

Landscape diversity slows the spread of an invasive forest pest species

Thibaud Rigot, Inge van Halder and Hervé Jactel

T. Rigot (thbdrgt@yahoo.fr), I. van Halder and H. Jactel, INRA, UMR 1202 BIOGECO, FR-33610 Cestas, France, and Univ. Bordeaux, BIOGECO, UMR 1202, FR-33400 Talence, France. TR also at: CIRAD, UMR 1062 CBGP, CS 30016, Campus International de Baillarguet, FR-34988 Montpellier-sur-Lez cedex, France.

According to the associational resistance hypothesis, diverse habitats provide better resistance to biological invasions than monocultures. Host-plant abundance has been shown to affect the range expansion of invasive pests, but the effect of landscape diversity (i.e. density of host/non-host patches and diversity of forest habitat patches) on invasions remains largely untested. We used boundary displacement models and boosted regression tree analyses to investigate the effects of landscape diversity on the invasion of Corsica by the maritime pine bast scale *Matsucoccus feytaudi* over an 18-yr period. Taking the passive wind dispersal of the scale into account, we showed that open habitats and connectivity between host patches accelerated spread by up to 13%, whereas landscapes with high tree diversity and a high density of non-host trees decreased scale spread by up to 14%. We suggest a new mechanism for such associational resistance to pest invasion at the landscape level, which we term ‘the pitfall effect’.

Biodiversity provides multiple ecosystem services (Millennium Ecosystem Assessment 2005, Balvanera et al. 2006, Cardinale et al. 2012). In particular, it contributes to the control of emerging infectious diseases (Keesing et al. 2010), in some cases limiting the establishment and/or impact of invasive pest species (Melbourne et al. 2007, but see also Sax 2002 or Gilbert and Lechowicz 2005). Indeed, depending on the spatio-temporal scale considered, biodiversity and biological invasions may be either positively or negatively correlated (Clark et al. 2013).

Although this ‘invasion paradox’ remains a matter of debate, a growing body of evidence suggests that forest pest damage can be limited by increasing the diversity of tree species (Jactel and Brockerhoff 2007, Vehviläinen et al. 2007, Castagneyrol et al. 2013a). Overall, a focal tree species grown in a mixed stand with non-host trees is more resistant to insect herbivores than the same tree species grown as a monoculture, in accordance with the associational resistance hypothesis (Barbosa et al. 2009). Two main mechanisms have been proposed to explain associational resistance. First, solitary host trees dispersed among non-host neighbours are less likely to be detected and colonised by insects (Jactel and Brockerhoff 2007), because of visual and semiochemical disruption of host finding (Jactel et al. 2011, Castagneyrol et al. 2013b). Second, more diverse plant communities can provide natural enemies with complementary food resources and shelter against adverse conditions, thereby increasing their capacity to control insect herbivores (Root 1973).

These two mechanisms have been studied principally at the stand scale. However, they may also operate at the landscape scale. Invasive species have to move through mosaics

of different patches of forest, grassland and crops to colonise new host trees, and the presence of non-host habitats may act as a barrier to spread (Jules et al. 2002, Mundt et al. 2011) or host colonization (Zhang and Schlyter 2004). Mosaics of diverse habitat patches also benefit natural enemies of pest insects (Gardiner et al. 2009, Rand et al. 2012). In particular, habitat complementation – i.e. the combined presence of different types of habitat patches providing non-substitutable complementary resources to organisms (Dunning et al. 1992, Dulaurent et al. 2011) – is critical for the maintenance of stable populations in many species, including predator species. For instance, the Eurasian hoopoe *Upupa epops*, requires a combination of three different types of land cover – pine forests, oak woodlands and grasslands – to build up its populations, thereby improving predation on the pine processionary moth (Barbaro et al. 2008).

In this study, we investigated whether landscape diversity also provides associational resistance to invasive pests, i.e. lower invasibility. In particular, we tested the hypothesis that landscape diversity can slow the spread of invasive species in forest. We estimated landscape diversity from both the number (= cover type richness) and the relative abundance (= cover type evenness) of different types of land cover (i.e. landscape compositional heterogeneity according to Fahrig et al. 2011). We also considered the spatial configuration of these land cover types (i.e. landscape configurational heterogeneity, Fahrig et al. 2011). Several studies have reported that the abundance and rate of spread of different invasive forest insects are affected by the relative abundance of host trees at the landscape level (Sharov et al. 1997b, 1999, Gilbert et al. 2005, Morin et al. 2009, but see Morin et al. 2007), but

none of these studies directly investigated the effect of landscape diversity. We are also unaware of any empirical model of the spread of an invasive forest insect taking landscape diversity into account.

Here we consider the invasion of Corsican forests by the maritime pine bast scale *Matsucoccus feytaudi* (Hemiptera: Matsucoccidae) between 1995 and 2012. We had several reasons for choosing this system, the most important of which relate to the life history traits of this species. Maritime pine bast scale is strictly monophagous on maritime pine *Pinus pinaster*, and the local effect of tree diversity on associational resistance is more pronounced for specialist than for generalist insect herbivores (Jactel and Brockerhoff 2007, Castagneyrol et al. 2013a). *Matsucoccus feytaudi* has only one generation per year, followed by a single dispersal event. Female adults are wingless and the species spreads through passive wind dispersal of the first-instar larvae. The invasion of Corsica by the bast scale has been monitored since this species first became established on the island in 1995, providing a time series of quantitative data (Jactel et al. 1996). Jactel et al. (2006) found that larval density on host trees was lower in mixed stands of maritime pine and Corsican pine *Pinus nigra* subsp. *laricio* var. *corsicana* than in pure stands of maritime pine, and that this lower density was positively correlated with the proportion of non-host trees in the mixed stands. These findings may reflect top-down control by predatory bugs *Elatophilus nigricornis* naturally preying on the native pine scale *Matsucoccus pini* in *P. nigra* and spilling over onto the introduced *M. feytaudi* on *P. pinaster* (Jactel et al. 2006). Alternatively, the presence of Corsican pine may simply have reduced the likelihood of *M. feytaudi* first instars landing on maritime pines in mixed stands. Finally, *M. feytaudi* infestations weaken trees, which are ultimately killed by bark beetles, leading to a general decline of the

forest. In addition to the pine plantations, several pine forests of high conservation and amenity value are now under threat on the island.

The objectives of our study were therefore 1) to estimate the effects of landscape diversity on the rate of spread of the maritime pine bast scale in Corsica, 2) to decipher the ecological mechanisms accounting for the slower spread of the invader in more diverse landscapes and 3) to provide a generic modelling framework for quantifying the relationship between landscape diversity and invasibility to forest pest insects.

Material and methods

Study organism

The maritime pine bast scale *Matsucoccus feytaudi* is endemic to the western part of the Mediterranean Basin and is currently spreading eastwards in France and Italy, following the distribution of its specific host, *Pinus pinaster* (Burban et al. 1999). In 1994, Jactel et al. (1996) recorded the first known presence of this species in Corsica (9.21489°E, 42.4258°N), which is located beyond the south-eastern limit of the bast scale's native distribution range. *Matsucoccus feytaudi* probably arrived on the island through long-distance wind dispersal of first-instar larvae. A trapping network in maritime pine forests monitors the spread of the bast scale across the region. The monitoring process involves sampling adult males with pheromone traps, as described by Jactel et al. (1996) or Branco et al. (2004). The pine bast scale was sampled across the island from 1995 to 2006 and at the fringe of the newly colonized areas from 1996 to 2012, with the exception of 2006 (= 384 trapping data) (Fig. 1A).

