Journal of Pest Science (2026) 99:67
https://doi.org/10.1007/s10340-026-02025-1

RESEARCH

Introduced or established? Convergent evidence indicates imported pine wood nematode vectors occupy gaps in native distribution

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Received: 8 October 2025 / Revised: 29 January 2026 / Accepted: 4 February 2026
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Abstract

Monitoring regulated quarantine plant pathogens and, when relevant, their vectors is compulsory in the European Union. Local *Monochamus* species (Coleoptera, Cerambycidae) vector the pine wood nematode, *Bursaphelenchus xylophilus*, a non-native pest already established in most of Portugal. Only 29 *M. galloprovincialis* individuals were trapped in Belgium in ten years (2013–2022), despite a dense coverage of pheromone-baited traps, suggesting absence or a very rare local occurrence in the country. In the northern neighbouring countries, only one single established population is known in The Netherlands and one in Denmark. A species distribution model based on pheromone-trap catches (negative and positive) of *M. galloprovincialis* from 4,914 traps in 29 European countries between 2008 and 2019 was developed, using the overall climate conditions and the distribution of seven pine tree species as explanatory variables. The effect of spatial scale was tested with a multi-scale approach. With a 225*225 km spatial grain, the major explanatory variables were the mean diurnal temperature range and, to a lesser extent, the presence of *Pinus* spp. The model predicted a low probability of presence in Belgium, the Netherlands, Great Britain and north-western Germany compared to southern Europe. Genotyping allowed to conclude that at least some of the beetles caught in Belgium originated from foreign locations. All catches were located close to entry points, suggesting introduction with imported material. The small size of most of the Belgian pine stands may also explain the absence or apparently transient status, or rareness of *Monochamus* spp. This study thus suggests that surveys in Belgium should privilege entry points rather than local forest stands.

Keywords *Bursaphelenchus xylophilus* · *Monochamus galloprovincialis* · Monitoring · Pest risk assessment · Pine wilt disease · Vectors

Key message

- The quarantine nematode, *Bursaphelenchus xylophilus,* is vectored by *Monochamus galloprovincialis*
- Only 29 potential vectors were trapped in Belgium in 2013–2022, with 45–95 traps deployed yearly
- A possible gap in the species' range, or at least rareness, is thus possible in Belgium

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Communicated by Andrea Battisti.

Retired: Jean-Claude Grégoire, Hans Casteels, Jean-Luc Flot, David Michelante, Hans Peter Ravn, Alain Roques, Martin Schroeder.

Deceased: Juan Pajares.

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Published online: 11 April 2026

- A species distribution model and genotyping support the foreign origin of the trapped insects
- The small size of Belgian pine stands could further explain the low probability of establishment.

Introduction

Favoured by increasing international trade and by climate change (Levine and D'Antonio 2003; Early et al. 2016; Fenn-Moltu et al. 2023), biological invasions growingly affect supporting services (nutrient and energy flows), provisioning services (material benefits and other services provided by ecosystems), regulating services (interactions within ecosystems) and cultural and human well-being (Vilà and Hulme 2017). Diagne et al. (2021) estimated the minimal overall cost of biological invasions at US$1.288 trillion over the period of 1970–2017. In this context, invasive animal pests and plant pathogens threaten forest health, with high ecological and economic impacts (reviewed, e.g. in Holmes et al. 2009, and Kenis et al. 2017). The affected sectors are multiple; Aukema et al. (2011) calculated that, for three insect guilds (wood- and phloem borers, sap feeders and foliage feeders), government expenditure (in prevention, mitigation and control) exceeded direct property losses. Fei et al. (2019) also identified significant increases in carbon emissions due to global biomass reduction in the USA.

In Europe, the pathogenic bacterium *Xylella fastidiosa* ssp. *pauca* (Xf), introduced in 2013 in Apulia (Italy), massively kills olive trees (EFSA Plant Health Panel 2018a). Were it to extend to the whole country, Xf would cause between 1.9 and 5.2 billion € losses in a worse case (orchards die off and production ceases), or between 0.6 and 1.6 billion € losses if the orchards could be restocked with resistant varieties (Schneider et al. 2020). The impact over 22 years (2008–2030) on pine forestry in the European Union (EU) of another alien pathogen, the North American pinewood nematode (PWN), *Bursaphelenchus xylophilus* (Steiner Buhrer) Nickle, was estimated at 22 billion € (Soliman et al. 2012).

When identified by pest risk assessments as potentially harmful, non-native pests and pathogens must be monitored upon entry. Efficient monitoring allows eradication before establishment, or at least containment in contingency areas. Plant pathogens can be monitored directly in the country of arrival, e.g. by molecular analysis of imported material (plants for planting, wood and wood products, or solid wood-packaging material (SWPM) or of potentially contaminated plants. Insect-borne plant pathogens can also be traced in their vectors. *Xylella fastidiosa* is transmitted by a range of xylem sap-feeding Hemiptera (Redak et al. 2004), and local potential vectors can be identified (e.g. Hasbroucq et al. 2020 in Belgium) and used as "sentinel vectors" if the pathogen can be detected in their foregut by PCR (Cruaud et al. 2018; Godefroid et al. 2019). Other invasive pathogens that could be monitored by trapping their vectors include, among others, *Harringtonia lauricola*, the fungal agent of laurel wilt in North America, transmitted by the introduced ambrosia beetle *Xyleborus glabratus* (Coleoptera, Curculionidae, Scolytinae) (Hughes et al. 2017), and the agent of the North American thousand canker disease, *Geosmithia morbida*, vectored by the bark beetle *Pityophthorus juglandis* (Coleoptera, Curculionidae, Scolytinae), both recently introduced in Europe (Montecchio et al. 2016; EFSA 2020). This targeted surveillance involves a thorough understanding of the distribution of potential insect vectors.

Here, we discuss issues regarding the monitoring in Belgium of *Monochamus galloprovincialis* (Coleoptera, Cerambycidae), recognised in Europe as a vector of the pine wood nematode (PWN), *Bursaphelenchus xylophilus*.

B. xylophilus was introduced in Japan in the early twentieth century and caused massive damage before spreading throughout Asia. It was reported in Portugal in 1999 (Mota et al. 1999) where it colonised most of the country, mainly attacking maritime pine, *Pinus pinaster*, and local infestations have been eradicated several times in Spain, except in Galicia, where eradication is now not considered possible any more (EPPO 2025). PWN has also been established in Madeira (Zhao et al. 2014). Its only known vectors are *Monochamus* species (Coleoptera, Cerambycidae) endemic to each region of the world, where PWN has established (EFSA Plant Health Panel 2018b). PWN infection is symptomatic (trees wilting and dying) only in areas characterised by a mean air temperature higher than 19.14 °C in July (Gruffudd et al. 2016), e.g. Portugal, Spain and southern France. However, asymptomatically infected wood in northern latitudes would nevertheless face quarantine constraints on exportation, resulting in economic losses. As eradicating the disease when symptoms are not visible would prove extremely difficult (Økland et al. 2010), early detection in areas still free from the PWN is of prime importance.

In the European Union, non-European *Monochamus* spp. and *B. xylophilus* are quarantine organisms (European Commission 2019). Emergency measures to prevent the spread of PWN within the Union (European Commission 2012) request member states to conduct annual surveys on susceptible host trees. In Belgium, the Federal Agency for the Safety of the Food Chain (FASFC) has led since 2000 visual controls at import sites, and surveys in pine stands, public green areas, and logging and wood processing facilities. A nationwide trapping network for vectors was also deployed since 2013. This campaign (+ interceptions and citizen observations) yielded only 23 M. *galloprovincialis*, three *M. sartor urussovii*, one *M. sutor* and four *Monochamus* sp. between 2013 and 2022 (SuppInfo_S1). In addition, the Belgian national collections include only 11 *Monochamus* specimens belonging to five species, among which two individuals were intercepted on imported goods (A. Drumont, pers. comm.). This scarcity of records raises the question as to whether *Monochamus* species are truly native to Belgium. This hypothesis is further supported by the catalogue of Tavaklilian and Chevillotte (2025) and by the review by Akbulkut and Stamps (2012), which do not list the country in the genus' distribution range. In The Netherlands, *M. galloprovincialis* has been known as established in only one site (Schoorl), since 1949 (see Sect. "Phylogenetics studies", Phylogeographic studies, below, and SuppInfo_S3), and in Denmark, the species was considered absent until 2015 and then regularly trapped in one single location, Oksbøl (Sect. "Phylogenetics studies"; SuppInfo_S3). So, in these two countries, *M. galloprovincialis* appears to have established relatively recently and very locally.

Our study, a species distribution model (SDM) based on pheromone trapping data covering the whole of Europe, was thus designed to model the distribution range of *Monochamus* spp. and identify possible gaps therein, where the genus is sparsely distributed or absent. As *M. galloprovincialis* was by far the most abundant species caught, the SDM focused on this species only. In a second approach, in order to define the genetic diversity and structure within *M. galloprovincialis* phylogeography in Europe, the insects caught in Belgium and some specimens from the Dutch and Danish breeding populations were genotyped and analysed in comparison with specimens from other European areas. Finally, as the existence of one stable local population in The Netherlands and in Denmark suggests that local stand conditions may favour or impede establishment even in areas of low probability of occurrence, a comparative study in Belgium, the Netherlands and Denmark was also carried out, focusing on stand size as a major factor determining the availability of reproductive material for the beetles (dead branches or dead trees), a necessary condition for the maintenance of stable populations.

Materials and methods

A fourfold approach was followed. We first analysed the trap data to delineate the distribution of *M. galloprovincialis*. We then developed an SDM based on these occurrences and absences. This was followed by phylogeographic studies. A comparative study of pine coverage in Belgium, the Netherlands and Denmark complemented work, to highlight monitoring priorities in Belgium.

