Spatial structure of natural boxwood and the invasive box tree moth can promote coexistence.

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Abstract

In the absence of top-down and bottom-up controls, herbivores eventually exhaust their host plants driving themselves to extinction. Poorly mobile herbivores may nevertheless go extinct only locally; then recolonize intact plant patches elsewhere, leaving time to previously over-exploited patches to regrow. However most herbivores such as winged insects are highly mobile, which may prevent the formation of spatial heterogeneity.

We test if long-distance dispersal can preclude coexistence using the invasion of box tree moth (*Cydalima perspectalis*) in Europe as a model system. We build a lattice model and estimate the parameters with a combination of field measurements, experimental data and literature sources. Space corresponds either to a realistic boxwood landscape in the Alps, or to theoretical landscapes of various sizes.

We find that both species persist under a large range of realistic parameter values, despite a severe reduction in boxwood biomass, with an alternation of outbreaks and near-to-extinction moth densities. Large landscapes are necessary for coexistence, allowing the formation of spatial structure. Low plant regrowth combined with long-distance dispersal could drive moths to extinction, because of resources depletion at the global scale even without a complete synchronization of the local dynamics. The spatial dynamics leads to formation of small plant patches evenly distributed in the landscape, because of a combination of local plant dispersal and global indirect competition between plants through their positive effect on moth population size. Coexistence is favored by such heterogeneous landscapes, because empty patches increase moth mortality during dispersal: the system thus creates its own stability conditions.

Key words: source-sink dynamics, green world, spatial asynchrony, metacommunity, invasive species

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Author contributions : CG, SI and JG originally formulated the idea, CG, SI, JG and LL developed methodology, LL conducted fieldwork, SI, JG and LL developed the mathematical model, LL performed the numerical analyses, all authors participated in writing the manuscript.

Introduction

In general, most herbivores do not polish their resources off because they are top-down controlled by their predators [Hairston et al., 1960] as well as bottom-up limited by the defense compounds and the poor nutritional quality of plants [Polis, 1999]. However, in some cases such top-down and bottom-up mechanisms are insufficient, turning the green world brown. In such cases, it has been suggested that the spatial dynamics of plant-herbivore metacommunities may favor their coexistence [Wilkinson and Sherratt, 2016]. This hypothesis builds upon long-standing theoretical work which has shown that spatial structure promotes the persistence of otherwise unstable prey-predator systems [Hassell et al., 1991, Comins and Hassell, 1996, Amarasekare, 2008], thanks to local extinctions followed by recolonization, in line with metapopulation and metacommunity dynamics [Hanski and Gilpin, 1997, Holyoak et al., 2005]. These theoretical predictions have received robust empirical support by experiments based on animal prey-predator system [Taylor, 1991], as protists [Holyoak and Lawler, 1996, Fox et al., 2017] and field studies with arthropods [Nachman, 1988, Winder et al., 2001].

However, there is little evidence showing that the spatial dynamics resulting from interactions between plants and herbivores leads to a green world - or at least to a multi-coloured world with green and brown patches. Many herbivorous insect populations persist thanks to metapopulation dynamics [Tscharntke and Brandl, 2004], but this is generally due to other mechanisms than the depletion of their plant resources. For instance, local extinctions can depend on patch size [Eber and Brandl, 1996], on the fluctuation of plant resources (but for other reasons than the herbivore itself [Halley and Dempster, 1996]), or on a combination of ecological succession and catastrophic events [Stelter et al., 1997]. In the well studied ragwort / cinnabar moth system, the moth can go locally extinct following defoliation, but plant patches persist [Myers and Campbell, 1976, Myers, 1976]. Although cinnabar moths contribute to local plant extinction, local plant persistence ultimately depends on habitat suitability, which leads to a source-sink dynamics rather than to a classical metapopulation scenario [van der Meijden and van der Veen-van, 1997, Van der Meijden, 1979]. Moreover, the high dispersal ability of cinnabar moths prevents asynchronous local dynamics for the moth, which rules out a metapopulation model of coexistence [Harrison et al., 1995, van der Meijden and van der Veen-van, 1997]. As far as we know, the only documented plant-herbivore system where the plant goes locally extinct due to over-exploitation comprises the Apiaceae *Aciphylla dieffenbachii* and the monophagous weevil *Hadramphus spinipennis*, two species endemic to the Chatham Istands (New Zealand). Increased local weevil densities are associated with local plant extinction [Schöps, 2002], and numerical simulations have shown that spatial structure allows the persistence of the system, provided that the dispersal distance of the herbivore is intermediate [Johst and Schöps, 2003]. However, the ecological conditions which promote the persistence of this particular study system may not hold for other plant-herbivore interactions. In particular, the weevil *H. spinipennis* is wingless and of a large size, which considerably reduces its dispersal ability either by itself, by wind or by birds. In contrast, many insects can disperse at long distances [Wilson and Thomas, 2002, Gillespie et al., 2012]. Long-distance dispersal can promote metapopulation persistence, except when strong density dependence triggers local extinctions [Johst et al., 2002]. In that case, long-distance dispersal events synchronize local extinctions which eventually lead to the extinction of the whole metapopulation [Palmqvist and Lundberg, 1998, Johst et al., 2002]. In plant-herbivore metacommunities, strong density dependence occurs when herbivores overexploit their host down to local extinction.

In order to test if plant-herbivore metacommunities can persist despite high abilities of herbivores to disperse, we study the system formed by the common European boxwood *Buxus sempervirens* and the invasive box tree moth (*Cydalima perspectalis*) in Europe. The moth first arrived in Germany in 2006/2007 [Van der Straten and Muus, 2010] via the boxwood trade from Asia [Kenis et al., 2013, Van der Straten and Muus, 2010, Bras et al., 2019]. It is currently quickly spreading throughout Europe [Blackburn et al., 2011], which suggests human and/or natural long-distance dispersal. On the base of its climate envelope, the moth will likely invade most of Europe in the following years [Nacambo et al., 2014], with potentially major ecosystemic consequences [Mitchell et al., 2018]. Defoliation caused by the moth can lead to the death of the boxwood, especially when the bark is also consumed [Kenis et al., 2013]. After total defoliation, boxwood can either grow back or wither completely, if the defoliation becomes too recurrent [Kenis et al., 2013]. The local extinction of boxwood has already been observed in the Nature Reserve of Grenzach-Whylen in Germany [Kenis et al., 2013]. In the meantime, the moth goes extinct locally after total defoliation of boxwood stand, even if it grows back several years after the moth outbreak. Within its area of origin, the moth is regulated by its natural enemies [Wan et al., 2014] and no local extinction of either plant and insect species is observed, but potential european natural enemies do not significantly alter the invasive moth dynamics [Kenis et al., 2013, Leuthardt and Baur, 2013]. Moreover, although box trees contain highly toxic alkaloids [Ahmed et al., 1988, Loru et al., 2000, Devkota et al., 2008], the moth larvae can sequester them in their body [Leuthardt et al., 2013], which may rule out bottom-up control. In contrast, in the ragwort / cinnabar and Apiaceae / weevil systems mentioned earlier, both insects are native and may therefore be top-down controlled by local natural enemies. Given that both top-down and bottom-up controls are disabled in the case of the invasive boxwood moth, will the European boxwood stands remain green?

Metacommunity dynamics with local moth extinctions followed by recolonization may be an alternative mechanism to top-down and bottom-up control favouring coexistence in Europe. In the particular context of biological invasions, spatial effects have not been widely addressed [Melbourne et al., 2007], although they may favour coexistence. The metacommunity mechanism requires spatial heterogeneity among local communities, which is likely because boxwood has a fairly fragmented distribution in Europe, and because the box tree moth was not simultaneously introduced in every patch. As long as the invasion does not start simultaneously in all stands, the moth may disperse from its current totally defoliated stand to a green intact stand. The defoliated stands may then grow back and be recolonised lately. Thus, despite local extinctions and recolonizations, local fluctuations may be averaged on a large spatial scale, leading to a global stationary regime which has been called 'statistical stability' [De Roos et al., 1991, Holyoak et al., 2005, Amarasekare, 2008]. However, unlike the wingless weevil *H. spinipennis*, *C. perspectalis* is highly mobile, because it can fly or it can be transported by exogenous factors (wind, human activities) [Bras et al., 2019]. Its high mobility may prevent spatial heterogeneity and therefore precludes coexistence by spatial effects [Johst et al., 2002, Johst and Schöps, 2003]. Thus at large spatial scale, three ecological scenarios are likely to occur. First, the moth might very quickly overexploit its host, causing it own extinction but not the one of its host, which in turn slowly grows back. Second, the moth might persist long enough to exhaust its host, leading to the extinction of both species. Third, coexistence might result from the balance between local moth extinctions and recolonizations, without complete resource depletion. Our study focuses on the conditions which favor such coexistence, based on the following hypotheses :

1. Long-term coexistence of boxwood and moth is possible at the landscape scale through spatial stabilizing effects (1a). Those effects rely on asynchronous local dynamics (1b).

2. Despite cycles of local extinctions and recolonizations, the coexistence regime is stationary at the regional scale, which corresponds to statistical stability.
3. Dispersal is double-edged : very limited dispersal might prevent the colonization of green patches (3a), whereas long-distance dispersal may synchronize local dynamics (3b).
4. The coexistence regime depends on the landscape characteristics, in particular the landscape size and the proportion of boxwood patches in the landscape. First, larger landscapes favor coexistence (4a). Secondly, the effect of the proportion of boxwood patches is uncertain, since it provides more resources to the moth, but also favors outbreaks and resource depletion (4b).

In order to address these four hypotheses, we develop a population model dynamics for the boxwood and moth system. First, a local model reproduces the local invasion dynamics, which invariably leads to moth extinction in the field. Then, a spatially explicit model simulates the dynamics of the moth in a landscape. Our model is calibrated from the literature, *in situ* measures, and through mesocosm experimentation.

Study system & theoretical model description

Species involved : boxwood and box tree moth

The box tree moth, *Cydalima perspectalis*, is an herbivorous lepidoptera belonging to the Crambidae family [Mally and Nuss, 2010]. Five to seven stages of development are necessary to the larvae to become nymphs for about ten days before emerging as moths [Kawazu et al., 2010]. During the winter, the larvae are at the beginning of their development in stages two or three and form cocoons to enter in diapause [Nacambo et al., 2014]. The moths live for two weeks during which they reproduce and lay eggs on boxwood leaves. The moth has a high fecundity rate, with between 300 and 400 eggs laid per female [Kawazu et al., 2010, Wan et al., 2014]. In Asia, two to five life cycles are possible per year, with a break during the winter when the caterpillars are dormant [Maruyama et al., 1987, 1991]. In its invasion range, the moth completes from 2 (in the north) to 4 (in the south) generations per year [Nacambo et al., 2014, Göttig, 2017]. The mean intrinsic dispersal distance of moths has been estimated around ten kilometers per year [Van der Straten and Muus, 2010].