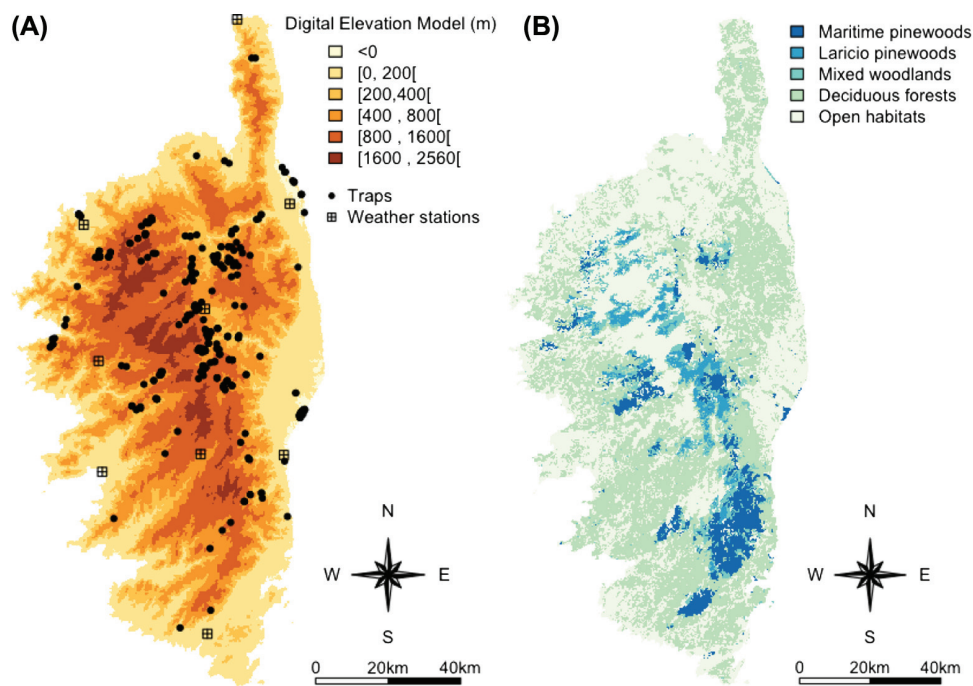


Figure 1. Maps of Corsica: (A) topography with sampling sites (black dots) and weather stations (open squares); (B) distribution of the major forest types found on the island (adapted from the classification provided by the National Forest Inventory).

Rate of spread

The model developed for inferring the rate of spread of *M. feytaudi* was based on the boundary displacement method described by Sharov et al. (1995, 1997a). In brief, this method involves calculating the distance between the limit of the distribution range of a given invading population at a given moment and the distributional limit found at the next time step. These limits of the distribution range are referred to as boundaries, and are characterized by the probable area occupied, a density threshold and a spatial scale (Sharov et al. 1995). The mean rate of spread is inferred by dividing the mean calculated distances by the time separating two steps in the invasion process (here, a year). This method has the advantage of estimating the mean rate of spread by taking into account the differences in spread rates between the occupied area and the newly colonized area. It can therefore be used to quantify anisotropic spread, in different directions, from the point of origin of the invasion. This method also facilitates the evaluation of environmental effects, such as those of landscape features, on spread rate, which may vary by spatial direction (Sharov et al. 1997a).

Several methods have been developed for defining the probable area occupied (i.e. the endemicity zone) by forest insects at each time step. Most of these methods have been borrowed from the field of geostatistics (Gribko et al. 1995, Sharov et al. 1995, Gilbert and Grégoire 2003). Here, we used point pattern analysis (Rowlingson and Diggle 1993). In particular, we computed an isotropic Gaussian kernel smoothed intensity function on a 250×250 m resolution grid covering Corsica. We included edge correction, according to the method described by Diggle (1985). The function was parameterized on the basis of pheromone trap records ($n = 289$, see below for the 95 trapping data removed). This

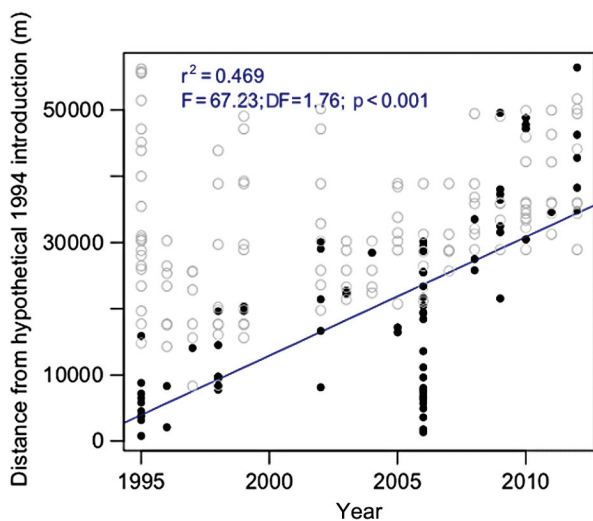


Figure 2. Regression distance plot, obtained by regressing the distance to the point of origin of the invasion, as a function of time of detection. The slope of the regression line provides an estimate of the mean rate of spread, 1.79 km yr^{-1} in this case. The data retained were filtered on a 2×2 km grid. Grey points indicate the sampling sites at which *M. feytaudi* was not detected.

method has the advantages that 1) no assumption about the frequency distribution of observations is required, 2) it can be fitted to presence-only data, and 3) the evaluation of only one parameter (bandwidth) is required to map population densities and to delineate the most probable occupied area at a given time step.

Many studies have been published on the various methods available for bandwidth evaluation (Kelsall and Diggle 1998, Baddeley and Turner 2006, Hengl 2009). In this study, we approximated the bandwidth parameter by the distance (= range) at which the semivariance of the empirical semivariogram, constructed from the cumulative distribution of records, reached its carrying capacity (= sill). A spherical model with an initial partial sill, range and nugget fixed to 0.6, 9000 and 0.3, respectively, was fitted to the data, and the range parameter was extracted. We assume that this estimate of bandwidth minimises spatial autocorrelation while capturing major trends in the data.

Once the probable area occupied had been defined and the relative density distribution maps had been constructed (Supplementary material Appendix 1, Fig. A1), we defined a threshold probability of presence (= TH), below which the likelihood of finding a positive case (the presence of the invasive insect) was minimal (or above which it was maximal). TH was also used to characterise the minimum probability of presence required to consider a location to be colonised. In practice, we selected several TH values, from 0.1 to 0.6 (in steps of 0.01). For each time step and for a fixed spatial scale (here the pixel size, i.e. 250×250 m), we split the area into presence/absence pixels, superimposed the presence/absence records from insect trapping and identified the TH minimising the number of grid cells misclassified, i.e. minimising type I (false-positive) and II (false-negative) errors (see the best cell classification method described by Sharov et al. 1995).

At this point, it should be noted that the distance between traps can influence the accuracy of spread rate estimation, particularly if traps are not uniformly distributed (Sharov et al. 1997a). Traps located too close to each other should, therefore, be removed, as recommended by Sharov et al. (1997a). We therefore applied a grid of 2×2 km cells to the entire area. If a cell was found to contain more than one trap, we randomly selected one trap for the analyses, excluding all the others from that cell. Ninety-five traps were thereby removed.