M. galloprovincialis occurrences

The study was based on a trapping network of 37 contributors in 32 European countries deployed in the summer from 2008 to 2019. The most widespread species caught was *M. galloprovincialis*, and we thus focused on this species. The compiled dataset consists of 4914 observations (absence or presence) defined by the traps and lures used, the geographical coordinates of the traps, the number of beetles caught, the contributor and the year. For a summary, see SuppInfo_S2; full data: https://doi.org/10.5281/zenodo.13629934.

As the different lures and traps used vary in efficiency, a confidence score (0–2: SuppInfo-S2) was established for each lure and trap, based on a literature review. Only the observations with the best scores (2) for both lures and traps were analysed, resulting in a total of 1,790 out of 2,341 presences and a total of 1,165 out of 2,573 absences (Fig. 1). The trap systems retained included a Crosstrap® (Econex, Murcia, Spain), multifunnel and cross-vane traps baited with a Galloprotect Pack® as a lure (SEDQ, Barcelona, Spain; components: monochamol (2-undecyloxyethan-1-ol), α-pinene, ipsenol and 2-methyl-3-buten-1-ol).

The species distribution model

Species distribution models (SDMs) are tools that spatially associate a species occurrence or abundance, on the one hand, and environmental data, on the other hand, to relate "species distribution data (occurrence or abundance at known locations) with information on the environmental and/or spatial characteristics of those locations", and "provide understanding and/or to predict the species' distribution across a landscape" (Elith and Leathwick 2009).

Explanatory variables

Nine variables related to climate (Hijmans et al. 2005), *Pinus spp.* distribution (de Rigo et al. 2016) and topography (Amatulli et al. 2018), such as mean annual temperature (°C); mean diurnal temperature range (°C); temperature seasonality (°C); temperature annual range (°C); annual precipitation (mm); precipitation seasonality (mm); precipitation of the warmest quarter (mm); elevation (m), the probability of *Pinus spp.* presence, all available in a raster format, and the total number of traps (nbT), were considered. The spatial resolution and extent of this dataset were harmonised at 30 arc-seconds ranging from − 19 to 47 degrees of longitude and from 31 to 72 degrees of latitude. Although the climatic data used in our analyses cover the period 1950–2000, we assume that the spatial patterns they represent remain relevant for our study. Indeed, our objective was not to capture short-term climatic fluctuations but to characterise broad scale and relative climatic gradients across Europe. These gradients (e.g. temperature and precipitation contrasts among regions) have remained largely consistent over time, even under recent warming trends.

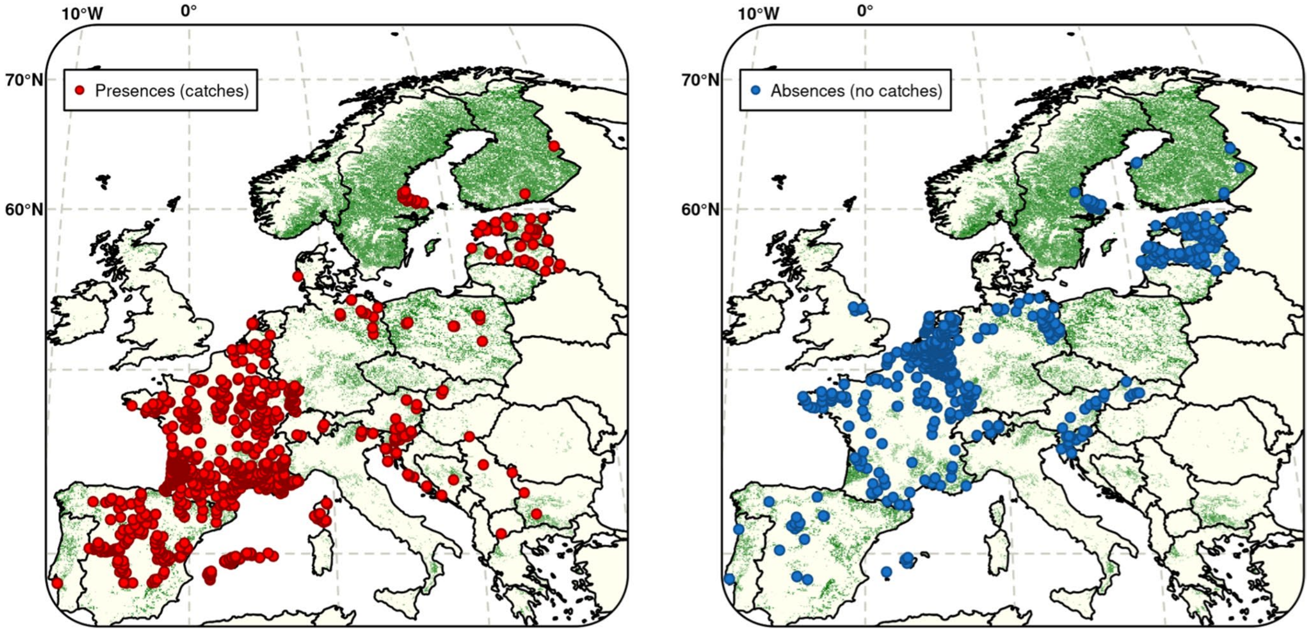

Fig. 1 Presences and absences of *M. galloprovincialis* at the trap locations (2008–2019)

A multi-scale approach

The spatial grains at which a species responds to its environment and the grains at which those relationships are analysed are critical aspects of species distribution models (Mertes and Jetz 2018). Species distribution models trained at inappropriate spatial scales can lead to apparent poor model fitting and could potentially lead to increasing the spatial autocorrelation of model residuals (Bradter et al. 2013).

Thus, a multi-scale modelling approach was selected to analyse the distribution of *M. galloprovincialis*. First, regular square tessellations covering the study area were created using the “st_make_grid” function from the “sf” package (Pebesma 2018). Tessellations were obtained by varying the size of the edges of basis tiles from 50 to 300 km with steps of 5 km. This resulted in 51 sampling grids at various resolutions (fine to coarse) but of constant geographical extent. It is assumed that uncertainty regarding the initial position of regular square tessellations (RST) should be accounted for. Therefore, the initial position of RST was shifted every 5 km on longitudinal and latitudinal axes, and the analyses were replicated over different sets of RST. The total number of possible shifts varies from 100 to 3600 depending on the size of the edges of basis tiles that form the RST. Fifteen different initial positions of RST were randomly selected for each RST resolution and were considered for the analysis. Then, the values of cells of predictor variables and the distribution of *M. galloprovincialis* were extracted and summarised at the locations of basis tiles for each sampling grid using the following procedure:

1) *M. galloprovincialis* First, the duplicate observations falling in the same pixel defined by the explanatory variables were summarised to label each pixel as presence (1224 pixels) or absence (593 pixels). Then, the number of presences or absences and the total number of pixels with observations were extracted for each basis tile.
2) *Climatic data and elevation* The mean pixel value, weighted by the fraction of each pixel that is covered by the basis tiles, was obtained.
3) *Pinus* spp. The proportion of basis tiles covered by forest was approximated by interpreting the relative probability of presence of *Pinus* spp. as the proportion of pixels covered by *Pinus* spp. First, the pixel values were summed and weighted by the product of the pixel area and the fraction of each pixel that is covered by the basis tile. This weighted sum is then divided by the area of the basis tile covered by pixels.

Modelling

GLMs were used to quantify the effect of predictor variables on the “proportion of pixels with the presence of”*M. galloprovincialis*” (as evidenced by trap capture). GLMs were fitted using a binomial distribution with the number of “presence” results as the number of successes in a binomial experiment and the total number of pixels with traps as the number of trials. The presence of spatial autocorrelation in the model residuals was evaluated using the Moran I statistic for areal data (Cliff and Ord 1981). Deviance ratios for GLM fits (Chambers and Hastie 1992) were used to quantify the model error reduction due to the inclusion of each term of the formula in the GLM. A forward variable selection was used to select the predictor variables of the final models, beginning with a model that contains the total number of traps (nbT) as a control variable of potential sampling bias and then adding the most important variables (highest deviance ratio) one after the other. Only the deviance ratio greater than or equal to 0.1 was considered in the model comparison process to focus on the main effects influencing the spatial distribution of *M. galloprovincialis*. The goodness of fit of the final models at each spatial scale was calculated using Pseudo-R^2 (Cohen and Cohen 2003). Ultimately, a single spatial grain was selected to compute a prediction map of the proportion of pixels with the presence of *M. galloprovincialis* across Europe. The spatial grain selected represented a good trade-off between the goodness of fit of the model (as high as possible) and the degree of spatial autocorrelation among residuals (as low as possible). At this step, spatial generalised linear mixed models (GLMMs) were used to consider spatial autocorrelation among residuals of the models and to produce a spatially smooth map of the proportion of pixels with the presence of *M. galloprovincialis.* Random effects with a Besag York Mollie (BYM) conditional autoregressive (CAR) prior (Besag et al. 1991; Blangiardo and Cameletti 2015) were used to that end. A BYM model includes both an intrinsic CAR model and an independent and identically distributed Gaussian random effect model (iid) to include spatially and non-spatially structured error terms. BYM, CAR and iid models were fitted and compared using the widely applicable information criterion (WAIC) (Watanabe 2013). The models with the lowest WAIC values were considered the best trade-offs between a reduction of the model errors and the over-parametrisation of models. The models were fitted using the integrated nested Laplace approximation (INLA) (Gomez-Rubio et al. 2021) specifying parameters of prior distributions to log-Gamma (1, 0.00005) for the spatially unstructured and structured random effects, which is the default specification of these parameters in R-INLA. Only the basis tiles covered by at least 20% of the predictor variables and that include at least five separate traps were used to train the model, while the model predictions were calculated for the basis tiles covered by at least 20% of the predictor variables, regardless of the number of traps in the tile.