The moth exhibits no preference for any particular boxwood species [Leuthardt and Baur, 2013], so the common European boxwood *Buxus sempervirens* is widely consumed, as well as Caucasus boxwood *Buxus colchica*, and even the rarer European species *Buxus balearica* [Kenis et al., 2013]. These natural boxwood stands, which have already undergone a major decline over the last millennia [Di Domenico et al., 2012], are now subject to this additional threat. In Asia, *C.perspectalis* also consumes other species, including holly (*Ilex purpurea*), charcoal (*Euonymus japonicus*, and *E.alatus*). Fortunately this is not currently the case in Europe [Göttig, 2017]. Despite natural regulation by native predators and parasites, this moth remains a threat to ornamental boxwood in Asia, where its potential targets are protected by insecticides [Wan et al., 2014]. Instead, in Europe *Bacillus thuringiensis* is commonly used as a sustainable control method. However, its efficiency is offset by its low persistence; current efforts are being made to develop more long-term treatments. Biological control solutions are also being explored, such as the use of nematodes [Göttig and Herz, 2018] and parasites from the genus *Trichogramma* [Göttig and Herz, 2016]. Efforts are also being made to seek out predators and parasites from the box tree moth's area of origin that might act in areas of invasion [Göttig, 2017]. The use of pheromone traps is widespread, both for monitoring and control [Santi et al., 2015, Göttig and Herz, 2017], but their effectiveness appears to be insufficient at a large scale. Even if effective control for ornamental boxwood could be introduced, natural boxwood and associated ecosystems will likely suffer dramatically from the *C.perspectalis* invasion.

Boxwood has a fairly heterogeneous distribution in Europe that consists mainly of small and fragmented stands, but some large areas of continuous boxwood occur in the French Pyrenees, the Pre-Alps and the Jura [Di Domenico et al., 2012]. It is a long-lived, slow-growing shrub that thrives on calcareous substrate. It can tolerate a wide gradient of light incidence, and can therefore be found in a range of plant communities, from canopy areas in heaths to under cover in forests [Di Domenico et al., 2012]. It can play an important role in structuring ecosystems, by trapping sediment and storing water. It also influences the establishment and survival of tree species in woodland succession [Mitchell et al., 2018]. A total of 286 species are associated with the shrub, including 43 fungi that are exclusively observed on boxwood [Mitchell et al., 2018]. However, boxwood is scarcely predated by native species.

Demographic model on the local scale

Our model projects the population size m of Box Tree Moths (BTM) and the population density of Box Trees (BT), which are separated in two variables : leaf density l and wood density w, from moth generation n to $n+1$. This time representation is used to avoid the problem of multiple generations per year and its variation with space location. However, we are able to project the population of BTM and BT from year to year if we know the number of generations per year in each specific location. We write

$$\left\{\begin{array}{lcl} l_{n+1} & = & S_l(\mu_n)\, F_l(l_n) l_n + r_0 w_n \\ w_{n+1} & = & S_w(\mu_n, \rho_n)\, F_w(w_n, \rho_n) w_n \\ m_{n+1} & = & S_m(\mu_n)\, F_m\, m_n \end{array}\right. \tag{1}$$

to indicate that during the projection interval, BT and BTM grow and reproduce (F), and survive (S). The BT reproduction functions were constructed using a Ricker model, which includes the intrinsic population growth rates r_f, r_w and the carrying capacity of the environment L_{max}, W_{max}, while the BTM reproduction function is linear and only includes the fecundity of adults f and their survival s. The survival of the species is determined by the consumption of leaves and bark by the BTM as well as the intraspecific competition for the resource faced by BTM. The survival and reproduction functions F and S depend on both the current population l, w, m, and the environmental descriptors μ and ρ.

Environmental descriptors. The environmental quality is described using two descriptors μ and ρ defined by ratios of population densities:

$$\mu_n = \frac{f m_n \alpha}{l_n} \quad \text{and} \quad \rho_n = \frac{l_n}{w_n}$$

The ratio μ corresponds to the ratio between the number of leaves needed by all the larvae to fulfil their cycle and the number of available leaves (α is the amount of leaves needed per larva). The number of larvae depends on the number of moths (m_n) through its product by the moth fecundity (f). And each larva needs α leaves to complete its cycle. The ratio μ thus quantifies the pressure for the resource, which plays a direct role in the intensity of consumption of leaves and wood, and therefore the survival of the larvae.

The ratio ρ is the quantity of leaves per unit of wood. This represents the level of boxwood defoliation, which has an impact on the growth of the wood.

Reproduction. The increase in foliage biomass is the result of two processes: the growth of leaves F_l, which depends on the current foliage (Figure 1a), and the production r_0 of new shoots by the wood after defoliation (Figure 1b). Without herbivory, the growth of leaves is limited only by senescence and carrying capacity L_{max}. Thus, growth F_l is represented by a Ricker model in the following form

$$F_l(l) = \exp\left(r_f(1 - \frac{l}{L_{max}})\right)$$

where r_f is the intrinsic growth rate of the leaves.

The wood growth function F_w (Figure 1c) is constructed using a Ricker model. Positive growth ($r_w > 0$) is constrained by carrying capacity. Negative growth ($r_w \leq 0$) occurs after an important defoliation because branches or even a proportion of trunk can die after defoliation. For each projection interval n, the intrinsic growth rate of the wood $r_w(\rho_n)$ is defined as the balance between the production of new wood b_w, which critically depends on the density of leaves per unit of wood ρ_n, and the mortality induced by severe defoliation d_w.

$$F_w(w,\rho) = \begin{cases} \exp(r_w(\rho)(1 - \frac{w}{W_{max}})) & \text{if } r_w(\rho) > 0 \\ \exp(r_w(\rho)) & \text{if } r_w(\rho) \leq 0 \end{cases} \qquad \text{with} \quad r_w(\rho) = b_w(\rho) - d_w(\rho)$$

When the density of leaves is large ($\rho \gg 1$), the BT is healthy and its production of wood reaches a maximum $r_{w,max}$. Conversely, when the density of leaves per unit of wood collapses due to severe defoliation, the production of wood is low while the mortality increases until a maximum $-r_{w,min} < 0$ which forces the growth rate to be negative. The production function b_w and the mortality function d_w takes the following form :

$$b_w(\rho) = \frac{\rho^{\beta_r}}{\rho^{\beta_r} + \theta_r^{\beta_r}} r_{w,max} \qquad\qquad d_w(\rho) = (1 - d^{\frac{1}{\rho}}) r_{w,min} \tag{2}$$

where β_r, θ_r and d are shape parameters (see Table 1).

The reproduction rate of BTM (Figure 1d) does not suffer from density dependence and is equal to the product of adult fecundity f and adult survival s

$$F_m = f\,s$$

Survival. The leaves may die by senescence at rate v, or be consumed by BTM at a rate which increases with the pressure of BTM on BT, μ, (Figure 1e). In the absence of BTM, 0% of leaves are consumed, while if BTM have saturated the environment, 100% of the leaves are consumed. Thus the survival function of the leaves is defined by

$$S_l(\mu) = v\,(\sigma_l^{\mu}) \tag{3}$$

where σ_l is a shape parameter (see Table 1).

The wood can suffer from both defoliation (Figure 1c), which decreases its intrinsic growth rate, and from the consumption of bark by the BTM (Figure 1f).

The wood mortality due to consumption increases with both the BTM pressure, μ and the BT health ρ. More precisely, the wood mortality saturates to d_{max} when the foliage is abundant (large ratio $\rho \geq 1/3$). However, when the foliage is small (low ratio $\rho \leq 1/3$), the bark consumption occurs while the superficial woods is available. Thus recently defoliated boxwood with small bark coverage (ρ close to 0) cannot be consumed by the larvae.

$$S_w(\mu, \rho) = 1 - \frac{\mu^{\beta_s}}{\mu^{\beta_s} + \theta_s^{\beta_s}} D_{max}(\rho) \tag{4}$$

where β_s and θ_s are shape parameters and D_{max} is the maximal mortality rate which grows linearly with ρ until a threshold 1/3, at which point it saturates to its critical value d_{max}.

$$D_{max}(\rho) = \begin{cases} 3d_{max}\,\rho & \text{if } \rho < 1/3 \\ d_{max} & \text{if } \rho \geq 1/3 \end{cases} \tag{5}$$

This step function takes into account that the consumption of superficial wood depends on the presence of available softwood, and thus a certain amount of foliage. The threshold value 1/3 for BTM pressure ρ corresponds to the approximate ratio when there is as much foliage as wood, the density of the wood being three times greater.

Survival of BTM during the larval stage depends mainly on the amount of available resource per larva μ. If the larva has enough available resource to complete its six stages, it will evolve into a moth, while a lack of resource during its growth will cause its death. The survival rate also takes into account intraspecific competition for resource caused by interference between the larvae. The survival function is defined using a shape parameter σ_m as

$$S_m(\mu) = \begin{cases} S_{m,max}\left(1 - (\sigma_m)^{\frac{1}{\mu}}\right) & \text{if } \mu < 2 \\ 0 & \text{if } \mu > 2 \end{cases} \tag{6}$$

The threshold $\mu = 2$ fits a given situation that occurs when there is a shortage of resource for the larvae, even if some larvae die during their evolution.

Spatially explicit model

The local model allows us to describe the interaction between BTM and its host BT at a small homogeneous spatial scale. Next, we build a cellular automaton in order to investigate the BTM invasion over a regional heterogeneous landscape. From field observations provided by the National Alpine Botanical Conservatory, we obtain a map of the French Alps composed of 570 by 351 cells of 29 hectares each (about 58 000km^2, see Online Resource 1 in Supporting Information). It should be noted that these data focus on natural boxwood and neglect the presence of ornamental boxwood in urban areas. We focus on the French Alps because detailed botanical data are available, but in theory our model could be extended to the whole area of invasion. Green cells correspond to areas with BT, grey cells correspond to areas without BT, while blue cells represent urban areas. We use the basemap from OpenStreetMap based in Qgis®. In each cell with BT, BTM can mate and lay eggs according to the local model, while in cells without BT, BTM cannot become established. After the reproduction phase, BTM moths disperse over the landscape to find new areas to breed and lay eggs. BT can also disperse over the landscape to recolonise extinct areas. Simulations are initialized with a single moth invading a patch chosen at random, and carried out on a maximum of 1000 iterations if no specifications are given.