For the quantification of boundary displacements, we drew n radial axes from the approximate origin of the invasion to the boundaries of consecutive occupancy maps (Supplementary material Appendix 1, Fig. A2), providing $n \times t$ segments, where t is the number of time steps. In practice, we defined 72 segments (angle of 5°) and 15 boundaries, corresponding to the 15 yearly time steps available. This provided a discrete population of 1080 possible spread rates (SR), making it possible to assess the effects of environmental variables on spatial variation in SR. Finally, for comparisons with the distance regression method, an overall radial SR was calculated and compared with the slope of the regressing distance to the point of origin of the invasion, as a function of time since first detection (Liebhold et al. 1992, 1997).

Ecological variables

Landscape diversity and configuration.

First, we characterise landscape diversity on the basis of the composition of habitat patches, estimating the density of patches of host and non-host tree species and the diversity of forest habitat patches (i.e. landscape compositional heterogeneity according to Fahrig et al. 2011). Second, we calculated the mean patch sizes and the connectivity between patches as a measure of functional landscape configuration (i.e. landscape configurational heterogeneity, Fahrig et al. 2011). A patch was defined as the sum of connected pixels found in the landscape matrix belonging to a given cover class. Patches were constructed on a raster matrix with a resolution of 250×250 m, on the basis of the land cover classification provided by the French National Forestry Inventory (IFN). Two different land cover typologies were built. The first (no. 1) consisted of five land cover types: one type with the host tree: 1) maritime pine forests (pure stands or mixed with undifferentiated *Pinus* spp.), three types with non-host trees: 2) black pine *Pinus laricio* forests, 3) deciduous forests, 4) mixed stands of coniferous and broadleaved trees and one type with 5) open habitats (Fig. 1B). The second typology (no. 2) included 11 types of forest habitat, corresponding to the main tree species or assemblages of tree species found in Corsica. A map and the description of these 11 classes are provided in Supplementary material Appendix 1, Fig. A3.

Then, landscape metrics were calculated within each delineating segment computed before (see the section entitled 'Rate of spread'). In particular, the first typology (no. 1) was used to quantify the mean patch size (area), relative density of host and non-host patches and their connectivity (i.e. minimum and mean distances separating two patches of the same type, aggregation, cohesion and adjacency metrics, as defined in McGarigal et al. (2002), Supplementary material Appendix 1, Table A1). The second typology (no. 2) was used to quantify the number of forest patches with different tree species (S) and the number of forest pixels (N). S and N were then combined into Margalef's index (DA), a density-independent diversity index (after Whittaker 1972, $DA = (S - 1)/\log N$).

For an accurate evaluation of the extent to which landscape diversity influenced the rate of spread of the pest scale, it was important to control for covarying features that could reduce, accelerate or orientate insect spread. As *M. feytaudi* is dispersed by a passive mechanism, we assumed that these features were mostly linked to the interplay between wind and topography. Other climatic conditions, such as temperature and rainfall, were considered less likely to influence the invasion process and were therefore not taken into account in this study.

Wind data

Meteorological data were obtained from the CLIMATIK web portal (INRA) and from the French Meteorological Service (Météo France). We retrieved data collected between 1994 and 2012 at nine weather stations distributed across Corsica (Fig. 1A) for two variables: daily wind speed at an altitude of 10 m and wind direction at maximum wind speed. We transformed the wind data into two vectors, u and v , parallel to the x and y axes, respectively, of the landscape

raster (Supplementary material Appendix 2). These vectors of wind events were then averaged or summed by year, over the dispersal period of *M. feytaudi* larvae, from February to May (Riom 1994). Yearly means and sums of vectors were then interpolated across the study area, by ordinary kriging (Pebesma 2004). We modelled the empirical semivariogram, using a circular model with an initial partial sill, range and nugget fixed at 0.45, 65 000 and 0.1, respectively. The goodness-of-fit of the semivariogram model was evaluated by leave-one-out cross-validation (Pebesma 2004). Output resolution was set at 250×250 m, according to the resolution selected for landscape analyses. This procedure was applied to both the mean and the sum of vector values within each segment ($= u_{\text{mean}}, v_{\text{mean}}$ and $u_{\text{sum}}, v_{\text{sum}}$, respectively).

Topography

Digital elevation data from the Shuttle Radar Topography Mission (SRTM) (Supplementary material Appendix 1, Table A1) were resampled to obtain a raster file of 250×250 m resolution, restricted to Corsica (Fig. 1A). We assumed that mountainous relief and high altitude might slow the spread of *M. feytaudi*. We therefore calculated the mean and maximum altitudes encountered within each segment.

Statistical analysis

The statistical relationships between calculated spread rates and environmental variables were modelled with a generalised boosted regression tree (BRT) (Ridgeway 1999). This algorithm was initially developed in the field of machine learning (Olden et al. 2008), but is increasingly being used in ecology (Elith et al. 2006, Roura-Pascual et al. 2009, Sinka et al. 2010). BRT has several strengths, namely it: 1) relaxes the assumption of a linear relationship between dependent and explanatory variables, 2) takes into account interactions between explanatory variables, 3) provides improved evaluation tools, such as internal cross-validation with a selectable bag fraction (Elith et al. 2008), 4) outperforms classical models in terms of explanatory power, ability to limit the effects of overfitting (Elith et al. 2006) and ability to account for spatial autocorrelation (Crane et al. 2012).

We reduced the bias linked to the collinearity of explanatory variables (Dormann et al. 2013), by constructing a matrix of Pearson coefficients for the selection of a subset of covariates. Our selection approach involved 1) grouping topoclimatic, forest composition and physical connectedness variables, 2) constructing Pearson's matrices for each group of variables, 3) identifying pairs with coefficients higher than $|0.7|$ (Dormann et al. 2013) and 4) selecting the variable within the pair that maximised the likelihood of the linear correlation between the explanatory variable and spread rate.

At last, we added an autoregressive cofactor (lag SR) to the model to control for the possibility of movements being correlated between time steps.

Bootstrap and model evaluation

Thirty BRT models were independently computed from a random sample of half the dataset. This bootstrap