Phylogeographic studies

Monochamus samples used for genetic analysis

The *M. galloprovincialis* specimens analysed originated from the Belgian national collection (1870; 1940) and from the 2013–2022 trapping campaign in Belgium, as well as from Dutch and Danish sites (Schoorl and Oksbøl, respectively) harbouring an established population. Regular catches have been reported yearly at one unique site in each of these two countries, indicating the existence of an established population (NL since 1949: Heijerman et al. 2009, 2011, 2013, 2014; Heijerman and Noordijk 2016, 2017, 2018; DK since 2015: Euphresco 2018; Miljø- og Fødevareministeriet 2018). A detailed list is provided in Table 1 in Suppinfo_S3.

DNA was extracted from one or two legs of each specimen using a Nucleospin Kit (Macherey–Nagel, Düren, Germany), following the manufacturer's instructions. Individuals were previously sequenced for the mitochondrial DNA fragment gene COI (primers used C1-J-2183a and TL2-N-3014, Simon et al. 1994) to confirm the specific status of each specimen trapped.

Microsatellite genotyping

Each specimen was genotyped at 10 microsatellite loci (Mon17, Mon23, Mon27, Mon30, Mon31, Mon35, Mon41, Mon42, Mon44, Mon45), following Haran and Roux-Morabito (2014), plus two newly defined polymorphic loci (Mon106 Mon116, see Table 2 in SuppInfo-S3). Multiplexed PCR was performed following Haran et al. (2017a), while the two new loci were amplified separately. Genotypes were scored using GENEMAPPER V 4.1 (Applied Biosystems®). Due to numerous missing data, loci Mon30 and Mon45 were excluded from further analysis.

Data analysis

Allele frequency, observed and unbiased expected heterozygosity, and the number of private alleles were estimated using GENALEX 6.5 (Peakall and Smouse 2012). The deficit of heterozygote was tested using GENEPOP on the web (Rousset 2008). The genetic population structure was inferred with the Bayesian model-based cluster analysis implemented in Structure 2.3.4 (Pritchard et al. 2000). The admixture model with correlated allele frequencies was run with no prior information about sampling locations. The genotypes were analysed by running 10 repeats for K values ranging from 1 to 10. Each run consisted of a burn-in period of 100,000 iterations, followed by 500,000 Markov Chain Monte Carlo (MCMC) iterations. Using the website Structure Harvester (Earl and von Holdt 2012), we used the Evanno method to visualise the evolution of Delta K (mean likelihood of K/ variance of likelihood for the same K: Evanno et al. 2005) and determine the number of clusters (K) that best-fitted the data.

To detect recent gene flow between the three countries, we estimated the frequency and origin of first-generation migrants using assignment tests implemented in GeneClass 2.0 (Piry et al. 2004). We tested the likelihood of each individual belonging to Belgium, The Netherlands and Denmark used the Bayesian-based approach (Likelihood (L) = L population of origin/L maximum in all populations) developed by Rannala and Mountain (1997). We used the Monte Carlo resampling method (Paetkau et al. 2004), using 1,000 simulated genotypes, with a threshold for migrant detection set to 0.01.

To assign Belgium, Danish and Dutch populations to reference European populations (used in Haran et al. 2017a), we performed population clustering with Structure 2.3.4 using previous settings with a burn-in period of 80,000 iterations, followed by 300,000 Markov chain Monte Carlo (MCMC) iterations. We finally performed assignment tests, considering Belgian, Danish and Dutch specimens of unknown origins using the function assign.X in the R package assignPOP (Chen et al. 2018) that employs supervised machine-learning methods. Assignment tests give the probability of an individual's multilocus genotype of belonging to reference populations described in Haran et al. (2017a). Due to assorted data samples, we retained a subset of eight shared loci between the two datasets (all except loci 46 and 47, Haran et al. 2017a) for both analyses.

A comparative study of pine coverage in Belgium, The Netherlands and Denmark

Belgium

The analysis was limited to Flanders, as there is very little pine (mostly *Pinus sylvestris*) in the rest of Belgium. To estimate the area of pine stands, we used the Flemish Biologische Waarderingskaart (BWK 2023). In this spatial vector dataset, the biotope is described by eight codes of decreasing importance. We included the polygons with any pine-related biotope (mostly *P. sylvestris* stands) in the three most important biotope descriptors (EENH1 to EENH3) of the eight available (to avoid including polygons with very few pines; robustness tests showed that including the EENH fields of lower importance had little effect on the result). To group spatially close polygons, we used the following approach: (1) add a 20-m buffer around the polygons; (2) merge covering polygons and then split the ones that do not touch; (3) add a negative buffer of 20 m; (4) calculate the area of the resulting polygons (ha). Consequently, all *Pinus* polygons less than 40 m apart were considered to belong to the same forest entity.

A comparison of pine stand size in Belgium, The Netherlands and Denmark

We used the Corine Land Cover (CLC) 100 × 100 m raster for 2018 and extracted the pixels corresponding to Coniferous forests and Mixed forests (CLC 2018). Touching pixels were considered as the same "forest entity"; the areas were computed in hectares. The advantage of CLC over BWK is that it is available all over Europe. However, it is less precise (100 × 100 m resolution) and does not contain information about *Pinus* trees but only about "coniferous trees". In Wallonia, coniferous and mixed forests do not contain much pine (Belgian National Climate Commission 2018), so Wallonia was excluded. In Flanders (Belgian National Climate Commission 2018) and in The Netherlands (Schelhaas et al. 2022), the conifers are mainly pines. Hence, these coniferous forests pixels were used as a coarse proxy to estimate areas of pine stands in the three countries, even though, in Denmark, pines represent only 23% of the conifers (Larsen et al. 2010).

Results

The species distribution model

Variables selection

Three predictors were selected in the final model: the total number of traps (nbT), the mean diurnal temperature range (DiurnalRange) and the probability of *Pinus spp.* presence (P.spp) based on the forward variable selection (Fig. 2).

The deviance ratios and coefficients of the GLM models run with the selected predictor variables are presented in Fig. 3.

The analysis of deviance and model coefficients of final GLM indicates that the mean diurnal temperature range was an important predictor variable in the final models regardless of the spatial grain considered. The mean diurnal temperature range was positively related to the proportion of pixels with the presence of *M. galloprovincialis*. The Pine Forest cover (*P.* spp) model coefficient was relatively high but decreased when the spatial grain became coarser and was positively related to the proportion of pixels with the presence of *M. galloprovincialis*. The effect of the total number of traps (nbT), the control variable of potential sampling bias, was low but increased when the spatial grain became coarser and was negatively related to the proportion of pixels where *M. galloprovincialis* was present.

Final models

The pseudo-R^2 and Moran's I statistics of final models for the different spatial grains are shown in Fig. 4.

The pseudo-R^2 increases continuously when the spatial grain becomes coarser, while the Moran I statistic decreases along the same gradient until a plateau is reached. The mean Moran's I is minimal around a spatial grain of 225 km of resolution. This grain was selected to obtain a spatial prediction

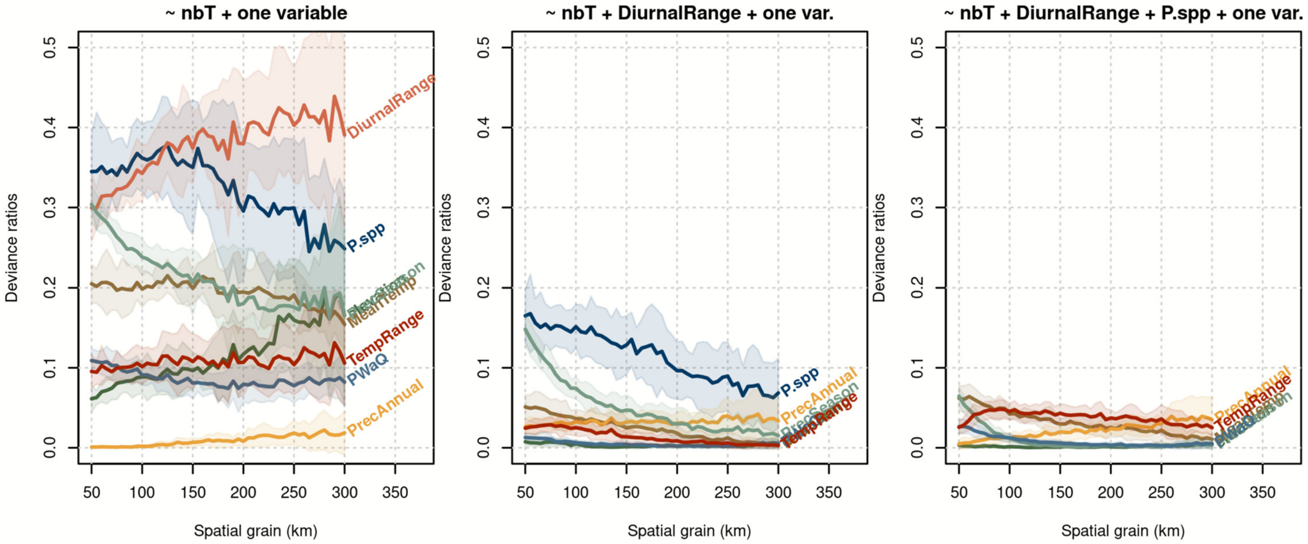

Fig. 2 Forward variable selection based on the deviance ratios between the deviance accounted for by a predictor variable and the null deviance of GLM models run with different sets of predictor variables and for different RST resolutions (spatial grain in km). The solid lines represent the mean deviance ratios of predictor variables over one RST resolution, whilst transparent polygons represent the standard deviation obtained by varying the initial positions of RST