Dispersal phase of BTM. A BTM dispersal event includes two stages: (1) emigrating from birth areas, and (2) searching for new areas (exploration) and settling to breed. Field observations suggest that the exploration phase is stochastic, composed of frequent short-distance dispersal by adult flight, and rare long-distance dispersal by anthropogenic action (boxwood trade) or long flight. *In situ* experimentation using a flight carousel has provided a mean dispersal distance per individual of 13km (Bras et al., personal communication), which is in accordance with the 10km dispersal distance observed by Van der Straten and Muus [2010]. Bras et al. have also observed rare long-distance flights in their experiments, which may correspond to long-distance dispersal events that we model using a fat-tailed dispersal kernel. To this end, we use an exponential power distribution from Klein et al. [2006] which makes it possible to compare different shape of distribution tails while maintaining a fixed average dispersal distance. For ecologically realistic calibration the tail shape parameter is 0.5 (i.e fat-tailed dispersal kernel) and the average dispersal distance is 25 cells (i.e $\approx$ 13km). In addition, to save computation time, we assume that BTM disperses as a swarm of 1000 individuals. This group dispersal may occur because BTM can be attracted by volatile boxwood compounds or avoid geographical barriers, or are influenced by weather conditions. Thus, during the searching and settling phase, each group of BTM settles in an area located at a random distance drawn in the exponential power distribution and chosen with a random turning angle run in a uniform distribution over $(0, 2\pi)$. The emigration rate for each location depends on the pressure for resource μ at the birth location. As long as pressure remains low, the moths have the possibility to find leaves to oviposit in their birth patch and thus dispersal is weak. When the resource pressure increases, there is not enough boxwood available for laying eggs and adults will disperse massively to another patch in search for resource. Such resource-dependent dispersal has also been modelled by the study of Johst and Schöps [2003]. The migration rate M_m of BTM depends on μ as follows

$$M_m(\mu) = (1 - \delta^{\mu})M_{m,max} \tag{7}$$

where the maximal dispersal rate $M_{m,max}$ takes into account mortality during the dispersal. Thus the number of dispersal events at each location is given by $\frac{M_m(\mu)m}{1000}$.

Dispersal of BT. Dispersal events for BT include (1) creation of seeds and (2) dispersal of seeds to surrounding areas by wind and birds. We assume that BT dispersal is very low and occurs only if the boxwood is in fairly good condition, meaning that it has sufficient foliage. Thus the dispersal rate of BT depends on the foliage ratio per BT,

ρ

$$M_w(\rho) = \begin{cases} (\omega_w)^{1/\rho} M_{w,max} & \text{if} \quad \rho > 1/3 \\ 0 & \text{otherwise} \end{cases} \tag{8}$$

As such, the initial density of wood in a newly dispersed seedling depends on the parent patch density. Foliage is produced in the next generation after recolonization through the production of leaves by the wood ($r_0 w_n$ in equation (1)). We assume that seeds from a location are transported randomly only in the 8 surrounding cells that has previously contained BT. We only make it possible for an extinct area to be recolonized by surrounding BT, and we make it impossible for BT to colonize new areas.

Theoretical landscape

To investigate the effect of the spatial structure we run our model on a square landscape with various initial size and proportion of boxwood patches. For each landscape, we also calculate an aggregation index by counting the number of pairs (adjacent boxwood patches) in the landscape and dividing it by the maximum number of possible pairs: $2n - |2\sqrt{n}|$, where n is the proportion of boxwood cells [Harary and Harborth, 1976]. For each landscape size and boxwood proportion, we randomly generate 1000 landscapes with possibly different aggregation indices. The final aggregation index equals the difference between the index of the landscape of interest and the average index of the randomly generated landscapes.

Cluster detection is done using the function Matlab® FINDCLU from the File Exchange of MathWorks. To fit the power-law to the cluster-size distribution, we define size-classes of five cells and evaluate the number of clusters in each class.

Parameter estimation

We use three measurement methods to calibrate the model parameters: 1) field measurements, 2) literature review, 3) mesocosm experiment. Some unmeasured parameters are estimated in order to obtain coherence between the simulations, the observations in the field, and the literature.

Fecundity parameter f

Females lay about 300-400 eggs at a time [Kawazu et al., 2010, Wan et al., 2014]. However, the model does not separate males from females, and survival is calculated for caterpillars but not for eggs. The sex ratio seems significantly skewed in favor of males, with only $43\% \pm 10\%$ of the population being females, according to Göttig [2017]. The hatchability rate is about $79.7\% \pm 2\%$ according to Kawazu et al. [2010]. The fertility parameter is therefore estimated with these bibliographic data using the value: f = number of eggs * percentage of female * hatchability rate = 120, with a range from 0 (i.e effects of oophagus predators and parasites) to 300.

Box tree moth survival function and wood consumption function

To determine the survival function according to the pressure for resource μ, the maximum caterpillar survival $S_{m,max}$ is estimated using the bibliographic data. Through lab experimentation, Kawazu et al. [2010] have obtained the following parameters: a larvae survival rate of 78%, a pupation rate of 70%, and an emergence rate of 89%.

Thereby, we estimate $S_{m,max} = 49\%$ which seems appropriate because in this laboratory experiment the caterpillars have not undergone any starvation stress. However, for this function, the second parameter σ_m also has to be set; this parameter is difficult to measure because it has no ecological interpretation. Nonetheless, it is possible to obtain different survival values for different μ in order to make a qualitative adjustment of the survival curve. To do this, we performed a mesocosm experiment from April 4 to late May 2018, located on the University of Savoie Mont Blanc campus, in an isolated grassy area (45°38'30.0"N 5°52'02.7"E). Climatic conditions were close to those of nearby natural boxwood stands. We created a pressure range for the resource by placing varying numbers of caterpillars on the box trees. The range included seven μ values, with four replicas for each and four controls. Each of the 32 boxwood were isolated in cages of 1m^3 covered by mesh (insect proof netting PE 22:30, 920x920; DIATEX, Saint Genis Laval, France) to prevent movement of the larvae between the boxwood. All of the boxwood shrubs came from the same supplier and had received no chemical treatment. They measured 30 cm high and were cultivated in 1 liter pots.

To establish the pressure range, we estimate the parameter α corresponding to the amount of leaves needed by a moth for its larval cycle, for each value of μ. Slansky Jr and Scriber [1982] provide a mean value of ingested food conversion efficiency (ECI) of 20% for herbivorous Lepidoptera. Knowing that ECI = B/I with B being gained mass and I being ingested food, we obtain I through measurements of dry caterpillar masses performed by T. Defferier and E. Tabone from the National Research Institute for Agriculture, Food and Environment (INRAE). Then, using the average dry mass of the leaves, we convert I into the number of leaves (I = 25 leaves). Finally, the number of leaves was counted for each boxwood. Therefore, the value of simulated μ could be determined when a certain number of caterpillars were deposited on a particular box tree. The range used was: $\mu = [2; 1; 0.75; 0.5; 0.25; 0.13; 0.07]$ (see Online Resource 2).

This experimentation also make it possible to calibrate the leaf consumption function. At the end of the experiment, when the surviving larvae had reached the adult stage, we counted the living leaves on the boxwood in order to obtain the percentage of leaves that were consumed. The insect-free controls allowed us to distinguish between mortality caused by caterpillars and mortality due to the environment. The qualitative calibration of the consumption curve is thus established using the consumption percentages as a function of μ.

Wood mortality function

Boxwood mortality by senescence is very low and some boxwood may be over 600 years old. However, box trees attacked by 2 or 3 successive generations may have high probabilities of death [Kenis et al., 2013]. It is necessary to calibrate mortality due to consumption of superficial wood by the late larva stage caterpillars, D_{max}, and notably the parameter d_{max}. Two wild boxwood locations are used to make *in situ* measurements. These boxwood areas are located on the eastern slope of the Epine massif in Savoie (45°38'23.7"N 5°50'43.6"E and 45°41'33.2"N 5°50'56.2"E) at an altitude of 500 and 630 meters, respectively. This massif has large stands of wild boxwood under trees in limestone soil. The peak invasion and defoliation of the boxwood occurred in July and August 2016, and mortality measurements were made in March 2017.

Mortality is assessed in terms of biomass rather than in terms of individuals, using the following procedure: the percentage of living biomass is measured on completely defoliated boxwood according to the level of branching (trunk or branch). For the trunk, the percentage of the total height of the boxwood with shoots (h) is measured, and for branches the percentage of branches with shoots (r), is measured. The mortality d_{max} is estimated by: $d_{max} = 1 - \frac{h+r}{2}$. The measurements made on 101 boxwoods give $d_{max} = 0.74$.

Shoot production parameter

The production of shoots from wood, r_0, is measured by estimating the biomass of shoots produced by wood whose 1) live biomass is estimated and 2) defoliation date is known. First, the average mass of a shoot is measured from 250 shoots. Then, for each measured boxwood (N = 49), the living wood biomass is estimated by considering the trunk as a cone whose volume could be calculated using its circumference and height, with the same calculations made for the branches. This volume, multiply by the density of the wood ($0.95 g.cm^{-3}$), gave the biomass of living wood. We count number of shoots and are able to obtain the biomass of the shoots. Thus, $r_0 = \frac{shoots\ biomass}{wood\ biomass} * \frac{1}{time}$ with *time* being the number of generations since defoliation.

For the 49 boxwoods measured, the amount of new growth varies from 1 to 154 with an average of 45, giving $r_0 = 5 * 10^{-5}$.

Wood growth function

Calibration of the growth function from empirical measurements is performed only for the maximum growth value $r_{w,max}$. For this, a method of dendrometry is used. We have cut some trunk sections with different circumferences (1.5, 2.4, 3.8, 4, 4.9, 5.6, 7.8 centimeters), and we have counted their rings number (respectively 11, 15, 20, 25, 32, 36, 50). We assume that boxwood is a cone whose increase in height is proportional to its increase in width, and its growth is proportional to its density. Thus we can infer the maximal growth rate per year $r_{w,max} = 0.134$ using a linear regression. Thus, the growth per generation in the case of two generations of moth per year is 0.067. We obtain a low estimate because we consider that the growth of individuals is already occurring, but not the formation of new individuals while $r_{w,max}$ takes it into account. From the simulation of the model in the absence of herbivory, and this experimental value, $r_{w,max} = 0.3$ is used to model a consistent boxwood growth rate.

Experimental results

Two functions are calibrated according to the experiment: a function for the consumption of leaves by caterpillars (Figure 2a) and a function for caterpillar survival (Figure 2b). These two functions are dependent on competition for the resource through μ. For the leaf consumption function, we quantify the mortality due to senescence from the difference between the average number of initial and final leaves in absence of moth pressure ($\mu = 0$), and then deduct that from the initial number of leaves for each boxwood. This allows one to express in the results only the proportion of dead leaves due to the action of the caterpillars, but it implies the hypothesis that all boxwood suffer about the same mortality due to senescence. Therefore, the control box trees had 100% of non-consumed leaves.

Leaf consumption reaches a threshold for $\mu = 1$, i.e. when resources present and resources needed are similar, above which the entire resource is consumed. Similarly, it is the threshold at which survival reaches its lowest value and nearly stagnates. The results presented here show survival until the pupal stage, but at the end of the experiment no moths emerge in the box trees when $\mu = 2$, which is why the survival function is set to 0 for $\mu = 2$.

These results are remarkable because they are similar to those expected with a defoliation saturation threshold at $\mu = 1$ and a drastic drop in moth survival. They support our model and minimise the uncertainties that we may have on other parameters.

Local model

Field observations show that when the box tree moth colonizes a patch, its population explodes within a few generations, eventually reaching a peak of density which results in total defoliation of the boxwood stand. At this point no more resources are available and the box tree moth disappears from this patch. We estimate the remaining model parameters in order to reproduce this qualitative behaviour, and to achieve plausible quantitative outputs (these parameters are referred as "estimate" in Table 1).