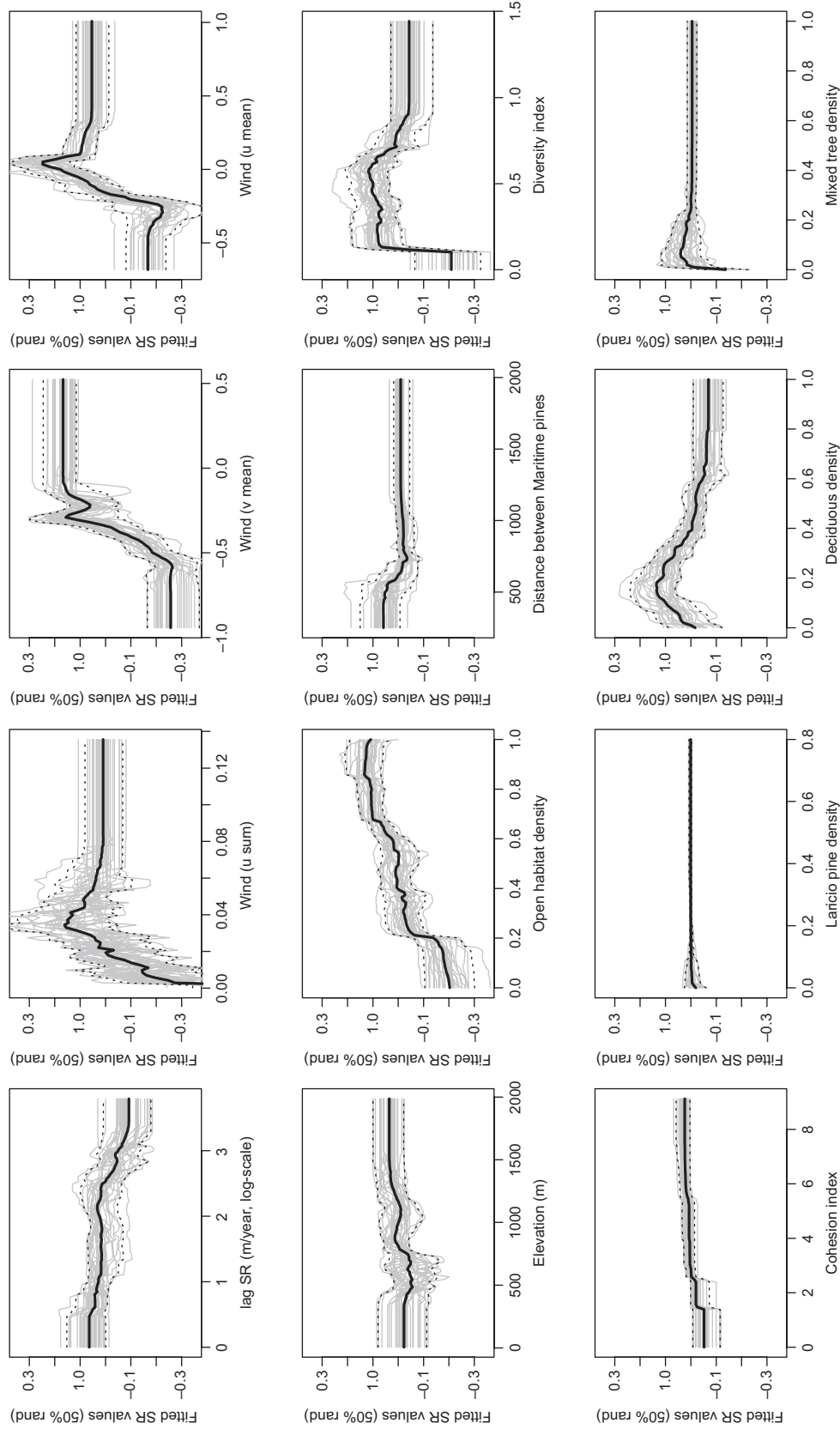


Figure 3. Relationships between selected explanatory variables and the relative fitted spread rates obtained at the landscape scale. For a more detailed explanation on the explanatory variables, their range and units, see the Material and methods section and Supplementary material Appendix 1, Table A1. Grey-line predictions were obtained by 30 iterations, from a random sample taken from half the dataset collected between 1995 and 2011. The black line shows the mean partial dependency between fitted values and each explanatory variable, within a 95% CI (dotted lines). A logarithmic scale has been used for the y-axes.

Table 1. Model characteristics and predictive performances, as evaluated on training data gathered between 1995 and 2011, or after removing 50% of the full dataset (external evaluation, $n_{\text{boots}} = 30$) (learning rate = 0.005, tree complexity = 5). Additional information about these indicators is provided in the 'Bootstrap and model evaluation' section of the methods.

	Full dataset	50% dataset/50%
N (positive spread rates)	294	147/147
Mean no. regression trees	6433	4733
% deviance (\pm SE)		
training	0.535 (\pm 0.014)	0.538 (\pm 0.158)
CV*	0.156 (\pm 0.020)	0.3583 (\pm 0.058)
r correlation		
training	0.988	0.854
CV*	0.841	0.612
independent	–	0.620 ($p < 0.001$)
RMSE		
training	0.117	0.391
independent	–	0.582

*cross-validation with a bag fraction of 0.5.

sampling complemented the internal cross-validation carried out within the BRT algorithm and provided estimated confidence intervals for the relative contribution of each explanatory variable. The external evaluation of the model was carried out on the half dataset not used for BRT model training. In addition, 1995–2011 data were used to predict spread in 2012. Partial dependence plots linking the fitted spread rate values and explanatory variables were also generated and averaged over the 30 runs, within a 95% confidence interval (CI). Finally, three measurements of goodness-of-fit were calculated for each run and averaged over the runs: 1) the deviance (dev), a criterion minimised during the model boosting process (Elith et al. 2008); 2) the root mean squared error (RMSE), which evaluates the accuracy with which the model fits the response variable; 3) the square root of the coefficient of determination (r), which can be used for comparisons with other regression methods.

All data processing and analyses were carried out with R software (ver. 2.14.2) (R Development Core Team). In particular, point pattern analyses and kernel functions were computed with the Spatstat package (Baddeley 2008), geo-statistics and spatial data manipulations were carried out with the Gstat (Pebesma 2004), Raster (Hijmans and Van Etten 2011), Maptools (Lewin-Koh et al. 2011) and Rgdal packages (Keitt et al. 2011). Landscape metrics were computed with the SDMTools package (VanDerWal et al. 2012), and BRT models were constructed with the gbm package (Ridgeway 2012), with custom code lines adapted from those of Elith et al. (2008).

Results

From 1995 to 2012, 384 pheromone traps were set up in Corsica (Fig. 1A). These traps caught 21 546 male maritime pine bast scales. The mean rate of spread of *M. feytaudi*, calculated by regressing the distances to the point of origin of the invasion in the Ponte Leccia area (Jactel et al. 1996), as a function of first detection time, was estimated at 1.79 ± 0.22 km yr⁻¹ (mean \pm SE) ($r^2 = 0.47$; $F = 67.23$, $DF = 76$, $p < 0.001$) (Fig. 2). The increasing distance travelled from

the point of introduction by the invading *M. feytaudi* population was accompanied by an exponential increase in the area of the maritime pine forests invaded (Supplementary material Appendix 1, Fig. A4). According to the distribution envelope for 2012 and a threshold probability of presence of 0.1, approximately 15 000 ha of maritime pine stands have been invaded by *M. feytaudi* since 1995, corresponding to about 29% of the total area under maritime pine forests on the island. The boundary displacement method provided a range of spread rates of 0.01 to 15.06 km yr⁻¹. On average, the spread rate was 1.89 ± 0.10 km yr⁻¹ (mean \pm SE), very close to the value obtained with the distance regression method.

Overall, the BRT models yielded satisfactory agreement between observed and predicted spread rates for the period 1995–2011 ($r_{\text{CV}} = 0.84$, Table 1). Nevertheless, model accuracy was low at spread rates below 250 m yr⁻¹. BRT model deviance did not decrease significantly following the removal of the least informative cofactors (up to five at a time).

Wind components made the largest contribution to the explanatory power of the model (63.0%) (Table 2).

The density of open habitat contributed to 8.1% of model deviance. On average, spread rates were greater for open landscapes, by up to 0.13 km yr⁻¹, corresponding to 6.6% of the mean spread rate ($r_{\text{Pearson}} = 0.92$) (Fig. 3).