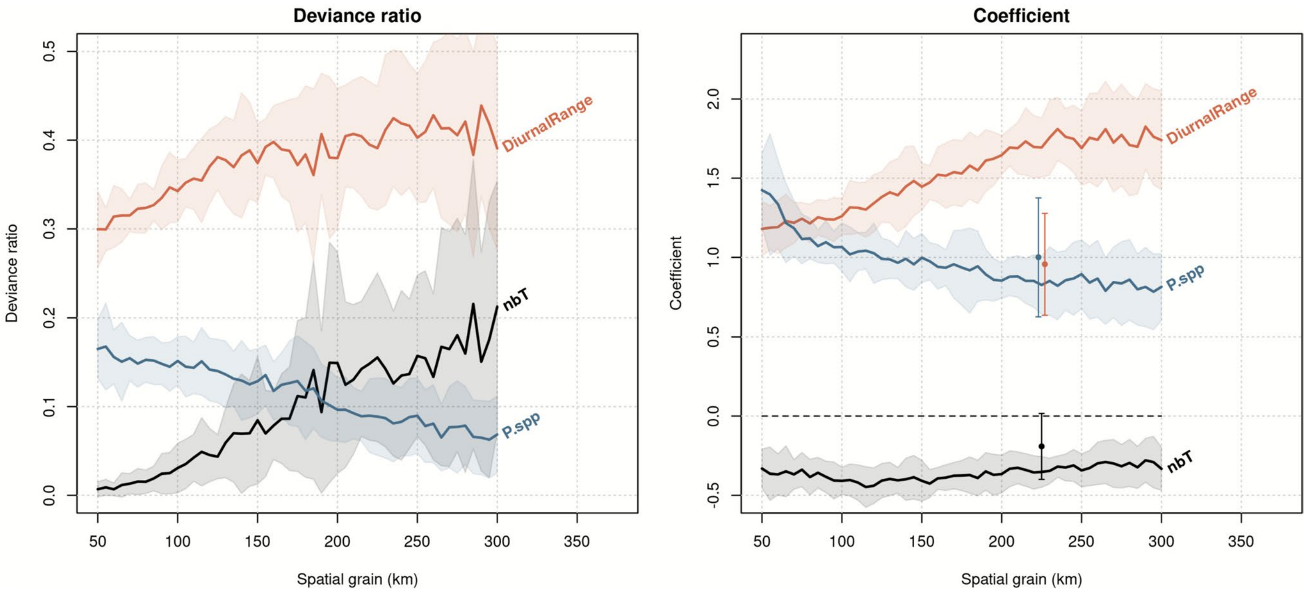

Fig. 3 The deviance ratios (left panel) between the deviance accounted for by a predictor variable and the null deviance of GLM models run with two predictor variables (the number of traps and the mean diurnal temperature range) and the regression coefficients of those predictor variables (right panel) for different RST resolutions. The solid lines represent the mean deviance ratios and the mean coefficient calculated over one RST resolution, whilst transparent ribbons represent the standard deviation obtained by varying the initial positions of RST. The posterior marginal distribution of variables' coefficients of the CAR model was also shown in this figure at 225 km of resolution

of the area occupied by *M. galloprovincialis* across Europe, while minimising the effect of spatial autocorrelation in the model. At this grain, two different models were compared to account for spatial autocorrelation among model residuals: the CAR model and the BYM model. The lower WAIC was obtained in 82% of cases with the CAR models and in 18% of cases with the BYM models. Therefore, the CAR model was selected to fit the final models (Fig. 5).

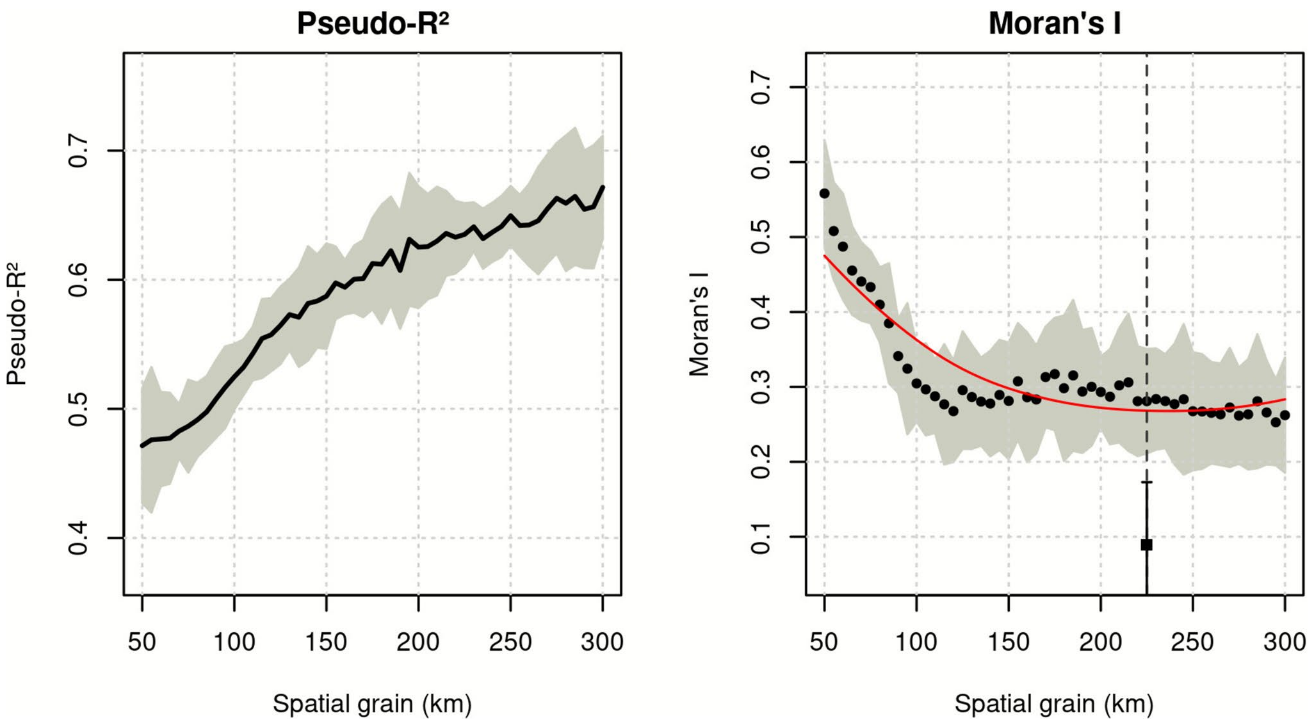

Fig. 4 Model assessment (pseudo-R^2 and Moran's I) at different spatial grains**.** The black lines or dots represent the mean pseudo-R^2 and Moran's I calculated over one RST resolution, whilst the grey areas represent the standard deviation obtained by varying the initial positions of RST. A local polynomial regression (Chambers and Hastie 1992), represented by the red line in the right panel, was used to examine the level to which Moran's I is minimal (dashed line). The mean Moran's I was obtained based on the raw GLM residuals (response variable—prediction). The Moran I of the CAR models was also shown in this figure (square with error bar at 225 km of resolution) and obtained based on the difference between the response variable and the posterior means of the models

Phylogeographic studies

Genetic analysis and structure of the Belgian, Danish and Dutch specimens

Because of the small sample size in each locality, genetic diversity analysis was conducted considering all Belgian specimens (trapped + museum) grouped as one population. The total number of alleles per locus ranged from two (Mon23) to 10 (Mon106) over the three populations analysed. Mean allelic richness and private allelic richness were highest among the Belgian specimens (Table 1). A significant departure from the Hardy–Weinberg equilibrium in favour of a heterozygote deficit was found in all three populations ($p < 0.0001$) with high F_{IS} values, especially in Denmark and the Netherlands, for which the fixation index reached 0.55 and 0.604, respectively.

The STRUCTURE analysis (Fig. 6) revealed two major genetic clusters grouping all Belgian (sites 1 to 12) and Danish specimens (population 14) in the same cluster, and Dutch specimens (population 13) in the second cluster. No genotype geographical distribution pattern could be identified in Belgium. When considering the clustering that best-fitted the data (k = 4–Fig. 7 left), four individuals were separated from the rest of the specimens from cluster 1 (Fig. 7 right). They exhibited similar divergent genotypes although originating from different Belgian sites and different collection dates, i.e. Famenne 2018 (1), Vallon de la Briserie 2018 (6) and Elsakker 2019 (12). Consequently, subpopulations from Vallon de la Briserie (6) and Elsakker (12) displayed contrasted genotypes regarding specimens trapped at the same site.

Regarding possible recent migration events between Belgian, Dutch and Danish specimens, likelihood-based statistics (Rannala and Mountain 1997) in combination with the resampling method of Paetkau et al. (2004) allowed us to assign four Belgian specimens, putative migrants, or of migrant ancestry, to the Denmark population, one trapped at Malmedy ($p < 0.0001$) and the three others at Vagevuurbossen, Tessenderloo and Elsakker ($p < 0.03$) (Table 2).