Figure 3 simulates the invasion dynamics as expected. The boxwood (leaf and wood) starts at its carrying capacity, which is calculated from a simulation without moths, and a single box tree moth is added to the patch. Within six generations, the moth population reaches its peak abundance. During the 7th generation, the ratio μ between the number of leaves needed by the larvae and the available leaves becomes too large and the survival of the moth drops to 0. At this point, the effect on boxwood density is maximal. Leaves are entirely consumed by the early larval stages, which cannot reach their final stages and die from starvation. Still, leaf density does not reach 0 because new leaves grow from wood (at rate $r_0 w$). In a more ecologically accurate representation, the density of the leaves would drop to 0 and then new leaves would only be produced in the next generation, but this would not change the model's outputs. Moreover, this phenomenon is implicitly present since all of the moths in the 7th generations die from starvation and cannot consume the new leaves produced, so it is comparable to a production of new leaves during the next generation. In natural conditions, however, intact boxwood patches will be more likely invaded by a larger number of moths. In the spatial version of the model, dispersal events occur with groups of 1000 individuals due to volatile compounds or other exogeneous attractors, and in that case the peak is reached as early as the 4th generation, and the moth population crashes at the 5th generation.

Although the moth population collapses for realistic parameter values, with different parameters the model allows a positive equilibrium for the three state variables, i.e. the coexistence of moth and boxwood (wood and leaves). We therefore built map of the final model state in function of moth fecundity and moth survival, two key parameters which may vary during the course of the outbreak in Europe. The accommodation of native predators and parasites could indeed reduce the survival rate of caterpillars, and moth fecundity could be reduced by oophagous insects. The final state map (Online Resource 3) clearly shows that coexistence is only possible in a very narrow range of parameters values, which are far from the actual measured values. Two connected patches instead of one can sometimes be enough to favour coexistence in plant-insect interactions [Kang and Armbruster, 2011], but simulations conducted on a two-patch model show only a slight expansion of the coexistence area, which is far from sufficient to lead to coexistence with realistic parameters (Online Resource 3).

Modelling results and discussion

Results for hypothesis 1

Using a spatially explicit model, including local population dynamics and short to long range dispersal events, we show that coexistence of the moth/boxwood system occurs across a wide range of parameters. At a regional scale, dispersal allows box tree moth persistence in a cycle outbreak dynamic [Berryman, 1987], through recurrent recolonization of patches that have been previously defoliated and which have had time to recover. The spatial structure therefore allows coexistence, in line with hypothesis 1a. The coexistence mechanism is similar to the rock-paper-scissors game with the corresponding states: patches of defoliated box tree, patches of box tree with foliage and patches of box tree invaded by the moth. These three states compete with each other following a circular hierarchy, as defoliated box trees 'lose' against box trees with foliage, which are in turn invaded by box tree moths, which finally leads to defoliated box trees. Similar rock-paper-scissors games have been described in other ecological contexts such as polymorphic bacterial strains [Kerr et al., 2002] and plant-mutualist-exploiter systems [Szilágyi et al., 2009].

We also explore moth persistence over a larger range of fecundity and survival parameters than those estimated. Predation on the moth and on the caterpillars is currently low [Kenis et al., 2013], in part because the box tree moth accumulates boxwood alkaloids in its body [Leuthardt and Baur, 2013]. However, native predators may become efficient to feed on the moth following phenotypic plasticity or adaptation [Carlsson et al., 2009]. Native egg parasites like trichograms often used in biological control may also become able to feed on the moth, thereby reducing its fecundity. We find that the moth could rapidly go extinct only for very low fecundity and survival rates (lower-left corners of Figure 4a and f). It is therefore unlikely that the accommodation of native natural enemies will trigger moth extinction.

One step further, hypothesis 1b postulates that long-term coexistence is due to asynchronous dynamics, and that moth extinction is due to the synchronisation of the local dynamics. If we artificially ensure that the invasion begins with a moth in each cell, we observe that all boxwood stands are defoliated simultaneously and that the moth disappears globally in a dynamic of type pulse outbreak [Berryman, 1987]: perfect synchronization indeed leads to moth extinction. But if all stands are initially invaded except a single one, this is enough for the occurrence of desynchronisation, and the whole system becomes viable. The moth can therefore disappear due to perfect synchronization, with 100% of the patches invaded simultaneously. However, any other mechanism that globally reduces drastically the resources may also cause moth extinction. Indeed, with high moth fecundity and survival rates (upper-right corners of Figure 4a and f) the moth depletes the resource until its own extinction. In contrast to the results obtained with *H. spinipennis–A. dieffenbachii* system, our results indicate that global resource depletion is responsible for moth extinction, rather than synchronisation of local dynamics [Johst and Schöps, 2003]. This is in line with the individual-based model of Uchmański [2019], who found that forest insect pests may go extinct when adult fecundity or larvae survival increase. Within the coexistence regime, the average density of moths and the average intensity of the invasion are insensitive to moth fecundity and survival; the moth either persists at the coexistence density or goes extinct (Figure 4).

Interestingly, the moth population can persist even when it periodically invades 99% of the patches (Figure 5 top), provided that leaves grow back fast enough to prevent global resource depletion. In this case the moth invades a significant proportion of the patches even during troughs (about 12%); the cyclic dynamics are therefore getting closer to a permanent outbreak [Berryman, 1987]. The same process occurred in the model of Uchmański [2019], where leaf growth rate was expressed by a parameter defining the number of years needed for their regeneration. In his model, when the leaf growth rate increased the dynamics of the cyclic outbreak was accelerated, with shorter periods between peaks and troughs. The system then transited to a permanent outbreak for very rapid leaf growth rates. On the contrary, a slow leaf growth rate led to the extinction of the insects (Figure 5).

Results for hypothesis 2

We further postulate that, despite local cycles of extinction and recolonization, the coexistence regime is stationary at the landscape scale (hypothesis 2), a phenomenon called statistical stability [De Roos et al., 1991, Holyoak et al., 2005, Amarasekare, 2008]. Instead, we find that the coexistence regime is periodic at the landscape scale (Figure 6a). A similar pattern has been observed in the *H. spinipennis*–*A. dieffenbachii* system [Johst and Schöps, 2003] and in Uchmański [2019]. The global period ranges between 20 generations (high leaf growth rate, Figure 5 top) and 40 generations (low leaf growth rate, Figure 5 bottom). In contrast, the invasion of a local patch lasts 5 generations when 1000 moths are introduced at once, and 7 generations when a single moth colonizes the patch (Figure 3). This discrepancy between the local and global timescales suggests that periodicity at the global scale results from the combination of the local time scale and the pace of dispersal. During peaks, between 60 and 99% of the boxwood patches are simultaneously invaded by the moth, and 1-5% during periods of minimal abundance, depending on parameter values. This corresponds to periodic travelling waves, which have been described in prey-predator systems [Lambin et al., 1998, Sherratt, 2001]. However, such prey-predator systems are locally periodic as well, and long-term coexistence does not require spatial structure. In contrast, in our study system, the periodic waves emerge from the spatial structure, instead of being a mere consequence of local periodicity.

If the mean dispersal distance is very low (1 cell on average, keeping rare long-distance events), the amplitude of the oscillations is also very low (Figure 7b) and the system tends to be statistically stable.

Results for hypothesis 3

Hypothesis 3 posits that asynchronous local dynamics require intermediate dispersal distance [Myers, 1976, Myers and Campbell, 1976], because very limited dispersal might prevent suitable boxwood patches from colonization (3a), whereas very long-distance dispersal may synchronize local dynamics (3b). However, with the measured parameter values we find that the long-term probability of moth persistence is insensitive to dispersal distance. This is shown in Figure 7a, where the measured value for the production of new leaves from wood after total defoliation r_0 equals $5 * 10^{-3}$ (-2.3 on a log scale). In that case, the moths persist whatever the mean dispersal distance is (1, 25 or 70 cells), because boxwood produces new shoots after total defoliation fast enough to enable moth persistence even when the global leaf biomass is low. Meanwhile, previously infected areas produce enough leaves to support another moth outbreak. Conversely, when r_0 equals $2 * 10^{-3}$ (-2.7 on a log scale, which may happen under climatic stress for instance), it turns out that the moth does not persist when the mean dispersal distance equals 70 cells (Figure 6b). The moth initially invades 99% of the patches (Figure 6c) and reaches very high densities (Figure 6d). This reduces the global leaf biomass (Figure 6e) and the moth eventually collapses due to resource depletion. In the case of coexistence (Figure 6a) the maximal % of invaded patches is around 60-70%, the maximal moth density is 3 times lower and the minimal leaf biomass is 5 times higher than in the extinction case.

We also find that when the mean dispersal distance is very short (1 cell on average) the probability of moth persistence is not affected by the offshoot production rate. Because of short-distance dispersal, the moth does not generate periods of global invasion and intact patches are always present at the border of its slow moving invasion front. In that case, relatively high offshoot production rates are unnecessary as the moth do not rely on the new growth of recently defoliated patches. In contrast, when the average dispersal distance is larger (e.g. 25 and 70 cells), the probability of persistence increases with the offshoot production rate (Figure 7a). In such cases, the moth needs to recolonize recently defoliated patches because during peaks a large proportion of patches are defoliated at the same time. Therefore, relatively high offshoot production rates are necessary to avoid global over-exploitation.

The influence of the mean dispersal distance on moth persistence is therefore studied with a relatively low offshoot production rate, $r_0 = 2 * 10^{-3}$. As expected by hypothesis 3b, frequent long-distance dispersal events lead to the extinction of the moth due to global resource depletion (Figure 7b, continuous line). This effect of long-distance dispersal was not present in Uchmański [2019], this can be explained to the use of a thin-tailed Gaussian kernel characterized by very rare long-distance dispersal events, thus insect pests could not reach the distant trees which had time to regenerate after their last defoliation.

Furthermore, hypothesis 3a posits that the moth goes extinct in the case of limited dispersal, because it would not be able to escape over-exploited patches. However, the fat-tailed dispersal kernel prevents such phenomenon: even when the mean dispersal distance is very low (1 cell), the moth can persist thanks to frequent long-distance dispersal events. Things change when we constrain dispersal to a uniform distribution, which ranges between 1 cell and a given maximum of cells. In that case, when the maximum number of cells is low enough (up to 4 cells), the moth invasion can get stuck in a landscape dead end and it disappears because of local resource depletion, and not global resource depletion (Figure 7b, dotted line). Prey-predator systems subject to limit cycles was also stabilized by limited dispersal in the individual-based model of Cuddington and Yodzis [2000], where limited dispersal reduced the average predation rate and thereby avoided local instability. However, if dispersal is too limited the consumer can go extinct because of a drastic reduction in the rate of predation, as is the case in our model when long distance dispersal events are extremely rare due to uniform dispersal kernel (Figure 7b, dotted line).

The results obtained using the fat-tailed dispersal seems the most plausible, indeed rare long-distance dispersal events mediated either by wind or by human dispersal likely occur in the case of the box tree moth. With a fat-tailed dispersal kernel, multiple invasion fronts are created far away from invaded patches because long-distance dispersal events are frequent [Shaw, 1995]. This created a fragmented landscape of defoliated and intact boxwood, in which the moth does not end up in a dead end. Such a fragmented invasion front can be observed in Europe. The moth was first observed in Germany in 2006/2007; in the same year it spread to Switzerland and the Netherlands. It then spread to France [Feldtrauer et al., 2009] and the United Kingdom [Salisbury et al., 2012] in 2008, to Austria in 2009, to Italy [Bella, 2013] in 2010, and to Portugal, Iran and Armenia in 2016 [Bras et al., 2019]. Long-distance dispersal might be due to the boxwood trade between European countries, and probably to a much lesser extent by the natural dispersal of moths. We therefore expect that in practise only frequent long-distance dispersal can lead to the extinction of the moth, due to global resource depletion.