A total of 7.7% of the explanatory power of the model was attributed to densities of non-host forest patches (deciduous trees 4.2%; mixed forests 2.9%; Laricio black pines 0.6%). The presence of these non-host trees was associated with reduced spread rates ($r_{\text{Pearson}} = -0.86$, -0.66 , for deciduous density and mixed tree density, respectively) except for forests with a high density of Laricio pines ($r_{\text{Pearson}} = 0.7$) but this variable had a very small relative contribution to the model (0.6%).

It is worth noticing that the density of host patches was not retained by the model. However, the physical connectivity between maritime pine patches accounted for 2.8% of explanatory power. This connectivity between host patches was associated with accelerated spread, by up to 6.0%. An increase in the distance between maritime pine patches (i.e. reduced connectivity) from 0 to 1 km was associated with a decrease in spread rate, whereas no further influence of this factor was observed beyond this range. Interestingly forest diversity on its own accounted for 7.6% of explanatory power and spread rates decreased significantly with increasing landscape diversity. Spread rates were up to 13.6% lower in landscapes with relatively high tree diversity ($r_{\text{Pearson}} = -0.56$) and high density of non-host trees ($r_{\text{Pearson}} = -0.86$, for deciduous trees, and -0.66 , for mixed trees).

Topography accounted for 5.8% of explanatory power but had no clear effect on spread rate ($r_{\text{Pearson}} = 0.53$).

The autoregressive cofactor contributed to 3.7% of model deviance. It appeared to be inversely related to the fitted spread rate of the next time step, indicating that spread generally slowed after a period during which it was relatively high, and increased after a period in which it was relatively low (Fig. 3).

We evaluated extrapolation potential of the model, based on the range expansion for 2012, and found that the correlation between the observed spread rates and model prediction was moderately accurate (Spearman's $r = 0.51$). However,

Table 2. Explanatory variables retained in the study and their relative contributions to the fitted spread model. Ranges of values are given for the area colonised by 2011. The larger the relative (%) contribution of the explanatory variable, the greater its contribution to the model fit. Correlation coefficients (Pearson's r) indicate the direction of individual explanatory variable effects on the spread of the invasion. Decrease* and increase** provide numerical indications concerning the extent to which the magnitude of each explanatory variable decreases or increases the average fitted spread rate. They were calculated as the difference between the mean (SR) and the minimum (SR_{min}) or maximum (SR_{max}) fitted spread rate, respectively, for a given explanatory variable, keeping the other covariates constant, divided by SR (see table note * and **). A detailed description of the explanatory variables is presented in Supplementary material Appendix 1, Table A1.

Explanatory variables	Range	Contribution	r Pearson	% Decrease*	% Increase**
Wind (u sum)	0.00–0.14	39.03	0.18	19.41	5.47
Wind (u mean)	–0.68–1.01	12.40	–0.23	6.70	14.88
Wind (v mean)	–0.97–0.12	11.56	0.87	10.79	11.57
Open habitat density	0–1	8.08	0.92	13.10	6.64
Diversity index	0.00–1.44	7.55	–0.56	5.94	5.62
Elevation (m)	5.98–2148	7.16	0.63	3.73	3.41
Deciduous density	0–1	4.16	–0.86	3.12	4.70
lag SR (m yr ^{–1} , log-scale)	0.00–3.87	3.68	–0.72	7.11	2.87
Mixed tree density	0–1	2.95	–0.66	4.56	2.54
Distance [maritime p.]	250–1987	1.88	–0.63	1.89	4.12
Cohesion index	0.00–9.01	0.94	0.89	2.65	1.89
Laricio pine density	0–1	0.60	0.70	1.44	0.45

$$(*) \frac{\Delta(SR, SR_{min})}{SR}; (**) \frac{\Delta(SR, SR_{max})}{SR}$$

this relationship was not significant ($p = 0.059$), due to the small number of range increase events occurring between 2011 and 2012 ($n = 15$).

Discussion

In this study, we demonstrate that landscape diversity – and more generally landscape heterogeneity (both compositional and configurational) – has a significant influence on the rate of spread of the invasive maritime pine bast scale. Specifically, bast scales spread more slowly in heterogeneous forest landscapes with high densities of non-host deciduous trees and high tree species diversity, whereas they spread more rapidly in landscapes in which open habitats were more abundant. Moreover, the rate of spread of this pest increased with increasing connectivity between maritime pine forest patches, up to a distance threshold of about 1 km between two patches.

Inference of spread rate and wind dispersal

On average, maritime pine bast scale is colonising Corsican maritime pine forests rather slowly compared to other regions. Our estimate is about half that reported for the species in the Maures and Esterel forest stands in the south of France (Carle 1974). This low spread rate also contrasts with the higher rates of spread reported for other wind-dispersed invasive insect species, such as the felted beech scale *Cryptococcus fagisuga* (15 km yr^{–1}, Morin et al. 2007) or the gypsy moth *Lymantria dispar* (16–41 km yr^{–1}, Sharov et al. 1999), but unbiased interspecific comparisons would require the use of similar study protocols and methods to infer the rate of spread. Theoretically, the inference of spread rates by interpolation techniques generally overestimates the

true rate of spread, whereas methods that do not require interpolation (e.g. regression distance methods) underestimate the rate of spread (Gilbert and Liebhold 2010). If these assumptions hold for our study, then the rate of spread of *M. feytaudi* is likely somewhere between the estimates obtained with the regression distance and boundary displacement methods, i.e. on average, between 1.79 and 1.89 km yr^{–1}. That these contrasting methods reached similar conclusions suggests that we can have confidence in our estimates. The low rate of spread suggests that first-instar larvae of maritime pine bast scale, although transported by the wind, rapidly settle in the nearest neighbouring trees. Wainhouse (1980) showed that the dispersal distance of *C. fagisuga* was proportional to take-off height and wind speed. In another study, Raynor et al. (1974) showed that vertical air turbulence was about eight times stronger at mid-canopy level than at trunk level in pine forests. It therefore seems likely that the larvae of maritime pine bast scale, which are found predominantly on trunks (Jactel et al. 1996) and sporadically in the canopy (Schvester and Fabre 2001), would tend to settle predominantly on nearby trees, and only occasionally travel larger distances of up to ~18 km in a year. The distance travelled before settling may also reflect the mean distance to the nearest host stand in the area already colonised, which was 1.8 ± 3.4 km (\pm SD) in Corsica.

Landscape heterogeneity

Interest in the effect of spatial heterogeneity on biological invasions is increasing, but coverage of this topic remains uneven (Hastings et al. 2005, Melbourne et al. 2007). Most studies have addressed invasion by alien plant species (Davies et al. 2005, Theoharides and Dukes 2007, Schreiber and Lloyd-Smith 2009, Gonzalez-Moreno et al. 2013, Thomas and Moloney 2013); a few others have focused

on plant pathogens (Miller et al. 2002, Holdenrieder et al. 2004, Condeso and Meentemeyer 2007, Plantegenest et al. 2007, Haas et al. 2011) but, to our knowledge, very few have tackled the spread of phytophagous insects (Hunter 2002, Jeschke et al. 2012). In addition, most studies also have either focused on the local scale (Knops et al. 1999, Tilman 2004, Jactel et al. 2006) or have considered spatial heterogeneity in terms of habitat density and connectivity (With 2002, Sebert-Cuvillier et al. 2008), with very few taking habitat diversity into account (Onstad et al. 2003). Finally, landscape-scale studies investigating the link between spatial heterogeneity and invasions have mostly been carried out by simulations (Onstad et al. 2003, but concerning agricultural insect pests; Pitt et al. 2009, Fitzpatrick et al. 2012, but not taking diversity into account). The question posed by Melbourne et al. (2007): 'Does species richness confer resistance to spatial spread?' has thus remained largely unanswered, particularly for forest insects.