Origin of the Belgian, Dutch and Danish populations

We approached the question of ancestry employing population clustering and assignment tests combining genotyped specimens under study with reference populations previously genotyped at the European scale. STRUCTURE analysis performed for a subset of eight loci confirmed the

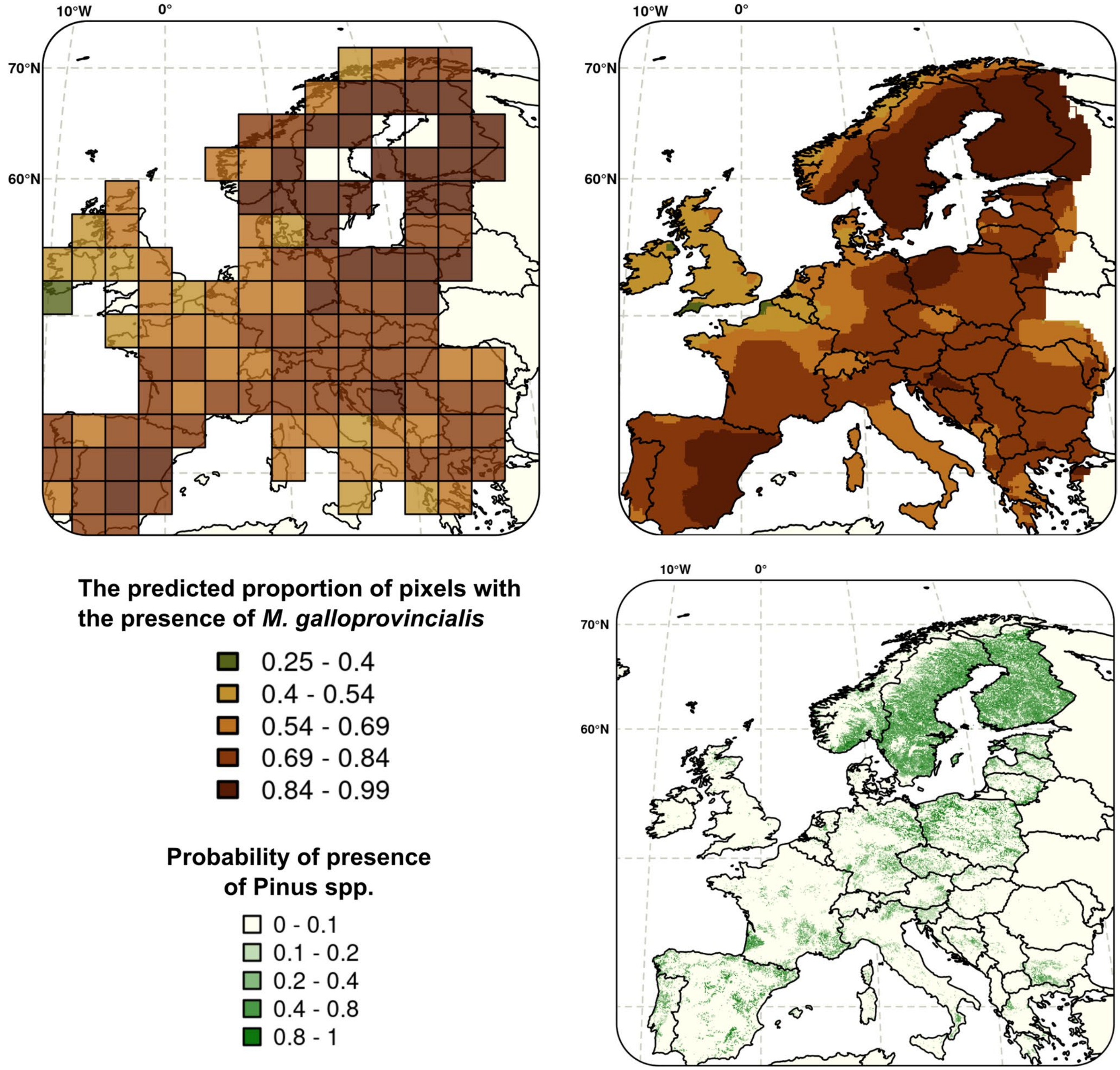

Fig. 5 Predictive maps of the posterior means of the proportion of pixels with the presence of *M. galloprovincialis* obtained with the CAR GLMM models for a spatial grain of 225 km of resolution. The top left panel represents one prediction for a specific initial position of RST, whilst the top right panel represents the mean predictive maps calculated over all the initial positions of RST for a 225-km resolution. The bottom right panel represents the relative probability of presence of *Pinus* spp

phylogeographic pattern already observed in Haran et al. (2017a) and mainly assigned the Belgian specimens to a main genetic cluster grouping most of the populations from North-Eastern Europe (Fig. 8).

Table 3 in SuppInfo-S3 shows the probabilities that a genotyped specimen is from, or has ancestry in, the other populations. None of the specimens analysed could be assigned to their source population. Specimens showed mixed genetic contributions, represented by multiple reference populations, and could not be confidently assigned in most cases. Nevertheless, these results confirm a partial ancestral origin for Belgium specimens from North-eastern Europe (13/19) and, to a lesser extent, a closeness to Danish samples (5/8). Dutch samples, however, showed higher genetic contributions from South-western Europe (including Portugal for two individuals and Spain for three individuals).

The small numbers of insects trapped and the low probability of local occurrence, according to the SDM, suggest

Table 1 Main genetic diversity parameters of the populations of *M. galloprovincialis* in Belgium, the Netherlands and Denmark

Populations		N	Na	Ne	Np	Ho	He	uHe	F
Belgium	*Mean*	18.300	5.200	2.867	1.200	0.384	0.574	0.590	0.296
	SEM	0.260	0.772	0.380	0.249	0.057	0.071	0.074	0.071
The Netherlands	*Mean*	9.900	3.400	2.243	0.300	0.201	0.460	0.484	0.604
	SEM	0.100	0.581	0.319	0.153	0.056	0.079	0.083	0.073
Denmark	*Mean*	7.500	3.100	2.274	0.200	0.241	0.472	0.505	0.550
	SEM	0.224	0.407	0.308	0.133	0.071	0.077	0.083	0.098

N: Sample size, Na: number of alleles, Ne: number of effective alleles, Np: private alleles, Ho: observed heterozygosity, uHe: unbiased expected heterozygosity, F: fixation index

that *M. galloprovincialis* has not established populations in the country but that the trapped insects are rather from exogenous origins. Even if we cannot exclude the fact that some specimens caught in Belgium had been resident in endemic low-level populations, native or introduced, our results rather suggest that they originated from other locations, thus supporting a higher priority of entry points in the monitoring strategy of the Belgian NPPO.

A comparative study of pine coverage in Belgium, The Netherlands and Denmark

Pine coverage in Belgium (Flanders)

Among the 7,095 identified pine stands, 6,912 (97.4%) are smaller than 50 ha, (Fig. 9) only three (0.04%) are larger than 1,000 ha, and two are larger than 3,000 ha (Tables 1, 2 and Fig. 1 in Suppinfo_S4). Overall, the Flemish pine landscape is composed mainly (98.8%) of small pine stands covering less than 100 ha, with a large majority (91% of the total pine coverage) of small patches occupying each less than 10 ha (BWK 2023).

A comparison of conifer stands areas in Belgium, The Netherlands and Denmark

There are more large stands in The Netherlands and Denmark than in Belgium (Table 3 and Fig. 9) (CLC 2018), with 12 stands larger than 500 ha in Belgium (Flanders), against 57 and 61 in Denmark and The Netherlands, respectively.

Size of the stands where *Monochamus* spp. were trapped

Table 4 provides information regarding the stands for which spatial information was retrieved (note that the catches did not always occur in forest stands). With the exception of Hoge Vijverbos (CLC: 875 ha; no data in BWK), the Belgian forests where *Monochamus* species were found are smaller than the habitats of the two permanent *M. galloprovincialis* populations in the Netherlands (Schoorl, NL: 709 ha–CLC) and Denmark (Oksbøl, DK: 1530 ha–CLC).

Synthesis—trap catches in Belgium, the Netherlands (Schoorl) and Denmark (Oksbøl)

Almost the whole of Belgium, north-western France, a small part of The Netherlands and a part of north-western Germany is characterised by a lower SDM status than the neighbouring areas (Fig. 10). One single *M. galloprovincialis* adult was generally caught at each locality in Belgium (Table 5), with a few exceptions: Elsakker (2013, 2018, 2019, 2021); Heidebos (twice the same year, but one month apart); Tessenderloo 2 (twice the same year but two months apart), Vagevuurbossen (2019, 2020, 2022), Vallon de la Briserie (2018 (two individuals on the same date), 2020), Vloethemveld (2018, 2022). One *M. sartor urussovii* was also caught in Kluisbos Kluisbergen (2019) and in Elsakker (2013). The *M. galloprovincialis* probability of occurrence inferred by the SDM at these locations (0.40 to 0.55) does not differ from that in Schoorl, NL (0.55) and in Oksbøl, DK (0.53) (Table 5). In all cases, the trapping sites were within flying distance to potential entry sites (ports, logistic sites, companies importing wood or goods with SWPM).

Discussion

The prevention or early management of biological invasions relies on strict trade regulations (Roy et al. 2014) and on carefully planned surveillance possibly combined with spread modelling (Alonso Chávez et al. 2025). In the case of Cerambycidae, the development of wide-ranging lures presently allows very efficient monitoring at European ports (Rassati et al. 2015; Hoch et al. 2020; Roques et al. 2023; Santoiemma et al. 2024). When a non-native pathogen is vectored by native insect species, as in the *M. galloprovincialis*–*B. xylophilus* association, the vectors should be monitored and tested for the pathogen both in their native habitat and at entry points. Demonstrating vector absence in local natural areas could then allow for reducing the high costs involved. In our study, the proximity of each site to potential entry points, and the scarce trapping results support

