in the left margin of the figure where DH stands for a dispersive herbivore and RH stands for resident herbivore. For each type of interaction, left to right comparison are related to landscape structure, top-down comparisons are related to types of interaction for the same landscape structure.

high ($H = 80$) levels of spatial correlation because it was previously demonstrated that these comprised contrasting scenarios for eco-evolutionary dynamics (Bonte et al. 2010a, b).

Plant and herbivore traits

We modelled the co-evolution of plant toxin production and herbivore resistance against the toxin in asexually reproducing organisms with discrete generations. Parthenogenetic reproduction is common in many invertebrate herbivores (e.g. aphids, root-feeding nematodes, etc) and in plants (for instance apicomictic Asteraceae). Individual plant seeds and herbivores disperse passively (without information) throughout the landscape according to a dispersal distance sampled from a Gaussian probability distribution (i.e. negexp density function) with a mean value of 0 and a fixed variance (σ). The variance measure σ , can be assumed to combine dispersal distance and propensity (low σ generates more philopatric individuals, with distance equalling zero, compared to individuals with

higher values of σ). Only propagules (either seeds or adult herbivores) that end up in suitable habitats survive. The position of both plant and herbivores are tracked in the grid (x, y coordinates).

Plants are characterized by an allele coding for toxin production (G_p). Allele values of 0 indicate that plants produce no toxins; the maximal production is in principle undefined but regulated by trade-offs with fecundity (see below). Similarly, both herbivores are characterized by toxin resistance alleles (also continuous traits, respectively G_r in the resident species and G_d in the dispersive species) within the same range as plant toxin production. Plants have one generation a year and are allowed to produce Λ_p seeds/plant. The resident and dispersive herbivores are allowed to produce Λ_r and Λ_d offspring, respectively, and have χ_r and χ_d generations per year. Because of the cost of toxin production (for plants) and resistance (for herbivores), the maximal number of offspring (respectively λ_p , λ_d and λ_r for the plant, RH and DH) is reduced to the values Λ multiplied by one minus the values of G (λ_p , λ_r and λ_d are respectively $1-G_p$, $1-G_r$, and $1-G_d$).

Population dynamics

Each habitat grid cell provides space for one individual plant. On each plant, herbivores may reach a certain number which is limited by the carrying capacity on the plant (respectively K_r and K_d) beyond which reproduction fails. Reproduction takes place after dispersal, i.e. after the establishment of local densities (respectively δ_a and δ_b). The realized number of offspring λ' for both herbivores is then sampled from a Poisson distribution determined by the local density K/δ . Reproduction of the herbivores fails for each individual with $G_r > G_r$ or $G_d > G_d$ i.e. when the toxin production by the plant is greater than the developed resistance by the herbivore. Realized plant reproduction λ_p' is relative to the experienced density of both herbivores and sampled from Poisson ($\lambda_p/(\delta_a + \delta_b)$). Therefore plant reproduction is affected by the density of both types of herbivores.

Initialization and evolutionary dynamics

The landscape is initialized with 3000 randomly distributed individuals of each species (except in single herbivore–plant interaction in which obviously only one herbivore was initialised). Initial allele values for toxin production or resistance were drawn from a uniform distribution [0,1]. We selected the initial number of individuals based on explorative simulations: lower initial values (<1500) resulted in rapid herbivore extinction and therefore were not suitable to address the questions of this study, and moreover, lower values dramatically increased the number of iterations to reach stable levels. Offspring inherit allele values from their mother during reproduction. Therefore at initialization, all individuals show similar allele values, but these values change according to the emerging properties of the study system and random mutation. Offspring inherit allele values from their mother during reproduction, but allele values are able to change by mutation every generation. We introduced a mutation rate of 1/10000 with values changing between the range $[x-0.1...x+0.1]$. Parameter values after mutation rates were constrained between zero and one.

Parameterization

As our modelling approach emphasises realistic interactions between herbivores and a plant species, we set different multiplication rates for the RH and the DH. Preliminary analysis showed that generation time did not affect the evolutionary outcome, but did affect the speed of the adaptive trajectory, so we assumed fast developing resident herbivores RH ($\chi_r = 4$ generations/plant generation) and dispersive herbivores (DH) with two generations per plant generation ($\chi_d = 2$). This mimics systems with fast developing below- or above ground, resident herbivores (like aboveground aphids, scale insects, or some species of root feeding nematodes) and winged, slowly developing aboveground herbivores like planthoppers. Therefore, individual development rate is seen here as an implicit cost of dispersal. Similarly, sensitivity analysis for reproduction (Λ) and carrying capacity (K) did not indicate substantial