Results for hypothesis 4

Next, we predict that the coexistence regime depends on the landscape characteristics, in particular its size (4a) and the proportion of suitable boxwood patches (4b). To do so, we use wrapped landscapes (with no edge effect) of different sizes and different proportions of randomly distributed suitable patches (Figure 8a). Below 200*200 cells, which corresponds to about 12 000 km^2, coexistence does not occur within the realistic range of parameter values, because previously defoliated patches are quickly recolonized by the moth and lack time to grow back. This induces a global resource collapse and drives the moth to extinction. Above the 200*200 threshold, the larger the landscape is, the more likely the coexistence occurs, in line with hypothesis 4a. In the previous sections, we restrict our model to the French Alps, but we expect that long term coexistence is even more likely on the European scale because larger landscapes favor coexistence. The influence of landscape size is also apparent in the real landscape, with a uniform and short-range dispersal kernel: when the invasion begins in a relatively isolated area of the landscape, coexistence is impaired by small size.

A priori, the effect of the initial proportion of boxwood patches on coexistence is unclear (4b) because on the one hand a higher proportion of suitable patches provides more resources to the moths, while on the other hand it may trigger moth outbreaks which ultimately leads to resource depletion. We find that the latter mechanism is on the driver's seat: reducing the proportion of boxwood patches increases the probability of moth persistence (Figure 8a). More precisely, the landscapes larger than 400*400 cells filled with less than 20% of boxwood patches almost always allow coexistence. In such cases, most dispersal events fail to find suitable patches, lowering the moth population density, which in turn leaves more time for leaves to grow back. On the contrary, a high proportion of suitable patches results in high moth densities which leads to global over-exploitation, despite a potentially higher leaf biomass.

The coexistence regime has interesting consequences on the final proportion of boxwood patches, which corresponds to the initial proportion minus the proportion of patches which wither completely due to over-exploitation. Under coexistence, the final proportion increases linearly with the initial proportion with a weak slope of about 0.1, whereas the slope is close to 1 in the case of moth extinction (Figure 8b). This indicates that the local extinction of boxwood patches is not responsible for global moth extinction. Instead, the final proportion of boxwood patches is a long-term consequence of coexistence and results from their gradual death (Figure 8c). During each moth outbreak, a small proportion of the boxwood patches disappears due to over exploitation. Then, right after the outbreak a few boxwood patches are recolonized from neighbouring patches (only previously occupied patches can be recolonized), which induces a clustered distribution of the boxwood patches. As a result of clustering, the aggregation index is always positive, which indicates that the landscapes created by long-term coexistence are more aggregated than random landscapes. Boxwood patches relatively isolated in the initial landscape experience larger extinction rates and create holes in the landscape. In contrast, areas where boxwood patches are initially more abundant persist more often, which creates clusters. Moreover, the aggregation increases with the average moth dispersal distance (Figure 8d). Boxwood patches favor moth outbreaks: increasing the boxwood patches proportion over the landscape produces severe outbreaks. This induces apparent competition between boxwood patches because of their shared pest. With low dispersal distance, apparent competition between patches is mainly local, which limits the formation of clusters. Instead, with high dispersal distance apparent competition is global and the aggregated pattern results from the interplay between local facilitation (recolonization of boxwood patches is purely local) and global competition, as in many spatially self-structured systems [Kéfi et al., 2007, 2008]. This is confirmed by simulations where boxwood recolonization is global, in that case the aggregation process vanishes (details not shown).

We further explore how the aggregation process creates boxwood clusters of different sizes, for various dispersal distance. To do so, we start with landscapes which are initially filled with boxwood patches, and run simulations after invasion by the moth. At the end of the simulations, we fit a power-law model to the final distribution of the cluster sizes (Figure 9 top). Clusters smaller than 5 boxwood patches are excluded from the fit. We find that small dispersal distance leads to a cluster size distribution closer to a power-law than large dispersal distance. When the dispersal distance is large (10 to 50 cells), the cluster size distribution follows a truncated power law (Figure 9 top), which indicates that large clusters are under-represented. Large dispersal distance leads to an increase of herbivory, which produces two distinct effects. On the one hand, it favors aggregation due to global apparent competition, as discussed earlier (Figure 8d). On the other hand, it increases the death rate of boxwood patches and thus reduces the final proportion of patches in the landscape (Figure 8e). This is why under large dispersal distance (10 to 50 cells) the final landscapes has a homogeneous aspect of equally spaced small clusters (Figure 9 bottom).

These regular patterns are similar to Turing instabilities [Turing, 1990, Murray, 2001] and result from "scale-dependent feedbacks" which combine short-distance positive feedbacks and long-distance negative feedbacks [Rietkerk and van de Koppel, 2008]. In the present case, short-distance positive feedback correspond to local facilitation of boxwood due to recruitment while apparent competition between boxwood stands because of their shared pest mirror long-distance negative feedbacks. Several studies have investigated how spatial patterns can emerge from such scale-dependent feedbacks in a variety of ecological scenarios, such as plant-water interactions [Klausmeier, 1999, von Hardenberg et al., 2001, Rietkerk et al., 2002, Meron et al., 2004, Kéfi et al., 2010], plant-plant interactions [Lejeune et al., 1999], or predator-prey interactions [Levin and Segel, 1976, Solé and Bascompte, 2012]. It has been shown that such spatial patterns emerge in predator-prey systems when the predator has a larger dispersal capacity than the prey [Gurney et al., 1998, de Roos et al., 1998]. We demonstrate here that this can also be the case in the context of a plant-herbivore system, using a model calibrated empirically.

Implications for management

First, the most important finding for management purposes is that the moth heavily impacts boxwood stands. With the estimated parameter values, we find that in the study area only 15% of the initial boxwood biomass remains (Figure 4b) and that 48% of the original boxwood patches completely disappear (Figure 4c), which represents 2414 square kilometres in the French Alps. Under low moth fecundity and high caterpillar survival, the moths could persist longer in heavily defoliated patches. The severe decrease in box tree biomass can impact the many species associated with boxwood, as well as the ecosystem services provided by the shrub (i.e sediment trapping and water storage) [Mitchell et al., 2018]. In stands where boxwood is severely weakened or extinguished, recolonization by neighbouring patches may be prevented by pioneer plants, potentially other invasive species such as *Buddleja davidii* or *Ailanthus altissima*, in a kind of 'invasion meltdown' process [Simberloff and Holle, 1999].

Next, the periodic invasion dynamics can lead to confusion regarding the persistence of the box tree moth. A period of low overall abundance should not be confused with a decrease in invasion, and moth control methods should take periodic invasion dynamics into account. Remote sensing methods may be appropriate in order to detect the few boxwood stands that provide refuge under low moth abundance [Kerr and Ostrovsky, 2003]. We suggest that detecting stands of undefoliated boxwood that allow moth persistence during a period of low abundance could provide an interesting management strategy, since control efforts could be increased on these particular patches.

Finally, management actions might consider preventing anthropogenic long-distance dispersal. However, we find that only very limited dispersal could lead to moth extinction, which occurs with a uniform distribution of dispersal events of no more than 4 cells (Figure 7b, dotted line). As soon as dispersal is higher, the moth could escape dead ends in the landscape and therefore persists. Even if anthropogenic long-distance dispersal is prevented, a few natural long-distance dispersal events might ensure moth persistence. It is therefore unlikely that management actions limiting dispersal can be able to eradicate the moth. However, such actions can reduce the impact on boxwood stands, since we find that long-distance dispersal increases the extinction rate of boxwood patches (Figure 8e).

Three scenarios may occur after the invasion of box tree moth in Europe: extinction of both species, extinction of the moth only, or coexistence. Our theoretical approach combined with field and experimental data suggests that coexistence is the most likely outcome, with cycles of moth outbreaks and crashes. Coexistence comes along with a severe reduction of boxwood biomass at the landscape scale: boxwood stands may therefore become closer to brown than green. Moth extinction can also occur, which indicates that the invasion dynamics of exotic pests can be mitigated even in the absence of predators and effective plant defenses.

We further show that plant-herbivore coexistence through spatial effects does not require poorly mobile wingless species, as in our model a wide range of dispersal values result in coexistence. Coexistence occurs in large landscapes, long-distance dispersal thus requires a spatial scaling-up for the persistence of the system. Particularly intense long-distance dispersal nevertheless leads to herbivore extinction, provided that plant grows back slowly. In that case, the herbivore depletes its resources at the global scale, which leads to its own extinction even without a complete synchronization of the local dynamics. Finally, coexistence is easier in patchy landscapes because unsuitable patches increase moth mortality during dispersal and thereby reduce the global insect population size. Interestingly, when plants disperse locally the spatial dynamics of the system lead to the formation of such a patchy landscape, with relatively small plant patches evenly distributed in the landscape. The system thus creates its own stability conditions.

Acknowledgements

- We thank all the student interns who participated in both field and experimental work: Aristide Chauveau, Alison Dilien, Jessica Barbe and Océane Guillot. We also thank Elisabeth Tabone and Thomas Defferier (INRAE) for their mass measurements on their farmed caterpillars, and Audrey Bras (INRAE) for the flight distance data and fruitful exchanges.
- This article is financially supported by AAP USMB and FREE federation. The PhD scholarship of L. Ledru is funded by the French Ministry for Education and Research. J. Garnier acknowledges NONLOCAL project (ANR-14-CE25-0013), GLOBNETS project (ANR-16-CE02-0009) and the European Research Council (ERC) under the European Unions Horizon 2020 research and innovation programme (grant agreement no. 639638, MesoProbio).

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Tables

Table 1: Model parameters. The values correspond to those most representative of actual ecological conditions. The parameters are either measured quantitatively, i.e. a direct value of the parameter concerned is measured, or qualitatively, i.e. the measurement of a process allows the calibration of the associated parameter. We estimate the unmeasured parameters from the model simulations, and aim to be consistent with the ecological situation. The parameters obtain from the literature come from : f [Kawazu et al., 2010, Wan et al., 2014], α [Slansky Jr and Scriber, 1982], $S_{m,max}$ [Kawazu et al., 2010]. The source listed as "experiment" corresponds to the measurements of moth weights made by the INRAE for α, and the mesocosm experiment for σ_m, σ_l and $S_{m,max}$. "Flight carousel experiment" corresponds to the measurements made by Bras et al. from the INRAE.