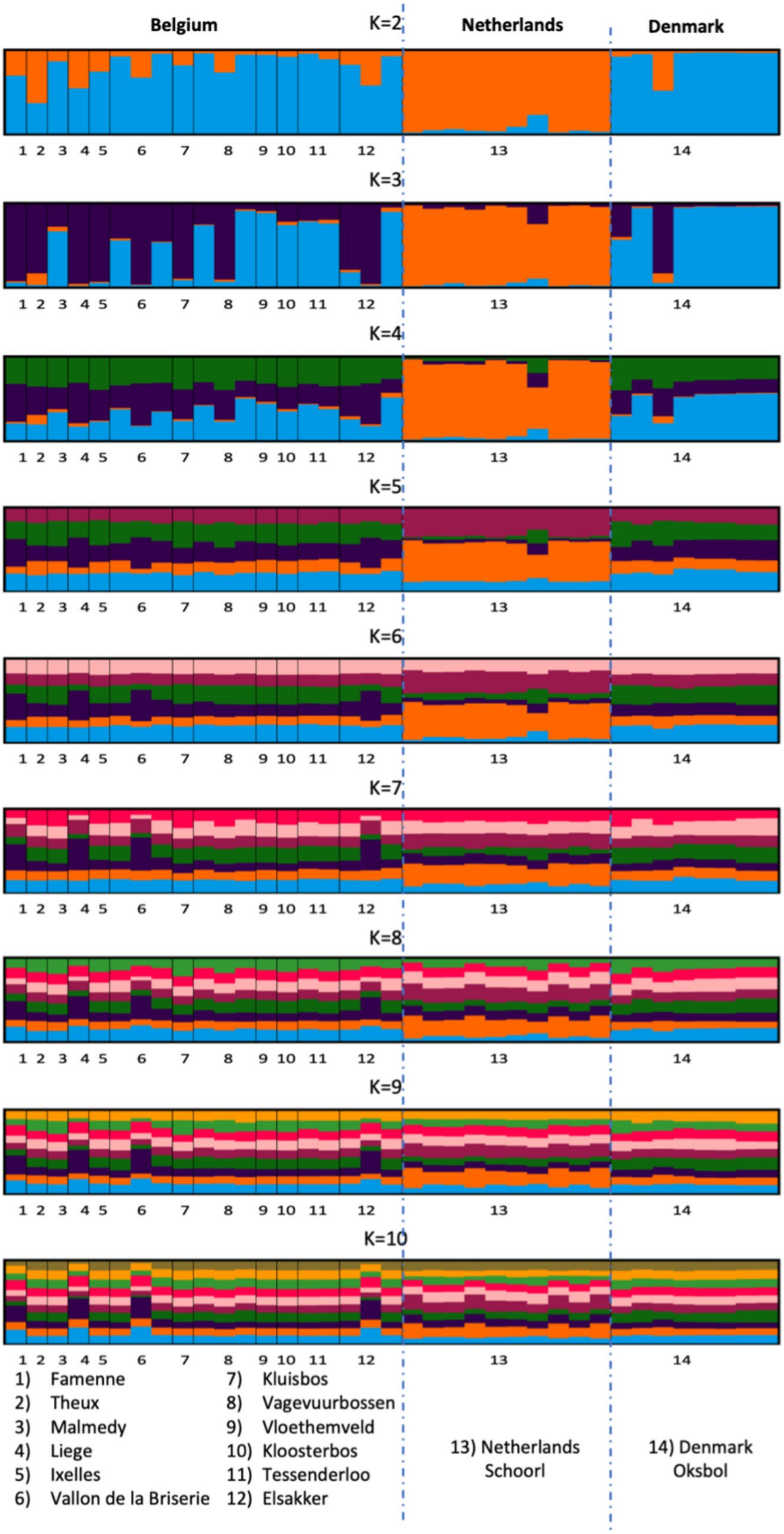

Fig. 6 Genetic clustering of *M. galloprovincialis* specimens from Belgium, The Netherland and Denmark inferred from STRUCTURE for 10 microsatellite loci. Barplots of individual assignments for each K are shown. Population numbers are, respectively: (1) Famenne 2018; (2) Theux 2022; (3) Malmedy 2022; (4) Liege 1940; (5) Ixelles 1870; (6) Vallon de la Briserie (3 specimens 2018, 2018, 2020); (7) Kluisbos 2020; (8) Vagevuurbossen (3 specimens 2019, 2020, 2022); (9) Vloethemveld 2022; (10) Kloosterbos 2013; (11) Tessenderloo (2 specimens 2020); (12) Elsakker (3 specimens 2013, 2019, 2021); (13) Netherlands Schoorl 2017; (14) Denmark Oksbøl 2016

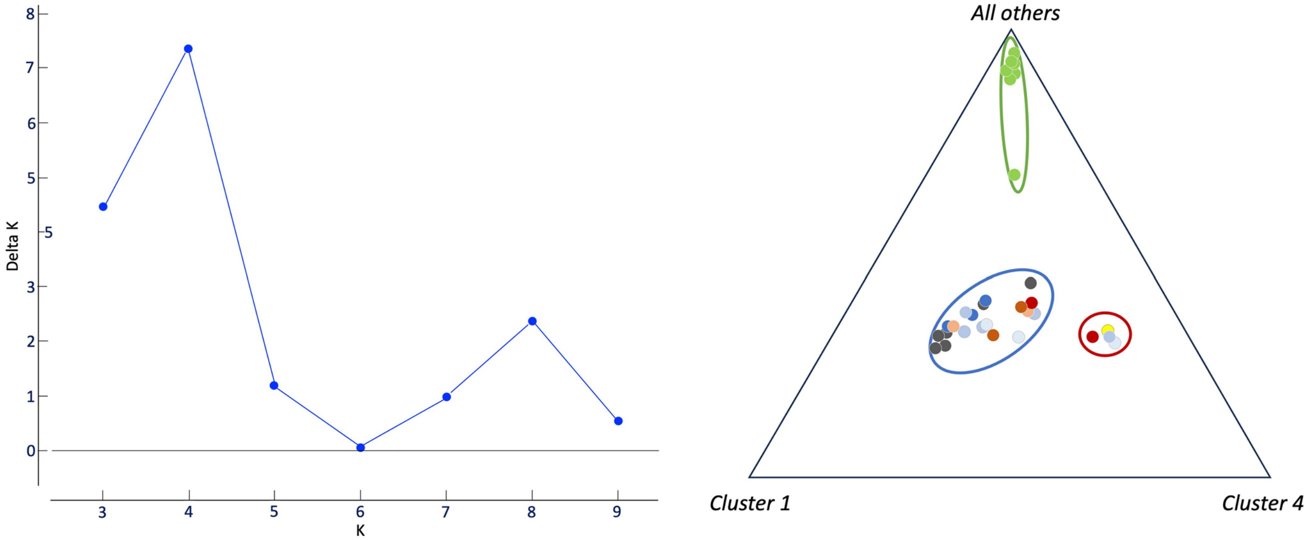

Fig. 7 Left: K = 4 was the highest ΔK value (Evanno et al. 2005). Right: Triangle plot at K = 4. Green circle = all specimens from The Netherlands; red circle = 4 Belgian specimens from (1) Famenne 2018, (4) Liège 1940, (6) Vallon de la Briserie 2018, (12) Elsakker 2019; blue circle = mix of specimens from Belgium and Denmark

Table 2 Putative immigrants between Belgium, Dutch and Danish specimens detected with Geneclass 2.0 ($p < 0.03$)

Sample	Origin	Probability	Belgium Log$_{10}$(L)	The Netherlands Log$_{10}$(L)	Denmark Log$_{10}$(L)	Nb of loci
Belgium_Malmedy_2022	Belgium	0.0000	14.880	17.745	11.106	10
Belgium_Vagevuurbossen_2019	Belgium	0.0189	10.810	16.938	10.096	10
Belgium_Tessenderloo_2020	Belgium	0.0291	10.239	13.836	9.505	10
Belgium_Elsakker	Belgium	0.0168	7.675	13.040	6.499	9

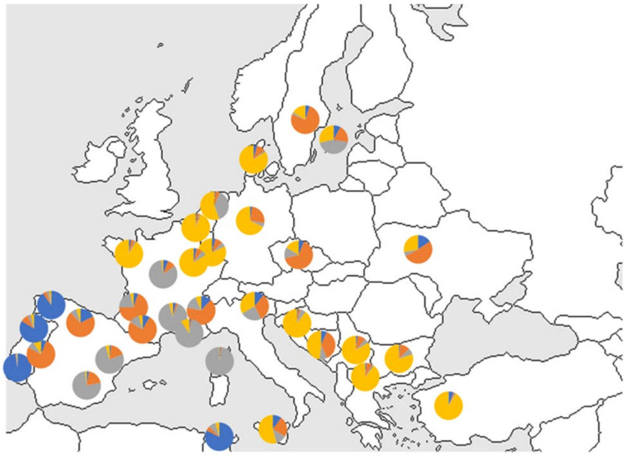

Fig. 8 Genetic clustering at eight loci inferred by STRUCTURE analysis. Membership of 35 European populations of *M. galloprovincialis* for the best K value, K = 4 genetic clusters

Table 3 Conifer stands in Belgium (Flanders), Denmark and The Netherlands

Area classes	Flanders	Denmark	The Netherlands
0–10 ha	2	26	44
10–50 ha	107	406	126
50–100 ha	92	288	91
100–200 ha	62	161	79
200–500 ha	34	122	75
500–1,000 ha	6	39	34
> 1,000 ha	6	18	27

the hypothesis of a likely exogenous origin of the insects trapped in Belgium, although we cannot totally exclude the existence of very small, probably unstable local populations. Similarly, natural entry by flight from neighbouring countries is not totally impossible, although the few observations of the species close to Belgium in France, Germany and The Netherlands in the GBIF records are located beyond flying