variation in the obtained results (unless extreme values are selected, e.g. multiplication of one species 10-fold higher or lower than the other species). Seed production was set to 10 ($\Lambda_p = 10$), and herbivore fecundity (Λ_d and Λ_r) to 4 (Bellows 1981, Cousens et al. 2008). Evolutionarily stable strategies were reached before 1000 plant generation time steps (see for example Fig. 1). The carrying capacities for both RH and DH (resp. K_r and K_d) were set to 10. In order to test the hypothesis that variation in herbivore and plant dispersal affects co-evolutionary dynamics, we tested scenarios in which plant and DH σ equaled 2, 4, 6, 8, 10, 12, 14, 16, 18, 20. Dispersal variance for RH (σ_r) was set to 2, hence only allowing for limited dispersal of the latter. We tested scenarios for two-species interactions (respectively plant-RH and plant-DH) and three-species interactions. We replicated each scenario 10 times in the four predefined landscape types. This resulted subsequently in $(2 \times 4 \times 100 \times 10 + 4 \times 20 \times 10 = 8800)$ simulations. For each simulation, we calculated the mean plant toxin level, the mean level of resistance for the RH and DH (if present).

Results

Toxin level

Evolutionarily stable levels of plant toxin production depend on the landscape structure, the number of species interacting and the dispersal capacity of seeds and DH herbivores (Fig. 1). Overall, greater availability of habitat (P) and higher levels of spatial autocorrelation (H) selected for greater levels of toxins in planta (see increasing levels in Fig. 1A–D, Fig. 1E–H and Fig. 1I–L, from left to right). In relation with the types of species interactions (i.e. RH-plant, DH-plant, or RH-DH-plant), the highest mean toxin values appeared under three species interactions (Fig. 1I–L). However, in the three cases compared non-linear relations between habitat structure (i.e. habitat availability and connectedness) and dispersal capacities of the DH and the plant (seed) appear.

In general, toxin production is lower in DH-plant interactions compared with three-species interactions for all studied scenarios (i.e. Fig. 1E vs Fig. 1I, Fig. 1F vs Fig. 1J, etc). However in two-species interactions (RH-plant vs DH-plant), the evolved maximal mean toxin values were similar and there was a strong dependency on the dispersal capacities of the species involved and the landscape structure. In scenarios where habitat availability is limited ($P = 20$), plant toxin production showed a non-linear relationship in relation to both plant and herbivore dispersal. For instance, when considering the plant-RH interactions in the fragmented landscapes (Fig. 1A), the highest toxin values evolved under intermediate seed dispersal ($\sigma = 10-14$), whereas in the connective landscape (Fig. 1B), they were observed for lower seed dispersal values ($\sigma \leq 12$). For scenarios where there was a greater habitat availability (Fig. 1C, D), there is a mean increase in toxin production from fragmented to connected landscapes, but seed dispersal does not impose a strong effect on the evolution of toxin production.

Toxin production in the DH-plant scenario evolved towards lower rates when herbivore dispersal increased

(Fig. 1E, 1F) and indeed, at very high dispersal rates, the system collapsed as both plants and herbivores went extinct (therefore toxin levels equal to zero are observed). Under high habitat availability (P80s), a homogeneous response was observed in the system and the role of both DH and seed dispersal is less relevant with high values, ca 0.45, in all situations.

In the three species interactions (RH, DH and plants), the effect of herbivore dispersal disappears when habitat availability is low (P = 20) (Fig. 1I–J), although again a selection to decreased toxin production was observed under conditions of high dispersal in the connected landscape (Fig. 1J). In landscapes with high habitat availability and high spatial autocorrelation, toxin production evolved towards the highest levels across all simulations and was independent of both the plant or the herbivore (DH) dispersal capacity (Fig. 1K–L).

DH resistance

In the absence of RHs, the highest levels of resistance to toxin evolved in the four landscapes when both herbivore and seed dispersal were lowest (Fig. 2A, B). Resistance evolved towards lower levels with increasing herbivore dispersal values. Mean levels of resistance increased with higher habitat availability and spatial autocorrelation and are higher than the evolved plant toxin levels (Fig. 2C–D vs Fig. 1G–H). Three-species scenarios evolved towards greater resistance levels over all (Fig. 2A vs Fig. 2E, Fig. 2B vs Fig. 2F, etc.). The pattern is similar for the two-species scenario in the landscape with low habitat availability (Fig. 2A vs Fig. 2F) although extinction occurs at lower dispersal values (i.e. 8). When habitat is freely available no variation emerges according to DH and plant dispersal (Fig. 2G, H).