	Settings	**Measured**	**Values**	**Unit**	**Meaning**	**Source**
Leaves	v	No	0.98	$\frac{1}{t}$	Leaf survival rate at senescence	estimate
	r_f	No	0.4	$\frac{1}{t}$	Leaf growth rate	estimate
	L_{max}	No	$\frac{1}{3}W_{max}$	$g.ha^{-1}$	Leaf carrying capacity	estimate
	r_0	Quantitative	$5 * 10^{-3}$	$\frac{1}{t}$	Offshoot production rate	field
	σ_l	Qualitative	0.01	-	Consumption function setting	experiment
Wood	W_{max}	No	$3 * 10^{9}$	$g.ha^{-1}$	Wood carrying capacity	estimate
	d_{max}	Quantitative	0.74	-	Saturation value of the maximum mortality function $D_{max}(\rho)$	field
	β_s	No	10	-	Setting of the wood mortality function by consumption (curvature)	estimate
	θ_s	No	1.2	-	Setting of the wood mortality function by consumption (inflection point)	estimate
	β_r	No	5	-	Setting of the wood growth function (curvature)	estimate
	θ_r	No	$5 * 10^{-5}$	-	Setting of the wood growth function (inflection point)	estimate
	$r_{w,max}$	Qualitative	0.3	-	Saturation value of the wood growth function	field
	$r_{w,min}$	No	1	-	Saturation value of the growth deficit function γ_0	estimate
	d	No	0.95	-	Setting of the growth deficit function γ_0	estimate
	ω_1	No	0.1	-	Setting of the wood dispersal function	estimate
	ω_{max}	No	$1 * 10^{-5}$	-	Maximum proportion of wood that can contribute to dispersal	estimate
Box tree moth	f	Quantitative	120	individual	Box tree moth fecundity	literature
	α	Quantitative	0.3	g	Amount of leaf needed by a box tree moth for its larval cycle	literature and experiment
	σ_m	Qualitative	0.85	-	Setting of caterpillar survival function	experiment
	$S_{m,max}$	Quantitative	0.49	$\frac{1}{t}$	Maximum caterpillar survival rate	literature and experiment
	s	No	0.4	$\frac{1}{t}$	Survival rate of adults (moths)	estimate
	$M_{m,max}$	No	0.01	$\frac{1}{t}$	Survival rate of adults during dispersal	estimate
	δ	No	0.01	-	Parameter of the dispersal function	estimate
	c	Qualitative	0.5	-	Tail shape parameter of the Exponential power distribution	flight carousel experiment
	α_d	Quantitative	25	cells	Average dispersal distance of the Exponential power distribution	flight carousel experiment

Figure legends

Fig. 1 Model of dynamics between the boxwood, separated into wood and leaves, and the box tree moth. The arrows show the interaction between the three variables

Fig. 2 Main results of mesocosm manipulation with measurement of defoliation intensity and box tree moth survival according to competition for the resource μ. (a) leaf consumption function $\frac{S_l(\mu)}{v}$. (b) box tree moth survival function $S_m(\mu)$.

Fig. 3 Visualization of invasion dynamics in the local model. Simulation with ecologically realistic parameters given in Table 1

Fig. 4 Final state maps in the real landscape in function of fertility f and maximum survival $S_{m,max}$. (a) landscape-scale probability of moth persistence, (b) landscape-scale wood biomass expressed as a percentage of the landscape-scale carrying capacity, (c) number of boxwood patches disappearing as a percentage of the initial number of boxwood patches, (d) landscape-scale moth biomass, (e) number of patches invaded as a percentage of the number of boxwood patches present, (f) time of moth persistence. The ecologically realistic parameter values are $f = 120$ and $S_{m,max} = 0.5$.

Fig. 5 Effect of the leaf intrinsic growth rate on the mean percentage of invaded patches. The percentage drop to zero when the moth do not persist in these conditions (when $r_f < 0.22$). The two inserts show the invasion dynamics for two growth rate values.

Fig. 6 Example of global population dynamics in the case of coexistence (a) and moth collapse (b). (c) maximum % of invaded patches. (d) maximum moth biomass. (e) minimum leaf biomass. Parameters values as in Table 1, except for r_0=$2 * 10^{-3}$ and for the average dispersal distance α_d which either equals 5 cells (moth persistence) or 70 cells (moth collapse)

Fig. 7 (a) Effect of the rate of new leaves production by the wood (r_0) on the probability of moth persistence. For each tested value, the probability of persistence is obtained by 50 simulations conduct on the realistic landscape with random initial patch of invasion. Three average dispersal distances are tested, a realistic distance of 25 cells, a very short distance of one cell, and a very large distance of 70 cells. (b) Effect of the average dispersal distance on the probability of moth persistence. For each tested value, the probability of persistence is obtained by 50 simulations conduct on the realistic landscape with random initial patch of invasion. Each time two dispersal functions are tested: a fat-tailed function, and an uniform function. The minimum dispersal distance is one cell. The inserts show the percentage of patch invaded over time for three selected average dispersal distances of 1, 5 and 70 cells with the fat tail dispersal function.

Fig. 8 Simulation in theoretical landscapes. (a) The probability of moth persistence depends on space size and on the initial proportion of boxwood patches. (b) In the case of coexistence, the final proportion of boxwood patches is much lower than the initial proportion because moth outbreaks cause patch extinctions. (c) The boxwood proportion in the landscape declines during each moth outbreak. (d) The aggregation index increases along with the average dispersal distance. (e) In coexistence, increasing the dispersal distance reduces the final proportion of boxwood patches in the landscape. All other parameter values are set to the realistic values.

Fig. 9 Effect of moth dispersal distance (increasing from left to right) on the size distribution of boxwood clusters at the end of the simulations (5000 time steps), in large theoretical landscapes of 550*550 cells. Top: regression lines correspond to the fit to a power-law distribution. The first size class (black square) has been excluded from the regression. Bottom : snapshot of the landscape at the end of the simulation, black cells indicate live boxwood patches. All other parameter values are set to the realistic values.

Figures

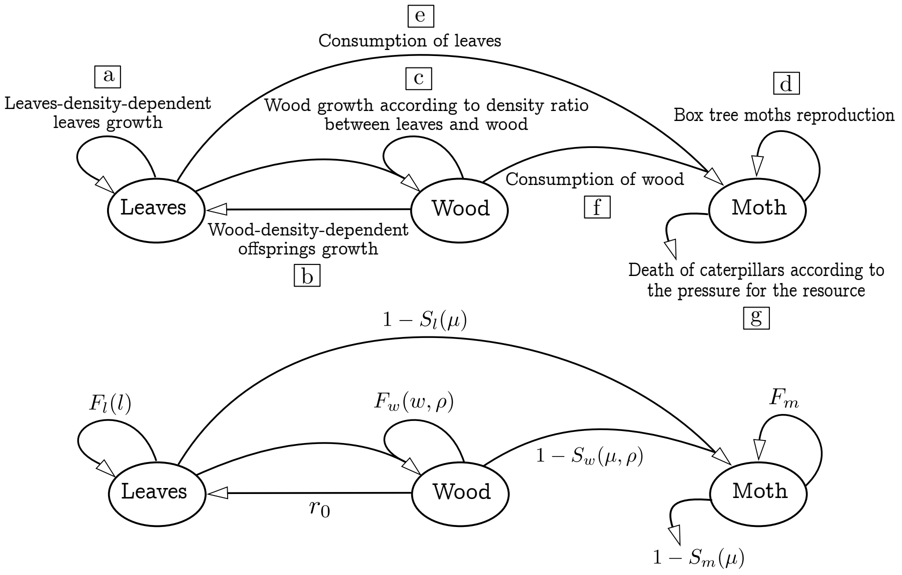

Figure 1

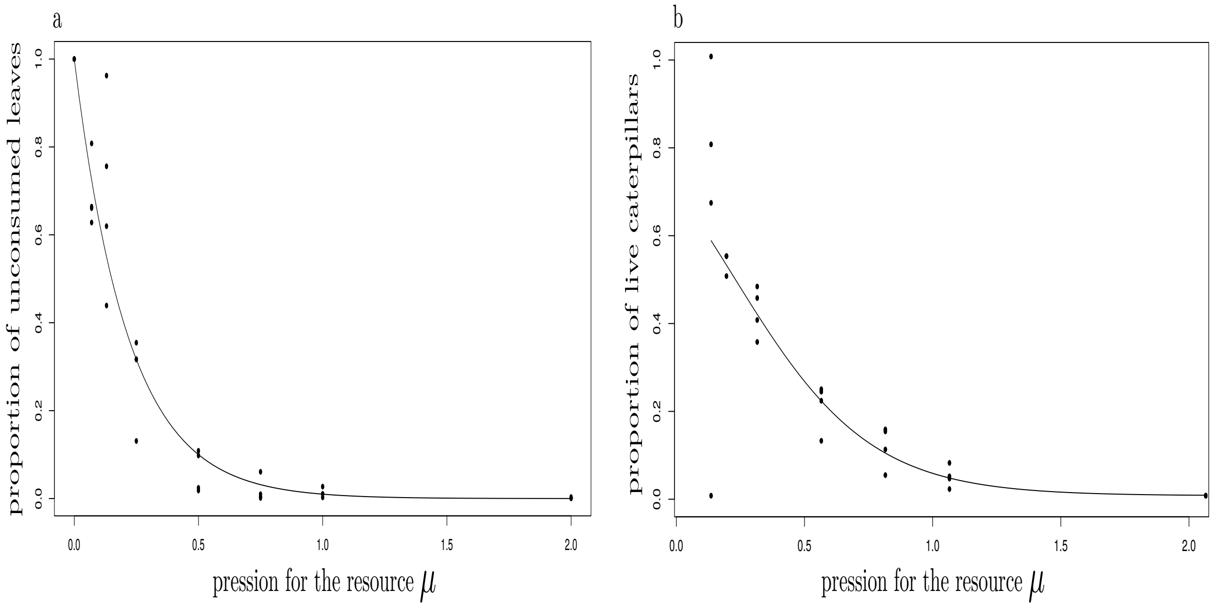
a
proportion of unconsumed leaves
0.0
0.2
0.4
0.6
0.8
1.0
0.0
0.5
1.0
1.5
2.0
pression for the resource μ
b
proportion of live caterpillars
0.0
0.2
0.4
0.6
0.8
1.0
0.0
0.5
1.0
1.5
2.0
pression for the resource μ

Figure 2

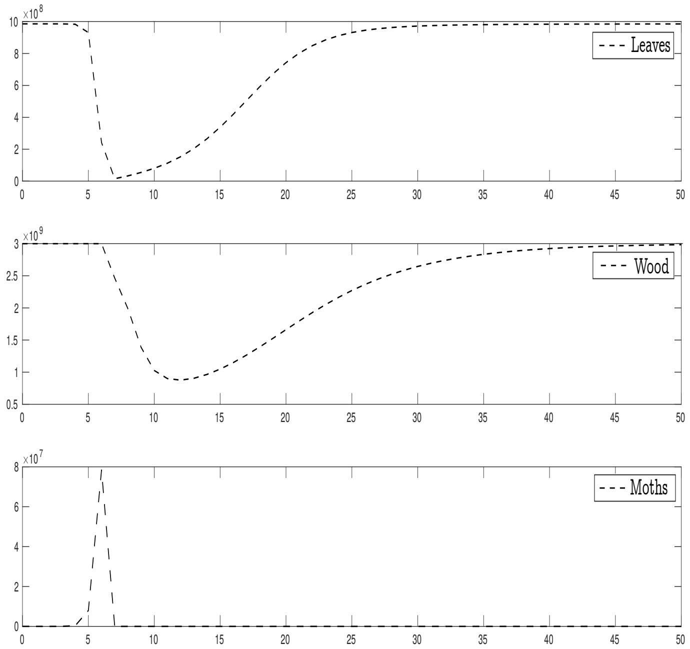
×10^8
10
8
6
4
2
0
Leaves
×10^9
3
2.5
2
1.5
1
0.5
Wood
×10^7
8
6
4
2
0
Moths
0
5
10
15
20
25
30
35
40
45
50