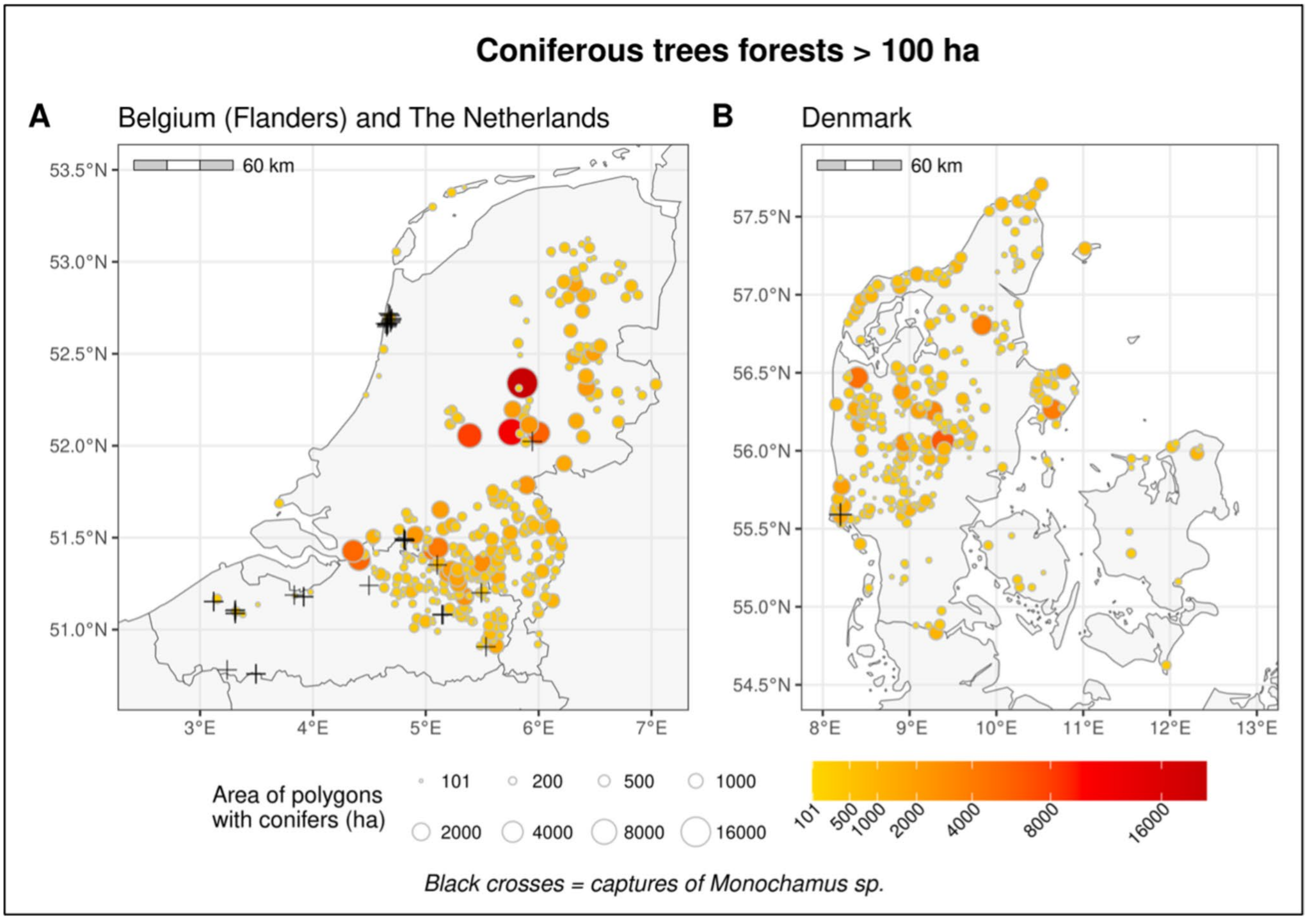

Fig. 9 Coniferous forests larger than 100 ha in Belgium (Flanders) and The Netherlands (**A**), and Denmark (**B**) with locations of *Monochamus sp.* captures (black crosses)

Table 4 Area of the forest stands in which *Monochamus* spp. were captured in Belgium, The Netherlands and Denmark

BWK_*Pinus* (ha)	CLC_mixed (ha)	CLC conifers (ha)	Location	Species
34.3	NA	117.3	Bezoensbeek	*M. galloprovincialis*
89.7	NA	NA	Bulskampveld	*M. galloprovincialis*
68.1	NA	89.1	Elsakker	*M. galloprovincialis* *M. sartor urussovi*
18.7	NA	NA	Heidebos	*M. galloprovincialis*
	NA	874.9	Hoge Vijverbos	*M. galloprovincialis*
	NA	128.2	Kloosterbos	*M. galloprovincialis*
	28.1	NA	Kluisbos Kluisbergen	*M. galloprovincialis* *M. sartor urussovii*
	NA	61.1	Kolisbos	*M. galloprovincialis*
5.0	NA	NA	Tessenderloo 1	*M. galloprovincialis*
70.5	NA	302.4	Vagevuurbossen	*M. galloprovincialis*
14.1	NA	35	Vloethemveld	*M. galloprovincialis*
	NA	709.4	NL—Schoorl	*M. galloprovincialis*
	NA	1529.9	DK—Oksbøl	*M. galloprovincialis*

Estimations based on various datasets: polygons containing *Pinus* from the BWK (2023), mixed coniferous forests from CLC distance (maxima of 45 km (males) and 65 km (females), according to David et al. 2014).

Monochamus galloprovincialis was already trapped at or around entry points in other countries (Rassati et al. 2014, 2015; Mas et al. 2023; Santoiemma et al. 2024). After introduction, the conditions for a successful establishment would be: (i) favourable climatic conditions; (ii) a minimal stand size guaranteeing sufficient reproductive resources (e.g. dead or dying pine branches or trees where the larvae could develop) and (iii) a minimal propagule size. Osada et al. (2018) analysed historical (1980–2011) records of *M. alternatus* abundance and Pine Wilt Disease infection in Japan and observed an Allee effect reducing the survival chance of sparse populations.

The beetles would mainly travel as immature stages in wood, with the young adults emerging after arrival. They would require 2–3 weeks for maturation feeding (Naves et al. 2006) on fresh pine twigs and do not respond to pheromones during this period (Etxebeste et al. 2016). They would thus need to fly to pine stands near the entry sites.

Genetic analysis revealed that none of the specimens analysed could be assigned to a source population when compared to European populations (membership probabilities: Table 3 in Suppinfo-S3). All trapped specimens showed mixed genetic contributions, represented by multiple reference populations, and could not be confidently assigned in most cases. Nevertheless, this approach helps to fill the phylogeographic gap in North-eastern Europe by incorporating data from three newly sampled countries, and confirms a partial ancestral origin of Belgium's specimens from North-eastern Europe (13/19) and, to a lesser extent, a closeness to Danish samples (5/8). Dutch samples, however, showed higher genetic contributions from South-western Europe (including Portugal for two individuals and Spain for three individuals).

The dispersal of *M. galloprovincialis* has been studied with flight mills by David et al. (2014). Over their lifespan (ca 100 days), males and females would fly an average distance of 16 km (maxima: 45 km for females; 63 km for males). In mark-release-recapture experiments, Mas et al. (2013) recorded maximal flights of 14 and 22 km, and Torres-Vila et al. (2015) reported an average of 107–122 m dispersal. Robinet et al. (2019), combining the results of flight mill experiments (David et al. 2014) and those of a release-recapture experiment, developed a random-walk flight dispersal model yielding a mean dispersal distance of ca 13 km as the crow flies, with ca 80% of the insects located further than 500 m from the emergence point at the end of their maturation period. Using this model (https://zenodo.org/record/1211489), we calculated that, after 120 days,

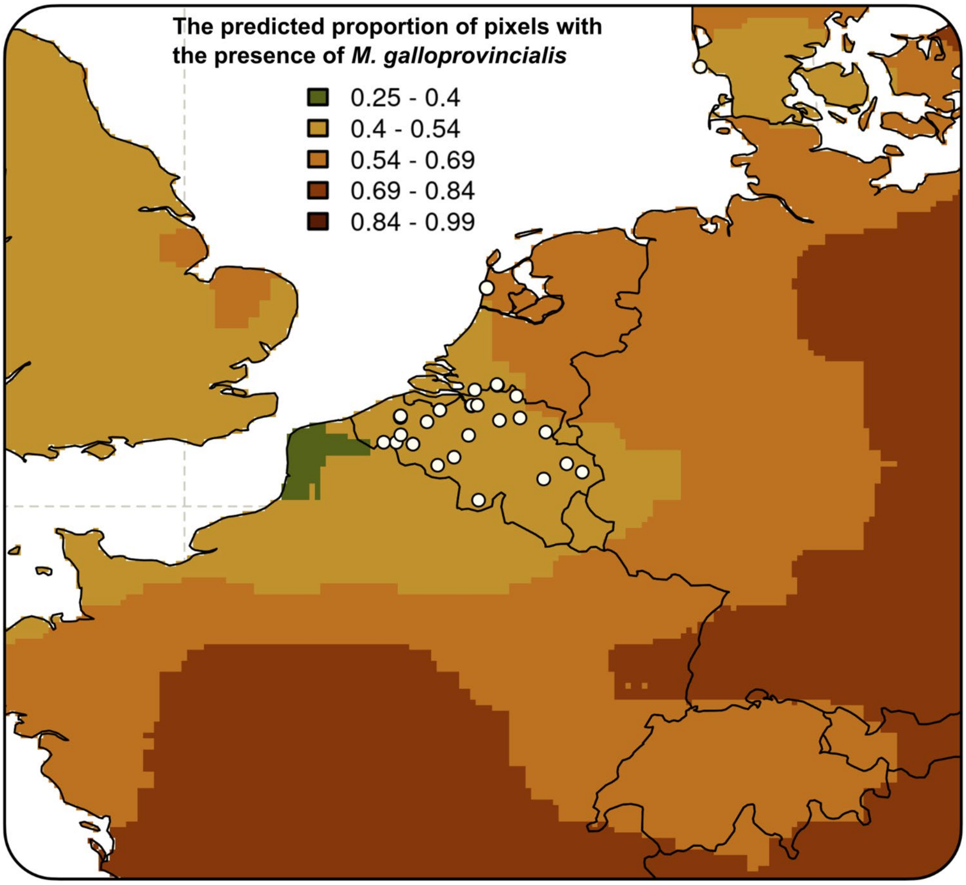

Fig. 10 SDM status (probability of occurrence for *Monochamus galloprovincialis*) in Belgium. White dots: trapping sites in Belgium

Table 5 Summary data regarding the *Monochamus* spp. catches/observations considered in Belgium, the Netherlands and Denmark