RH resistance

The evolution of RH resistance depended on the landscape structure and also on the number of species involved (Fig. 3). In general, resistance values showed an increasing trend in relation to habitat availability and connectedness (Fig. 3A–D and also Fig. 3E–H). However, selection resulted in increased levels of RH resistance when plant dispersal was low (Fig. 3A–B). In landscapes with high habitat availability, comparable tendencies in herbivore resistance resulted over the four possible scenarios that were compared (Fig. 3C–D and Fig. 3G–H).

Discussion

Our model showed the evolutionary outcome of plant-herbivore antagonistic interactions to be strongly influenced by the landscape structure and the dispersal capacities of both the plant and herbivores. Landscapes with greater availability of suitable habitat select for high plant toxin levels, and consequently for the evolution towards high resistance in herbivores. In landscapes with low habitat availability, the spatial autocorrelation of the available habitat and the dispersal capacities of the species are the main drivers of toxin/defense evolution. Therefore, non-linear co-evolutionary dynamics of plant toxin production and herbivore resistance occur and depend on complex feedbacks between interacting species, spatial structure and the dispersal capacities of the organism involved.

Herbivory acts as an important selection force in plant communities (Strong 1988, Rutter and Rausher 2004, Lau et al. 2008). The forces exerted by herbivores on plant species, and vice versa, vary spatially (depending on the geographic sites) and this leads to geographic structuring of plant-herbivore interactions (Thompson 1999). Here, we

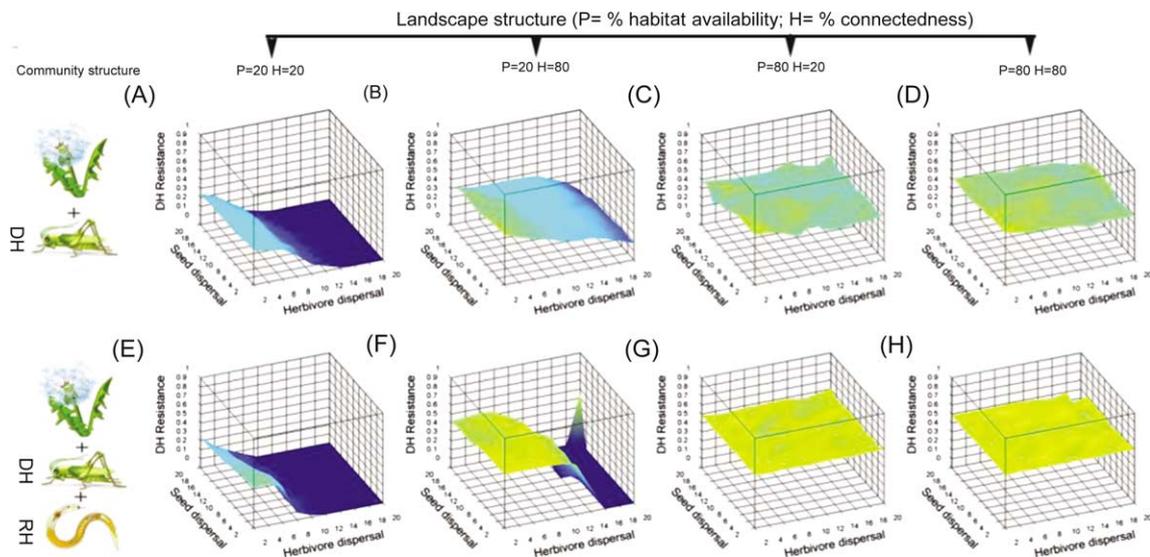


Figure 2. Mean resistance to toxin for DH as a function of types of species interaction, landscape structure and dispersal capacities of the species involved. Types of interactions are explained on the left margin of the figure where DH stands for a dispersive herbivore and RH stands for residential herbivore. For each type of interaction, left to right comparison are related to landscape structure, top-down comparisons are related to types of interaction for the same landscape structure.