We found that the rate of spread of maritime pine bast scale increased with increasing connectivity between maritime pine stands in the landscape, a feature that would tend to maximise dispersal success. Similarly, an increase in the percentage of host trees has been shown to increase the spread rate of gypsy moth (Sharov et al. 1999) and hemlock woolly adelgid (Morin et al. 2009), suggesting that connectivity between stands of host species favours invasion. This is probably because movement mortality decreases with decreasing distance between host patches (Fahrig 2007). However, we did not observe any effect of host (maritime pine) density on the spread rate of *M. feytaudi*. In contrast we found that a higher percentage of open habitats in the landscape increased the rate of spread of maritime pine bast scale, even though the presence of open habitats between maritime pine stands also reduces their connectivity. According to our model, minimising the proportion of open habitats in the landscape would decrease the mean rate of spread by up to 13.1%. A high percentage of open habitats would facilitate the wind-mediated transport of bast scale to sites further away from the source, thereby increasing the likelihood of establishment in remote host stands.

To our knowledge, our study is the first to demonstrate that high landscape diversity (i.e. high densities of non-host patches and high diversity of forest cover types) decreases the rate of spread of invasive species. The spread of maritime pine bast scale in Corsica was reduced by up to 13.6% in landscapes with high forest types diversity and high density of non-host trees. Kennedy et al. (2002) suggested that local biodiversity represents an important line of defence against the spread of invaders, but their study focused on processes operating at the local scale. Both the proportion of non-host tree species and the diversity of tree species at the landscape level were significantly negatively correlated with the rate of spread of maritime pine bast scale. These findings suggest that associational resistance processes operating at the stand scale may also be relevant at the landscape scale. First, according to the 'resource concentration hypothesis' (Root 1973), forest herbivores are more likely to find their host tree if it is present at high density, due, in particular, to a higher likelihood of immigration in monospecific patches (Hambäck et al. 2000). However, the proportion of host tree species and the number of monospecific patches of the host

tree decrease in proportion with forest diversity in the landscape. Moreover, just as neighbouring non-host trees can act as physical barriers to the colonisation of individual host trees (Jules et al. 2002, Dulaurent et al. 2012), the presence of patches of non-host trees may impede dispersal and the invasion of host tree stands at the landscape scale. In particular, in the case of passively dispersed forest invaders, such as the maritime pine bast scale, patches of non-host trees (here black pines or broadleaved trees) can filter swarms of flying insects. We refer to this mechanism as the 'pitfall effect'.

Second, according to the 'natural enemy hypothesis' (Russell 1989), natural enemies of herbivores are more diverse and control herbivores more effectively in more diverse forests (Riihimäki et al. 2005). Consistent with this hypothesis, Jactel et al. (2006) attributed the lower density of *M. feytaudi* in mixed stands of maritime and Corsican pines to the higher abundance of the predatory bug *Elatophilus nigricornis*, a native predator of the native *Matsucoccus pini*, a sibling species feeding on Corsican pine. In the light of these results, we expected the rate of spread of *M. feytaudi* to decrease with increasing area under Corsican pines in the landscape. However, we found that this factor had no influence. Presumably, *E. nigricornis* predation on *M. feytaudi* was not effective or rapid enough to affect the rate of spread of the bast scale at the landscape level. In a previous study, we found that the pheromone release threshold triggering the attraction of *E. nigricornis* (a kairomonal effect) was much higher than that for the attraction of *M. feytaudi* males (Branco et al. 2006). This suggests that the predator cannot detect low-density prey populations and may therefore be unable to control the invader when it first begins to colonise the area (Fabre et al. 2000). We can therefore conclude that 1) the pitfall effect may account for landscape diversity slowing the invasion of Corsica by the maritime pine bast scale in the short term while 2) tree diversity increases top-down control of the scale by native predators in the longer term (Jactel et al. 2006), supporting two complementary mechanisms of associational resistance operating at two different spatial and temporal scales.

Management implications

Our findings and the modelling framework we have developed have at least two applied perspectives that could prove useful for managing invasions, and particularly the ones of maritime pine bast scale in Corsica. First, we obtained encouraging results concerning the predictive capacity of the model. This aspect may be particularly valuable for identifying areas of the landscape in which there is an imminent risk of invasion and targeting forest areas on which surveillance and management efforts should be focused. Second, several landscape attributes emerged as key drivers of the spread of *M. feytaudi*, providing clues to potentially useful landscape management approaches. For example, the presence of open areas resulted in a more rapid spread of the insect, suggesting that the clear cutting of forest stands in a buffer area around colonised pine stands would be counterproductive. By contrast, the presence of patches of non-host trees slowed the spread of the insect, providing support for approaches based on the maintenance or improvement of landscape diversity,

by growing maritime pine stands in broadleaved woodlands, for example.

Acknowledgements – We would like to thank the ‘correspondants observateurs’ of the Forest Health Dept in Corsica for collecting some of the data. We also thank Fabrice Vétillard and Pierre Ménassieu for assistance with fieldwork and Martine Lettéré (INRA) for providing pheromone lures. We thank Aiko Gryspeirt and Marius Gilbert (Univ. Libre de Bruxelles) for fruitful discussions on the algorithmic optimisation of SR models and the three anonymous reviewers for their helpful comments. TR was supported by a postdoctoral grant from INRA. This research was funded by the French Ministry of Agriculture and ODARC.