Municipalities	SDM1	Area[1]	Nb caught	Species[2]	Proximity to entry points[3]
BE—Aalbeke	0.40	NA	1	*Mg*	< 3 km: wood importer; logistics hub
BE—Antwerp Center	0.48	NA	1	*Mg*	> 7 km: port of Antwerp (235 MT of freight in 2019)
BE—Bavikhove	0.41	NA	1	*M*sp.	< 1 km: machinery factory 37 km: port of Ghent (71.5 MT of freight in 2019)
BE—Bezoensbeek	0.50	34.3[4]	1	*Mg*	Kieleberg industrial park
BE—Braine-le-Comte	0.42		1	*M*sp.	< 4 km: stone quarry; < 5 km: stone quarry; < 8 km: polymer factory; cement and concrete plant
BE—Bulskampveld	0.41	89.7[4]	1	*Mg*	< 3.5 km: Beernem industrial park (furniture factories; tiling factory; plant nursery; machinery factory; wood importer) 24 km: port of Zeebrugge (45 MT of freight in 2019)
BE—Elsakker	0.52	68.1[4]	4/1	*Mg/Ms*	< 4–6 km: Hazeldonk industrial area (vast logistic hub (trucking and storage) on the E19 highway on both sides of the border with the Netherlands 38 km: port of Antwerp (235 MT of freight in 2019)
BE—Famenne Est	0.47		1	*Mg*	< 1 km: building materials company; carpentry company; Within 13.5 km: military camp Roi Albert
BE—Gent-Zuid	0.41		1	*Ms*	Port of Ghent (71.5 MT of freight in 2019) < 3–4 km: ring canal; many industrial plants
BE—Heidebos	0.46	18.7[4]	1	*Mg*	< 7 km: vast industrial park (major European steel mill; wood importer; cement plant; a pallet factory; large food products producer and seller; trucking, etc.) 16 km: port of Ghent (71.5 MT of freight in 2019)
BE—Hoge_Vijverbos	0.54	874.9[5]	1	*Mg*	< 2,7 km: plastic raw materials plant; within 6 km: Hoge Mauw industry park (building materials company; trucking companies, etc.) 49 km: port of Antwerp (235 MT of freight in 2019)
BE—Kloosterbos	0.45	128.2[4]	1	*Mg*	< 1 km: vast industrial park (major European steel mill; wood importer; cement plant; a pallet factory; large food products producer and seller; trucking, etc.); 13 km: port of Ghent (71.5 MT of freight in 2019)
BE—Kluisbos Kluisbergen	0.41	28.1[5]	1/1	*Mg/Ms*	3 km—Avelgem industrial area (carpet tiles, carpets; vinyl floors; lineseed oil refinery, etc.); 39 km: port of Ghent (71.5 MT of freight in 2019)
BE—Kolisbos	0.55	61.1[5]	1	*Mg*	Metal trade company; Kleine Brogel military airport, sheltering *USAF 701st Munitions Support Squadron*
BE—Les_Cripettes	0.46		1	*Mg*	1 km*:* stone quarry; 2 km: Couvin commercial park (large supermarkets); 2,5 km: wood for energy company
BE—Malmedy	0.49		1	*Mg*	< 1 km: stone quarry and concrete factory
BE—Molenbeek-St-Jean (Tour Taxi)	0.44		1	*M*sp.	Port of Brussels (5.2 MT of freight in 2019): concrete factory; commercial storage facilities; logistics companies; building materials company; …
BE—Ramsel	0.48		1	*M*sp.	8 km—Important industrial park (logistics company, etc.); 12 km: the Albert canal, with the Herenthals and the Geel industrial parks (logistics; building materials, etc.)
BE—Schoten	0.49		1	*Mg*	Industrial park (wood trading companies, logistics, container manufacturing, etc.; 6 km: port of Antwerp (235 MT of freight in 2019)
BE—Tessenderloo 1	0.51	5[4]	1	*Mg*	The Tessenderlo industrial park along the Albert Canal
BE—Tessenderloo 2	0.51		2	*Mg*	The Tessenderlo industrial park along the Albert Canal
BE—Theux	0.49		1	*Mg*	3.4 km: mineral water company; 10.7 km: Damré-Sprimont industrial Park (concrete producer; transport and container renting company; tiling; 9.3 km: Cornémont Industrial park

Table 5 (continued)

Municipalities	SDM1	Area[1]	Nb caught	Species[2]	Proximity to entry points[3]
BE—Vagevuurbossen	0.42	70.5[4]	3	*Mg*	5 km: Beernem industrial area (furniture factories; tiling; nursery; health products; machinery factory; wood merchant); 26 km: port of Zeebrugge (45 MT of freight in 2019)
BE—Vallon de la Briserie	0.43		3	*Mg*	2 km: Ghlin industrial area (chemicals; glass; ceramics; Logistic companies, etc.)
BE—Vloethemveld	0.42	14.1[4]	2	*Mg*	4 km: industrial park Zedelgem (WPM; machinery; slaughterhouse; etc.); 20 km: port of Zeebrugge (45 MT of freight in 2019)
NL—Schoorl	0.55	709.4[5]	NA	*Mg*	25 km: major European steel mill; 30 km: port of Amsterdam (86 MT of freight in 2019)
DK—Oksbøl	0.53	1529.9[5]	NA	*Mg*	6,500 ha large military area; 20 km: port of Esbjerg

[1] Probability of occurrence according to the SDM

[2] *Mg*: *M. galloprovincialis*, *Ms*: *M. sartor urussovii*, *M*sp.: unconfirmed *Monochamus* species

[3] ports, industrial or logistics sites, military camps

[4] BWK

[5] CLC

40.4% of a population leaving an entry point could have flown at least 15 km, 3.4% could have flown at least 30 km and 0.38% could have flown at least 40 km under continuous pine cover. Under the fragmented forest cover conditions in Belgium, these proportions are likely to have been higher, according to Etxebeste et al. (2016) and Haran et al. (2017b), which suggests higher dispersal under discontinuous pine cover. All the sites where *Monochamus* spp. were found or trapped are within 40 km of a potential entry point (Table 3). Release-recapture experiments (Nunes et al. 2021) showed that *M. galloprovincialis* tends to avoid non-host stands but is indifferent to clear-cut areas. Schroeder (2019) found no difference in the catches of *M. galloprovincialis* between traps in pine stands and traps in clear-cuts. Han et al. (2023) reached similar conclusions about *M. alternatus* in China, based on whole-genome resequencing.

When leaving entry points, the beetles may need to find "stepping-stones" (i.e. sites with limited resources where they could at least feed if not oviposit), as observed with the Black Woodpecker *Dryocopus martius* (Saura et al. 2014), and the pine processionary moth, *Thaumetopoea pityocampa* (Rossi et al. 2016).

The sites in Schoorl (NL) and Oksbøl (DK) have a *M. galloprovincialis* probability of occurrence similar to that of the Belgian sites; this could not explain the permanent populations they shelter. However, they contrast with all the Belgian stands, except Hoge Vijverbos, by their larger size (700–1,500 ha), providing more breeding sites (dead trees or dead branches on living trees) to the beetles. A comparative study of pine coverage in Belgium, The Netherlands and Denmark (SuppInfo_S4) shows a reduced pine coverage and a much lower number of large stands (> 500 ha) in Belgium than in the two other countries. Permanent beetle populations may be present in the few larger Belgian stands; this could be explored further by targeted monitoring.

Robinet et al. (2011) developed a spread model for Europe after the introduction of the pine wood nematode through the major European ports, with human-assisted transportation facilitating natural spread. They considered the ports as the main entry points. Their model implicitly assumes that a native vector population would contribute to spreading the nematode or that the introduced vectors would be able to establish. Our results suggest that local vectors are absent or very rare in Belgium, with local resources (mostly small and fragmented pine stands) likely insufficient to allow the establishment of introduced vectors.

The practical outcome of this study is that monitoring for *M. galloprovincialis* in Belgium should focus in and around entry points. If surveillance in natural areas is deemed necessary, it should concentrate on the larger pine stands.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10340-026-02025-1.

Acknowledgements This study was partly funded by the Belgian Federal Public Service Health, Food Chain Safety and Environment through contract RT 18/4 MONODIS 2, and by the Observatoire wallon de la Santé des Forêts.

Authors' contribution Jean-Claude Grégoire and Marius Gilbert conceived and organised the project; Jean-Claude Grégoire coordinated the whole study; Louis Van Geertruijden collected the data; Jean Artois, Marius Gilbert, Gilles San Martin, Julien Claude, Serge Morand, Louis Van Geertruijden and Jean-Claude Grégoire analysed the data; Géraldine Roux and Emmanuelle Magnoux performed the genetic analyses; Dimitrios Avtzis, Nick Berkvens, Jochem Bonte, Hans Casteels, Sandra Closa, Gyorgy Csoka, Alain Drumont, Natasha Farrugia, Jean-Luc

Flot, Jiří Foit, Antonio Miguel Franquinho Aguiar, Juraj Galko, Marcel Govaert, Liga Grisane, Tine Hauptman, Theodoor Heijerman, Gernot Hoch, Björn Hoppe, Birger Ilau, Hervé Jactel, Wim Jennes, Emmanuel Kersaudy, Quentin Leroy, Hugo Mas, Iryna Matsiakh, David Michelante, Jørn Misser, Christo Nikolov, Juan Pajares, Simone Prospero, Davide Rassati, Hans Peter Ravn, Julien Reiners, Loreta Rezgytė, Alain Roques, Géraldine Roux, Martin Schroeder, Lidia Sukovata, Olivier Vanhoutte, Liisa Vihervuori and Andrija Vukadin provided trapping data and/or biological samples; Jean-Claude Grégoire, Jean Artois, Géraldine Roux and Gilles San Martin wrote the manuscript. All authors reviewed the manuscript.

Funding FOD Volksgezondheid, Veiligheid van de Voedselketen en Leefmilieu

Data availability Used in this study are available at (https://zenodo.org/record/8375215https://zenodo.org/record/8375215https://doi.org/10.5281/zenodo.8375215).

Declarations

Conflict of interest The authors declare no conflicts of interest.

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