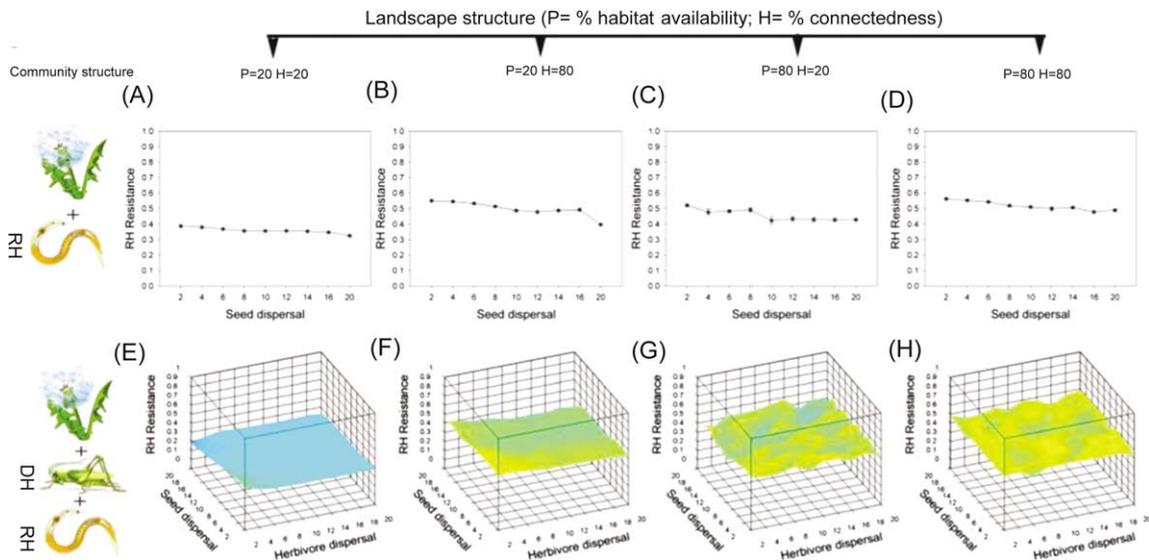


Figure 3. Mean resistance to toxin for RH as a function of types of species interaction, landscape structure and dispersal capacities of the species involved. Types of interactions are explained on the left margin of the figure where DH stands for a dispersive herbivore and RH stands for resident herbivore. For each type of interaction, left to right comparisons are related to landscape structure, top-down comparisons are related to types of interaction for the same landscape structure.

show that this spatial variation can be related to the structure of both the landscapes and the prevailing communities (e.g. the number of species interacting). We considered evolutionary patterns within each of the landscapes as a closed system and demonstrated clear variation in evolutionary dynamics in relation to the availability of habitat and its distribution. As expected, the evolution of toxin production (or broader defense strategies) in plants, and the consequent resistance strategies in the herbivores, strongly depended on the landscape context. Independent of plant and herbivore dispersal strategies, highest levels were reached in the landscape with high habitat availability. When habitat availability was low, defense and resistance evolved to higher levels in highly spatially autocorrelated landscapes (i.e. showing a high connectedness between the patches) compared with the values in fragmented ones. Consequently, the evolution of antagonistic interactions depends strongly on the community structure and this conclusion agrees with previous observations (Kruess 2003, Tschardt and Brandl 2004). We implemented 1) differences in the number of species in the interaction (i.e. one herbivore vs two herbivores), and 2) differences in species' dispersal rates, to test the effect of altered community structure on the plant/herbivore arms race. When the plant was interacting with two herbivores, toxin and resistance values were higher in comparison to the single-herbivore interactions. This result follows our initial expectation that an increased level of herbivore pressure would result in a strong selection towards higher toxin production in plants and subsequent emerging resistance strategies (Agrawal and Fishbein 2006).

While it is widely acknowledged that abiotic selection pressures related to different environmental factors (e.g. nutrient conditions and light availability) affect the evolution (local adaptation) of plant genotypes (Karban and Agrawal 2002), the importance of biotic interactions and herbivory in particular has been much less studied from an

evolutionary community perspective (i.e. the perspective beyond the single herbivore-plant perspective, Urban et al. 2008). As expected, multispecies interactions and the subsequently evolving antagonistic strategies strongly interact with the prevailing landscape structure through feedbacks with the spatial distribution of species, their fitness and colonization/extinction dynamics. Despite the necessary simplification of the magnitude and complexity of possible antagonistic interactions, our simulation model highlights the importance of the community complexity (in the number of interactions with herbivores) as a driver for plant and herbivore persistence and evolution. Variation in the community structure and also, in the properties of the species involved within the community has strong effects on the co-evolution of plant-herbivore interactions.