References

- Baddeley, A. 2008. Analysing spatial point patterns in R. – Technical report, CSIRO, 2010, ver. 4, <www.csiro.au/resources/pf16h.html>.
- Baddeley, A. and Turner, R. 2006. Modelling spatial point patterns in R. – In: Case Studies in Spatial Point Process Modeling, Lecture Notes in Statistics. Springer, pp. 23–74.
- Balvanera, P. et al. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. – Ecol. Lett. 9: 1146–1156.
- Barbaro, L. et al. 2008. Multi-scale habitat selection and foraging ecology of the eurasian hoopoe (*Upupa epops*) in pine plantations. – Biodivers. Conserv. 17: 1073–1087.
- Barbosa, P. et al. 2009. Associational resistance and associational susceptibility: having right or wrong neighbors. – Annu. Rev. Ecol. Evol. Syst. 40: 1–20.
- Branco, M. et al. 2004. Effect of trap design, trap size and pheromone dose on male capture of two pine bark scale species (Hemiptera: Matsucoccidae): implications for monitoring and mass-trapping. – Agric. For. Entomol. 6: 233–239.
- Branco, M. et al. 2006. Kairomonal response of predators to three pine bark scale sex pheromones. – J. Chem. Ecol. 32: 1577–1586.
- Burban, C. et al. 1999. Rangewide variation of the maritime pine bark scale *Matsucoccus feytaudi* Duc. (Homoptera: Matsucoccidae) in relation to the genetic structure of its host. – Mol. Ecol. 8: 1593–1602.
- Cardinale, B. J. et al. 2012. Biodiversity loss and its impact on humanity. – Nature 486: 59–67.
- Carle, P. 1974. Le dépérissement du Pin mésogéen en Provence : rôle des insectes dans les modifications d'équilibre biologique des forêts envahies par *Matsucoccus feytaudi* duc (Coccoidea, Margarodidae). – Ann. Sci. For. 31: 1–26.
- Castagneyrol, B. et al. 2013a. Effects of plant phylogenetic diversity on herbivory depend on herbivore specialization. – J. Appl. Ecol. in press.
- Castagneyrol, B. et al. 2013b. Plant apparency, an overlooked driver of associational resistance to insect herbivory. – J. Ecol. 101: 418–429.
- Clark, G. F. et al. 2013. Intrinsic time dependence in the diversity–invasibility relationship. – Ecology 94: 25–31.
- Condeso, T. E. and Meentemeyer, R. K. 2007. Effects of landscape heterogeneity on the merging forest disease sudden oak death. – J. Ecol. 95: 364–375.
- Crane, B. et al. 2012. A new method for dealing with residual spatial autocorrelation in species distribution models. – Ecography 35: 879–888.
- Davies, K. F. et al. 2005. Spatial heterogeneity explains the scale dependence of the native–exotic diversity relationship. – Ecology 86: 1602–1610.
- Diggle, P. 1985. A kernel method for smoothing point process data. – Appl. Stat. 34: 138–147.
- Dormann, C. F. et al. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. – Ecography 36: 27–46.
- Dulaurent, A.-M. et al. 2011. A case of habitat complementation in forest pests: pine processionary moth pupae survive better in open areas. – For. Ecol. Manage. 261: 1069–1076.
- Dulaurent, A.-M. et al. 2012. Hide and seek in forests: colonization by the pine processionary moth is impeded by the presence of nonhost trees. – Agric. For. Entomol. 14: 19–27.
- Dunning, J. B. et al. 1992. Ecological processes that affect populations in complex landscapes. – Oikos 65: 169–175.
- Elith, J. et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. – Ecography 29: 129–151.
- Elith, J. et al. 2008. A working guide to boosted regression trees. – J. Anim. Ecol. 77: 802–813.
- Fabre, J.-P. et al. 2000. Biology and ecology of *Elatophilus nigricornis* Zetterstedt (Hemiptera Anthocoridae) predator of *Matsucoccus feytaudi* Ducasse (Homoptera Matsucoccidae) in the south-east of France. – Ann. For. Sci. 57: 777–792.
- Fahrig, L. 2007. Non-optimal animal movement in human-altered landscapes. – Funct. Ecol. 21: 1003–1015.
- Fahrig, L. et al. 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. – Ecol. Lett. 14: 101–112.
- Fitzpatrick, M. C. et al. 2012. Modeling range dynamics in heterogeneous landscapes: invasion of the hemlock woolly adelgid in eastern North America. – Ecol. Appl. 22: 472–486.
- Gardiner, M. M. et al. 2009. Landscape diversity enhances biological control of an introduced crop pest in the north-central USA. – Ecol. Appl. 19: 143–154.
- Gilbert, M. and Grégoire, J. C. 2003. Site condition and predation influence a bark beetle's success: a spatially realistic approach. – Agric. For. Entomol. 5: 87–96.
- Gilbert, B. and Lechowicz, M. J. 2005. Invasibility and abiotic gradients: the positive correlation between native and exotic plant diversity. – Ecology 86: 1848–1855.
- Gilbert, M. and Liebhold, A. 2010. Comparing methods for measuring the rate of spread of invading populations. – Ecography 33: 809–817.
- Gilbert, M. et al. 2005. Post-storm surveys reveal large-scale spatial patterns and influences of site factors, forest structure and diversity in endemic bark-beetle populations. – Landscape Ecol. 20: 35–49.
- Gonzalez-Moreno, P. et al. 2013. Quantifying the landscape influence on plant invasions in Mediterranean coastal habitats. – Landscape Ecol. 28: 891–903.
- Gribko, L. S. et al. 1995. Model to predict gypsy moth (Lepidoptera: Lymantriidae) defoliation using kriging and logistic regression. – Environ. Entomol. 24: 530–537.
- Haas, S. E. et al. 2011. Forest species diversity reduces disease risk in a generalist plant pathogen invasion. – Ecol. Lett. 14: 1108–1116.
- Hambäck, P. A. et al. 2000. Associational resistance: insect damage to purple loosestrife reduced in thickets of sweet gale. – Ecology 81: 1784–1794.
- Hastings, A. et al. 2005. The spatial spread of invasions: new developments in theory and evidence. – Ecol. Lett. 8: 91–101.
- Hengl, T. 2009. A practical guide to geostatistical mapping. – Creative Commons Attribution-Noncommercial-No Derivative Works 3.0 license, <http://spatial-analyst.net/book/>.
- Hijmans, R. J. and Van Etten, J. 2011. Geographic analysis and modeling with raster data. – R package ver. 1.9-92, <http://raster.r-forge.r-project.org/>.
- Holdenrieder, O. et al. 2004. Tree diseases and landscape processes: the challenge of landscape pathology. – Trends Ecol. Evol. 19: 446–452.
- Hunter, M. D. 2002. Landscape structure, habitat fragmentation, and the ecology of insects. – Agric. For. Entomol. 4: 159–166.