Figure 3

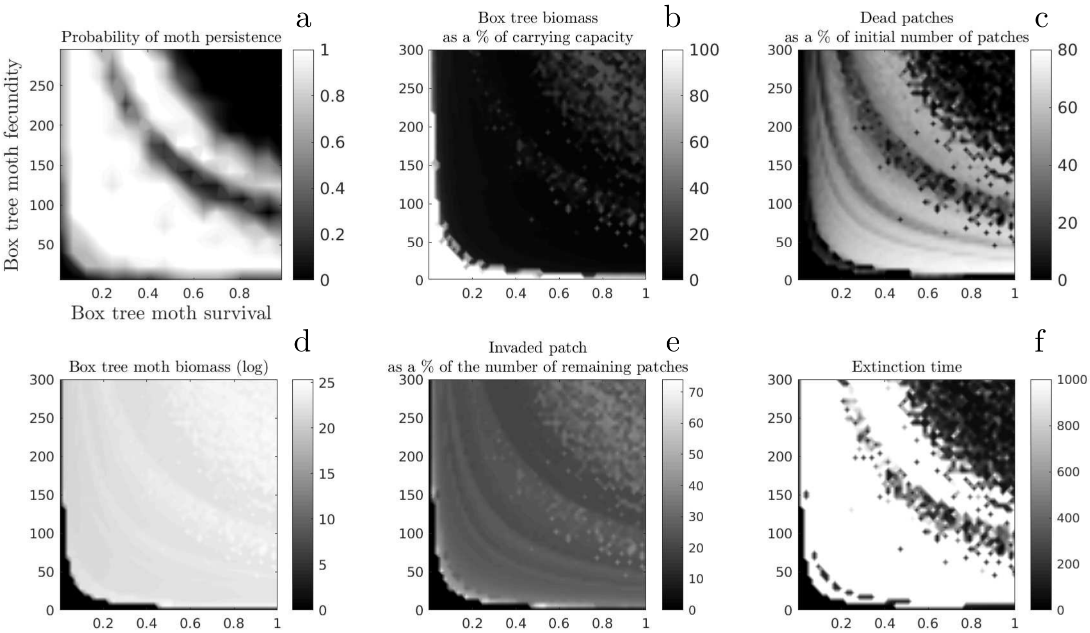
a
Probability of moth persistence
Box tree moth fecundity
Box tree moth survival
50
100
150
200
250
0.2
0.4
0.6
0.8
0
0.2
0.4
0.6
0.8
1
b
Box tree biomass
as a % of carrying capacity
0
20
40
60
80
100
c
Dead patches
as a % of initial number of patches
0
20
40
60
80
d
Box tree moth biomass (log)
0
5
10
15
20
25
e
Invaded patch
as a % of the number of remaining patches
0
10
20
30
40
50
60
70
f
Extinction time
0
200
400
600
800
1000
300

Figure 4

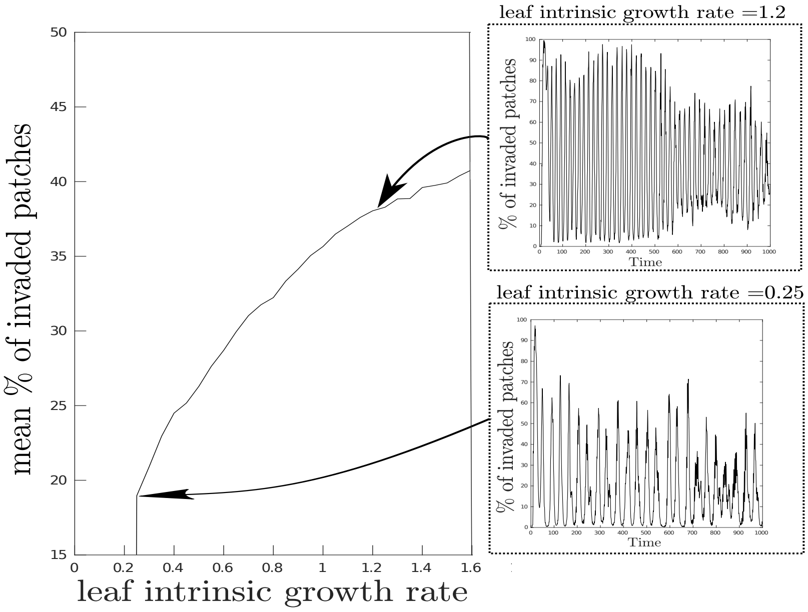
mean % of invaded patches
50
45
40
35
30
25
20
15
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
leaf intrinsic growth rate
leaf intrinsic growth rate =1.2
% of invaded patches
Time
leaf intrinsic growth rate =0.25
% of invaded patches
Time

Figure 5

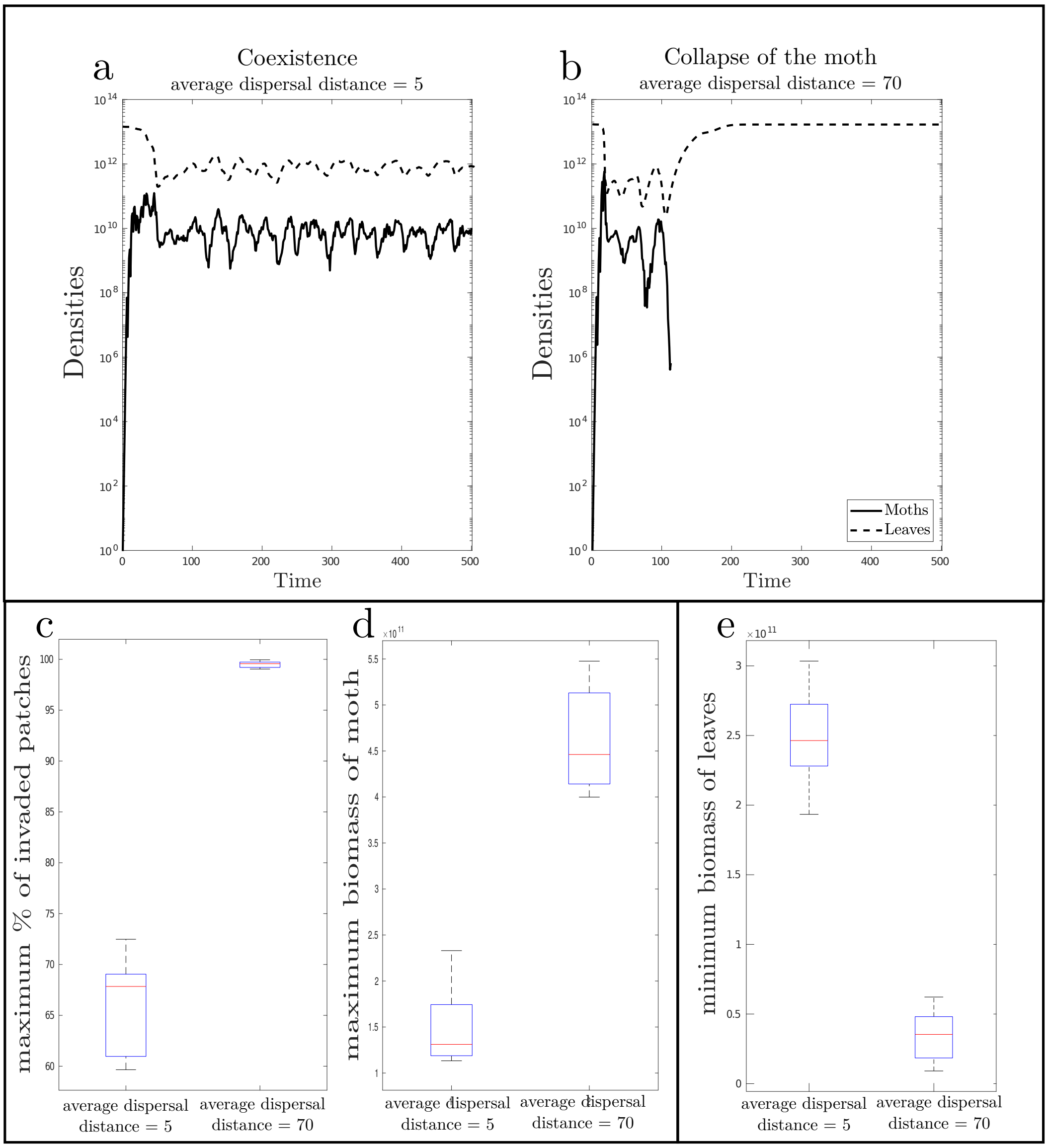
a
Coexistence
average dispersal distance = 5
b
Collapse of the moth
average dispersal distance = 70
Densities
10^{0}
10^{2}
10^{4}
10^{6}
10^{8}
10^{10}
10^{12}
10^{14}
0
100
200
300
400
500
Time
Moths
Leaves
c
maximum % of invaded patches
60
65
70
75
80
85
90
95
100
d
maximum biomass of moth
$\times 10^{11}$
1
1.5
2
2.5
3
3.5
4
4.5
5
5.5
e
minimum biomass of leaves
$\times 10^{11}$
0
0.5
1
1.5
2
2.5
3
average dispersal distance = 5
average dispersal distance = 70