In our model we showed that the evolutionary outcome of plant-herbivore interactions is strongly determined not only by the number of interactions, but also by changes in species' capacities to move and how this influences population persistence. These interactions strongly depend on the underlying landscape structural component. When habitat is freely available, dispersal mortality is low, as already predicted for other study systems (King and With 2002). Spatial connectedness in the low-habitat landscape ($P = 20$) resulted in strong effects of dispersal on the evolution of plant-herbivore interactions (King and With 2002). When taking into account the different single herbivore-plant interactions in these landscapes, toxin and resistance levels decrease with increasing plant dispersal only for the scenarios with low dispersive herbivores (RH, Fig. 1A, D). This is due to the decreasing possibilities for the plant and herbivore to interact, or the increased possibilities of plants to escape herbivore grazing pressure. For plant-DH, and three-species interactions, we found a contrasting pattern. In landscapes with low connectedness ($P20, H20$; Fig. 1E, I), there was a selection towards low toxin levels at low seed dispersal rates, whereas in clumped

landscapes (P20, H80; Fig. 1F, J), low seed dispersal resulted in higher levels of toxin. This unexpected outcome results from the feedbacks with population dynamics. High dispersal rates in heterogeneous landscapes result in a high mortality (Supplementary material Fig. S1). However, when the landscape is patchy, low dispersal increases the chances of establishment, which in combination with the effect of herbivory, explains the contrasting pattern at low seed dispersal (King and With 2002).

In contrast to our initial expectations that increased dispersal rates of DH would always induce selection for increasing antagonistic evolution (Rausher 2001), our simulations suggest this is not a general outcome. In fact, in two-species interactions, high dispersal capacities at low habitat availability resulted in the extinction of the herbivores and subsequently in low toxin levels (Fig. 1E, F). This can be explained in two ways: 1) high dispersal can result in dispersal to sites where there is no host plant available and subsequently in extinction and 2) because surviving herbivores in the system have developed high resistance strategies, trade-offs with fecundity induce a negative feedback on the colonization of single plant patches. In this case, if colonization is successful, despite low probabilities, local, isolated arms races will lead to fast evolutionary suicide in the herbivore due to local plant extinction.

We here analysed average trait levels at the landscape level. We should, however, keep in mind that, especially in landscapes with intermediate spatial autocorrelation and habitat availability, polymorphisms in strategies may arise (Bonte et al. 2010a, b). Here, spatial dynamics of herbivores in landscapes with a low autocorrelation gives rise to spatial variation in herbivore presence, eventually leading to coevolutionary selection mosaics, subsequently resulting in trait polymorphism in both, defense and resistance strategies. For information, we include evolutionary trajectories (Supplementary material Fig. S3) which demonstrate the evolution of polymorphism in landscapes with lower amount of habitat availability, but an in depth analysis of these patterns is topic for a following contribution. Nonetheless a preliminary analysis of the coefficient of variation (CV) in toxin production in plants (i.e. allele selection) showed that the highest CV mean values are obtained under low habitat availability (Supplementary material Fig. S2).

Empirical data and models have demonstrated that we can only understand plant–insect interactions if we take into account the landscape perspective (Valladares et al. 2006, Cagnolo et al. 2009). This is particularly important when habitat fragmentation (i.e. transformation of formerly extensive landscapes into smaller and isolated remnants surrounded by unsuitable habitat for the species (Valladares et al. 2006)) is a common characteristic of different natural habitats. The occurrence of species across a fragmented landscape depends of the size and connectedness of habitats, the landscape context in which the habitats are embedded, and the traits of the species. Landscape structure and especially habitat fragmentation will not affect all the species in the same way. Although the general trend is a negative effect of fragmentation on species diversity and species establishment (Cagnolo et al. 2009), basic life-history traits such as dispersal, body-size and position within a trophic cascade will determine the effect of

fragmentation in the community. In this study we show that the dispersal abilities of the species occurring in our artificial communities are extremely relevant to understand the evolutionary pathway of the system and not only that, but the effect of dispersal will be context (landscape) dependent and occur in a non-linear fashion.

Although this study has been developed as a theoretical approach to explore the effect of landscape structure and species dispersal on the (evolutionary) outcome of plant–herbivore interactions it is important to keep in mind real life scenarios. For instance, during the last decade there is increasing awareness and empirical evidence of the key role that biotic interactions occurring belowground play on aboveground plant–animal interactions and on ecosystem processes and properties (van der Putten et al. 2001, Wardle et al. 2004). From the literature we know that in some cases above and belowground herbivore fauna can trigger similar responses and in consequence, the effect of belowground herbivores in shaping evolutionary aboveground–insect herbivore needs to be elucidated (Bezemer and Van Dam 2005, Kaplan et al. 2008). Nevertheless, most theory has been developed from an above-ground perspective and we lack field studies in which the effect of such complex interactions are integrated. Interestingly, among the key features that distinguish these two groups of herbivores are the intrinsic capacities for dispersal. Therefore, the above and below-ground herbivore community structure may affect plant evolutionary strategies and plant-mediated herbivore evolution which will eventually feedback again on the persistence of herbivores in spatially structured systems.

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