- Jactel, H. and Brockerhoff, E. G. 2007. Tree diversity reduces herbivory by forest insects. – *Ecol. Lett.* 10: 835–848.
- Jactel, H. et al. 1996. Découverte en Corse de *Matsucoccus feytaudi* Duc (Homoptera: Margarodidae), cochenille du pin maritime. – *Ann. Sci. For.* 145–152.
- Jactel, H. et al. 2006. Tree species diversity reduces the invasibility of maritime pine stands by the bast scale, *Matsucoccus feytaudi* (Homoptera: Margarodidae). – *Can. J. For. Res.* 36: 314–323.
- Jactel, H. et al. 2011. Non-host volatiles mediate associational resistance to the pine processionary moth. – *Oecologia* 166: 703–711.
- Jeschke, J. et al. 2012. Support for major hypotheses in invasion biology is uneven and declining. – *NeoBiota* 14: 1–20.
- Jules, E. S. et al. 2002. Spread of an invasive pathogen over a variable landscape: a nonnative root rot on Port Orford cedar. – *Ecology* 83: 3167–3181.
- Keesing, F. et al. 2010. Impacts of biodiversity on the emergence and transmission of infectious diseases. – *Nature* 468: 647–652.
- Keitt, T. H. et al. 2011. rgdal: bindings for the geospatial data abstraction library. – R package ver. 0.7-1.
- Kelsall, J. E. and Diggle, P. J. 1998. Spatial variation in risk of disease: a nonparametric binary regression approach. – *J. R. Stat. Soc. C* 47: 559–573.
- Kennedy, T. A. et al. 2002. Biodiversity as a barrier to ecological invasion. – *Nature* 417: 636.
- Knops, J. M. et al. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. – *Ecol. Lett.* 2: 286–293.
- Lewin-Koh, N. J. et al. 2011. maptools: tools for reading and handling spatial objects. – R package ver. 0.8-10.
- Liebold, A. M. et al. 1992. Gypsy moth invasion in North America: a quantitative analysis. – *J. Biogeogr.* 19: 513–520.
- Liebold, A. M. et al. 1997. Forest susceptibility to the gypsy moth. – *J. For.* 95: 20–24.
- McGarigal, K. et al. 2002. FRAGSTATS: spatial pattern analysis program for categorical maps. – *Comp. Software Prog. Univ. Mass., Amherst*, <www.umass.edu/landeco/research/fragstats/fragstats.html>.
- Melbourne, B. A. et al. 2007. Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? – *Ecol. Lett.* 10: 77–94.
- Millennium Ecosystem Assessment 2005. Ecosystems and human well-being: biodiversity synthesis. – Island Press.
- Miller, T. E. et al. 2002. Effect of community structure on invasion success and rate. – *Ecology* 83: 898–905.
- Morin, R. S. et al. 2007. Spread of beech bark disease in the eastern United States and its relationship to regional forest composition. – *Can. J. For. Res.* 37: 726–736.
- Morin, R. S. et al. 2009. Anisotropic spread of hemlock woolly adelgid in the eastern United States. – *Biol. Invasions* 11: 2341–2350.
- Mundt, C. C. et al. 2011. Landscape heterogeneity and disease spread: experimental approaches with a plant pathogen. – *Ecol. Appl.* 21: 321–328.
- Olden, J. D. et al. 2008. Machine learning methods without tears: a primer for ecologists. – *Quart. Rev. Biol.* 83: 171–193.
- Onstad, D. W. et al. 2003. Does landscape diversity slow the spread of rotation-resistant western corn rootworm (Coleoptera: Chrysomelidae)? – *Environ. Entomol.* 32: 992–1001.
- Pebesma, E. J. 2004. Multivariable geostatistics in S: the gstat package. – *Comput. Geosci.* 30: 683–691.
- Pitt, J. P. W. et al. 2009. Predicting Argentine ant spread over the heterogeneous landscape using a spatially explicit stochastic model. – *Ecol. Appl.* 19: 1176–1186.
- Plantegenest, M. et al. 2007. Landscape epidemiology of plant diseases. – *J. R. Soc. Int.* 4: 963–972.
- Rand, T. A. et al. 2012. Landscape complexity differentially benefits generalized fourth, over specialized third, trophic level natural enemies. – *Ecography* 35: 97–104.
- Raynor, G. S. et al. 1974. Particulate dispersion into and within a forest. – *Bound.-Layer Meteorol.* 7: 429–456.
- Ridgeway, G. 1999. The state of boosting. – *Comp. Sci. Stat.* 172–181.
- Ridgeway, G. 2012. gbm: Generalized boosted regression models. – R package ver. 1.6-3.2, <http://CRAN.R-project.org/package=gbm>.
- Riihimäki, J. et al. 2005. Testing the enemies hypothesis in forest stands: the important role of tree species composition. – *Oecologia* 142: 90–97.
- Riom, J. 1994. Le dépérissement du pin maritime dans le sud-est de la France au cours des années 1960–1970: le rôle de la cochenille *Matsucoccus feytaudi* Duc. (Coccoidea, Margarodidae). – *Revue Forestière Française* 5.
- Root, R. B. 1973. Organization of a plant–arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). – *Ecol. Monogr.* 43: 95–124.
- Roura-Pascual, N. et al. 2009. Consensual predictions of potential distributional areas for invasive species: a case study of Argentine ants in the Iberian Peninsula. – *Biol. Invasions* 11: 1017–1031.
- Rowlingson, B. and Diggle, P. 1993. Splanx: spatial point pattern analysis code in S-plus. – *Comp. Geosci.* 19: 627–655.
- Russell, E. P. 1989. Enemies hypothesis: a review of the effect of vegetational diversity on predatory insects and parasitoids. – *Environ. Entomol.* 18: 590–599.
- Sax, D. F. 2002. Native and naturalized plant diversity are positively correlated in scrub communities of California and Chile. – *Divers. Distrib.* 8: 193–210.
- Schreiber, S. J. and Lloyd-Smith, J. O. 2009. Invasion dynamics in spatially heterogeneous environments. – *Am. Nat.* 174: 490–505.
- Schvester, D. and Fabre, J.-P. 2001. Le dépérissement du Pin maritime des Maures et de l'Estérel provoqué par *Matsucoccus feytaudi* Ducasse (Homoptera, Matsuccidae), connaissances acquises de 1964 à 1990 – I. – Historique et rôle des insectes. – *Forêt Méditerranéenne XXII*: 213–234.
- Sebert-Cuvillier, E. et al. 2008. Spatial spread of an alien tree species in a heterogeneous forest landscape: a spatially realistic simulation model. – *Landscape Ecol.* 23: 787–801.
- Sharov, A. A. et al. 1995. Gypsy moth (Lepidoptera: Lymantriidae) spread in the central Appalachians: three methods for species boundary estimation. – *Environ. Entomol.* 24: 1529–1538.
- Sharov, A. A. et al. 1997a. Methods for monitoring the spread of gypsy moth (Lepidoptera: Lymantriidae) populations in the Appalachian Mountains. – *J. Econ. Entomol.* 90: 1259–1266.
- Sharov, A. A. et al. 1997b. Correlation of counts of gypsy moths (Lepidoptera: Lymantriidae) in pheromone traps with landscape characteristics. – *For. Sci.* 43: 483–490.
- Sharov, A. A. et al. 1999. What affects the rate of gypsy moth (Lepidoptera: Lymantriidae) spread: winter temperature or forest susceptibility? – *Agric. For. Entomol.* 1: 37–45.
- Sinka, M. et al. 2010. The dominant *Anopheles* vectors of human malaria in the Americas: occurrence data, distribution maps and biometric précis. – *Parasites Vectors* 3: 72.
- Theoharides, K. A. and Dukes, J. S. 2007. Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. – *New Phytol.* 176: 256–273.
- Thomas, S. M. and Moloney, K. A. 2013. Hierarchical factors impacting the distribution of an invasive species: landscape context and propagule pressure. – *Landscape Ecol.* 28: 81–93.
- Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion,

- and community assembly. – Proc. Natl Acad. Sci. USA 101: 10854–10861.
- VanDerWal, J. et al. 2012. Species distribution modelling tools: tools for processing data associated with species distribution modelling exercises. – R package ver. 1.1-12, < <http://CRAN.R-project.org/package=SDMTools>>.
- Vehviläinen, H et al. 2007. Tree species diversity influences herbivore abundance and damage: meta-analysis of long-term forest experiments. – *Oecologia* 152: 287–298.
- Wainhouse, D. 1980. Dispersal of first instar larvae of the felted beech scale, *Cryptococcus fagisuga*. – *J. Appl. Ecol.* 523–532.
- Whittaker, R. H. 1972. Evolution and measurement of species diversity. – *Taxon* 21: 213–251.
- With, K. A. 2002. The landscape ecology of invasive spread. – *Conserv. Biol.* 16: 1192–1203.
- Zhang, Q.-H. and Schlyter, F. 2004. Olfactory recognition and behavioural avoidance of angiosperm nonhost volatiles by conifer-inhabiting bark beetles. – *Agric. For. Entomol.* 6: 1–20.

Supplementary material (Appendix ECOG-00447 at <www.oikosoffice.lu.se/appendix>). Appendix 1–2.