Figure 6

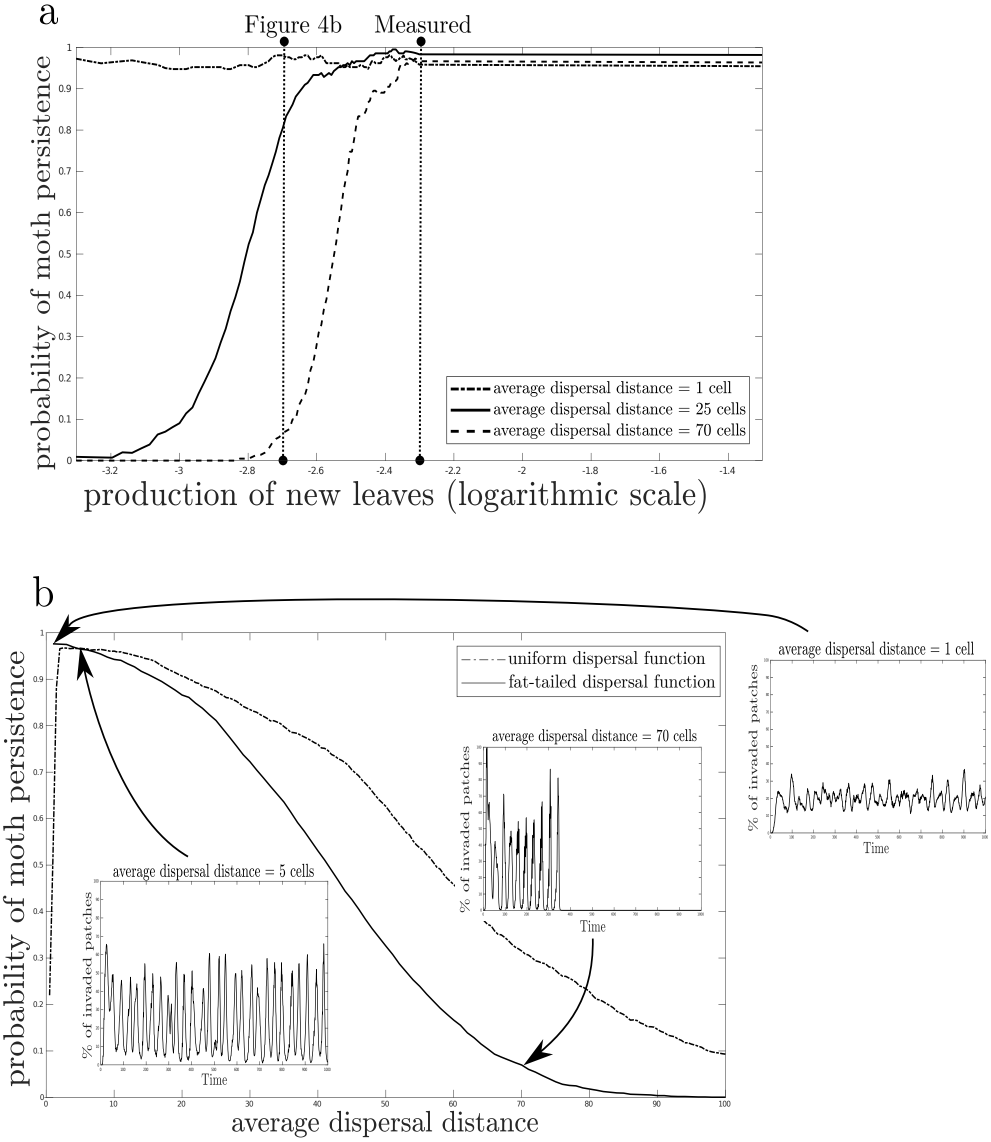
a
Figure 4b
Measured
probability of moth persistence
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
-3.2
-3
-2.8
-2.6
-2.4
-2.2
-2
-1.8
-1.6
-1.4
average dispersal distance = 1 cell
average dispersal distance = 25 cells
average dispersal distance = 70 cells
production of new leaves (logarithmic scale)
b
probability of moth persistence
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
10
20
30
40
50
60
70
80
90
100
uniform dispersal function
fat-tailed dispersal function
average dispersal distance = 1 cell
average dispersal distance = 70 cells
average dispersal distance = 5 cells
% of invaded patches
Time
average dispersal distance

Figure 7

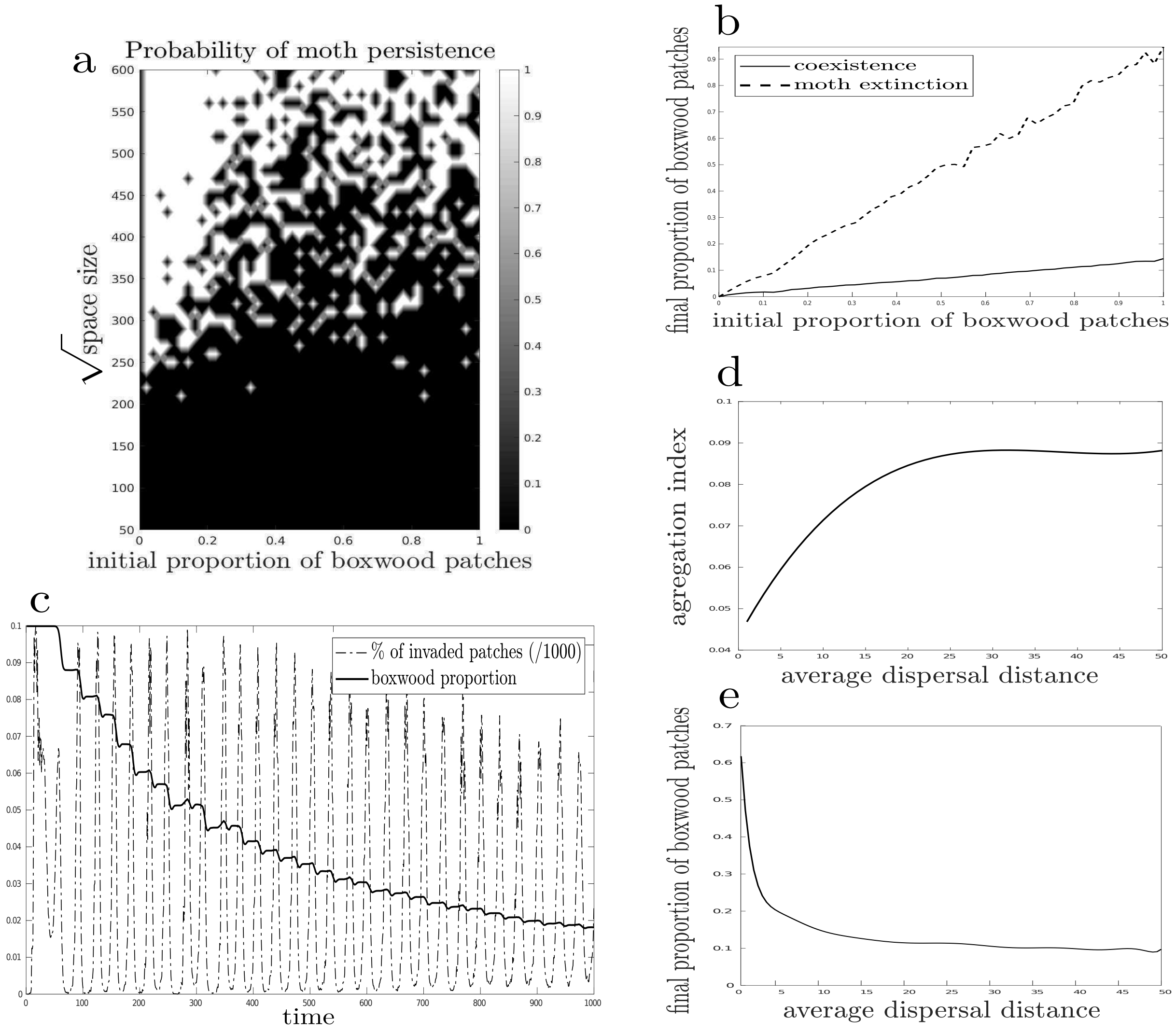
a
Probability of moth persistence
√space size
600
550
500
450
400
350
300
250
200
150
100
50
0
0.2
0.4
0.6
0.8
1
0.9
0.7
0.5
0.3
0.1
initial proportion of boxwood patches
b
final proportion of boxwood patches
coexistence
moth extinction
initial proportion of boxwood patches
c
% of invaded patches (/1000)
boxwood proportion
time
0
100
200
300
400
500
600
700
800
900
1000
0.01
0.02
0.03
0.04
0.05
0.06
0.07
0.08
0.09
0.1
d
agregation index
0.04
0.05
0.06
0.07
0.08
0.09
0.1
average dispersal distance
5
10
15
20
25
30
35
40
45
50
e
final proportion of boxwood patches
0.1
0.2
0.3
0.4
0.5
0.6
0.7
average dispersal distance

Figure 8

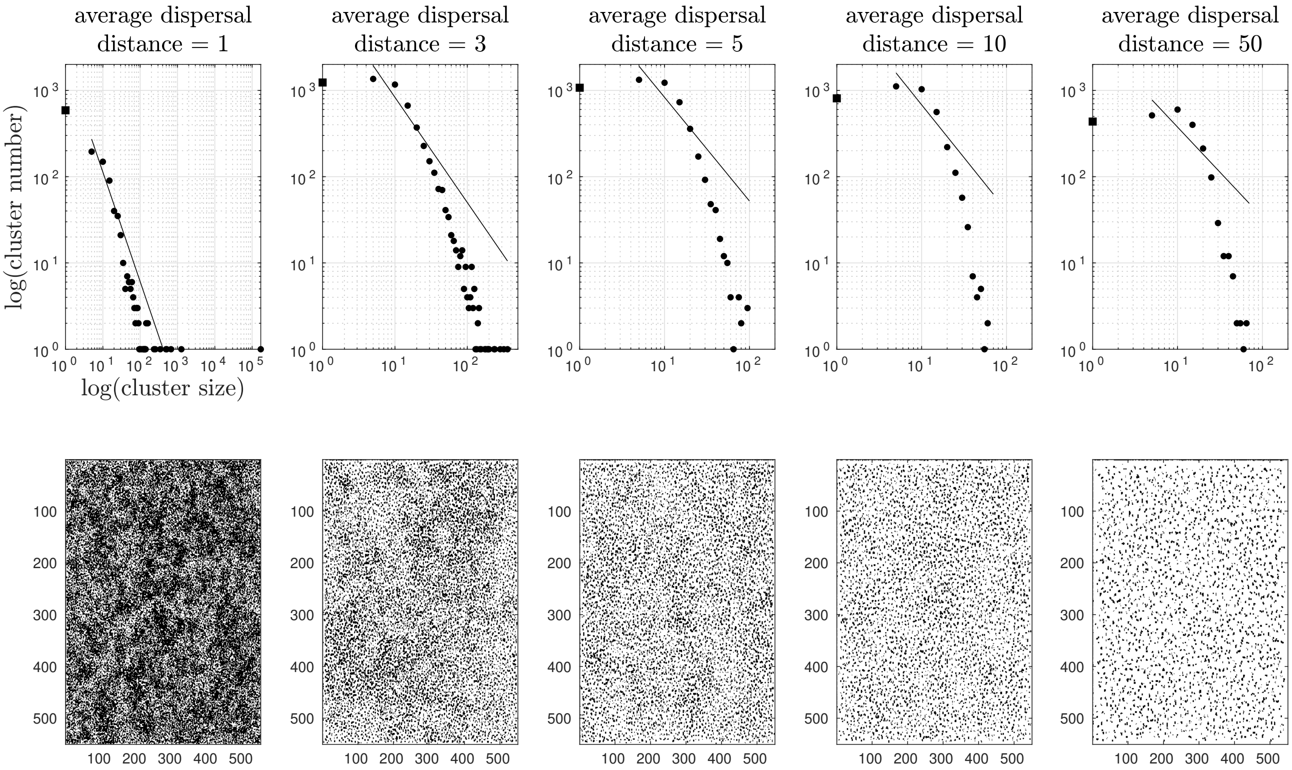
average dispersal distance = 1
average dispersal distance = 3
average dispersal distance = 5
average dispersal distance = 10
average dispersal distance = 50
log(cluster number)
log(cluster size)
10^0
10^1
10^2
10^3
10^4
10^5
100
200
300
400
500

Figure 9