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Spatio-temporal infestation patterns of *Ips typographus* (L.) in the Bavarian Forest National Park, Germany

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ABSTRACT

The Bavarian Forest National Park in Germany has experienced infestations of bark beetle (*Ips typographus* L.) since the 1980s, resulting in considerable ecological loss due to the destruction of almost 5800 ha of spruce forests. Although there have been numerous investigations on the physiology and ecology of the bark beetle, until now the spatio-temporal infestation and dispersal dynamics of the bark beetle over a longer period have still not been satisfactorily understood. The understanding of the structure and the dispersal of bark beetle infestations is however of significant importance for forest management systems in order to predict the risk of outbreaks, especially in the face of climate change.

The aim of this investigation was therefore (I) to analyse and describe the long term spatio-temporal infestation patterns of *I. typographus* in the Bavarian Forest National Park, Germany on the landscape scale, (II) to conduct investigations on spatio-temporal shifts of the focal points of bark beetle infestations from 1988 to 2010 and (III) to compare the quantitative spatio-temporal infestation patterns obtained at the landscape level with the dispersal patterns of the spatially explicit agent-based simulation model (SAMBIA) for *I. typographus* (Fahse and Heurich, 2011).

The results of the study show that a shift in the infestation pattern of *I. typographus* from 1988 to 2010 occurs at different time intervals both undirectionally as well as directionally. Furthermore, the dispersal pattern of the bark beetle was recorded quantitatively and described extensively over a period of 23 years on the landscape scale.

The quantification of the presence and dispersion pattern of *I. typographus* in the Bavarian Forest National Park allows us to gain a better understanding of the distribution pattern of the bark beetle on the landscape scale. In this way, both the pattern and structure of infestation patterns obtained for *I. typographus* serve as: (a) a basis for the criteria to improve the parameters of spatio-temporal simulation models, (b) a better understanding of the bark beetle pattern and existing processes such as disturbance patterns or damage patterns in the food web of spruces due to climate change, (c) a test for the hypotheses on the relationships between the presence of bark beetle and relevant habitat variables as well as (d) the compilation of forecast models on the dispersal of bark beetle. These predictions can help with the implementation of specific management strategies to prevent the dispersal of bark beetle.

1. Introduction

The Bavarian Forest National Park is the oldest National Park in Germany. The management principle for the National Park is the so-called natural process principle: nature within the park should be given the opportunity to take its own course as much as possible without human intervention. In fact, since 1970 a habitat has been created that acts as a unique refuge for many plant and animal species.

The severe thunderstorms that struck in 1983 and 1984 blew down many of the old tree stands, destroying a total area of 173 ha. Following the National Park's principle, the trees that had fallen within the nature zone of the National Park were left to take a natural course as was the outbreak of bark beetle. In the years that followed the bark beetle population increased dramatically so that even healthy trees became infested and died off. Following an initial fall in the activity of the bark beetle at the end of the eighties, unfavourable weather conditions in the early nineties (Heurich et al., 2001) resulted in annual increases in the area of ancient spruce stands dying off from 1992 onwards (slowly at first,

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but then escalating). Even until this day there have always been local infestations in the park which then spread to larger areas (Heurich et al., 2001; Nationalparkverwaltung Bayerischer Wald, 2001; Heurich, 2009).

In Europe there are around 154 species with different bark beetles infesting different tree species. The bark beetles that are found in the Bavarian Forest National Park are the spruce Ips (*Ips typographus*) and the six-toothed spruce bark beetle (*Pityogenes chalcographus*), both of which infest spruce trees (Heurich et al., 2001). Bark beetles are considered to be secondary pests, meaning that they only find favourable living conditions in weakened or dying trees. Storms and hurricanes (Coulson et al., 1999; Schroeder et al., 1999), snow, emissions or drought resulting from extreme weather events are known to weaken spruce trees that can then serve as ideal breeding grounds for the bark beetle, eventually leading to infestations under favourable weather conditions and sufficient breeding material (Netherer and Schopf, 2009).

Numerous investigations have already been conducted on the dispersal pattern of the bark beetle: in North-America (Powers et al., 1999; Negron et al., 2000; Klutsch et al., 2009), in Canada (Aukema et al., 2006; Wulder et al., 2006; Coops et al., 2009), in Slovenia (Jurc et al., 2006), in the Czech Republic (Svoboda and Pouska, 2008) in Poland and in Slovakia (Grodzki et al., 2003) in France (Gilbert et al., 2005) as well as in Germany (Heurich, 2001; Müller et al., 2009; Kautz et al., 2011; Lausch et al., 2011). Netherer and Schopf (2009) showed for example that global warming, temporal and spatial dynamics as well as the pattern, frequency and population dynamics can all alter the dispersal of the bark beetle. According to them, an increase in temperature can lead to a change in the number of generations per year, survival during the winter period as well as an increase in the susceptibility of the host vegetation. Baier et al. (2007) and Aukema et al. (2008) were able to prove a shift in the flight activity and dispersal for *I. typographus*. Investigations conducted by Jönsson et al. (2009) proved a change in development, reproduction rate, diapause and winter mortality of bark beetles.

Although the biology and ecology of the spruce Ips (*I. typographus*) has been investigated extensively (Wermelinger, 2004), until now there has been no satisfactory understanding in terms of its long-term spatio-temporal dispersal dynamics in forests on the landscape scale.

In many of the investigations covering dispersal dynamics only a short time frame of bark beetle dispersal was modelled as a result of insufficient data e.g. Powers et al. (1999) and Gilbert et al. (2005). Although Grodzki et al. (2003) and Jurc et al. (2006) were able to conduct analyses of bark beetle dispersal over a period of 7 and 11 years respectively, the presence/absence data, which they provided was point data as opposed to area data, as it is difficult to conduct a thorough analysis that covers entire areas.

Therefore the aims of this research were (I) to conduct investigations on the spatio-temporal shift in focal sites of bark beetle infestations from 1988 to 2010, (II) to analyse and describe long-term spatio-temporal infestation patterns of *I. typographus* (L.) in the Bavarian Forest National Park on the landscape scale and (III) to compare spatio-temporal infestation patterns obtained on the landscape level with the dispersal patterns of a spatially explicit agent-based simulation model (SAMBIA) for *I. typographus* (L.).

2. Data and methods

2.1. The study area

The study area known as the Rachel Lusen Region (Lat. E13°23′, Long. N48°53′) covers approximately 130 km^2 of the Bavarian

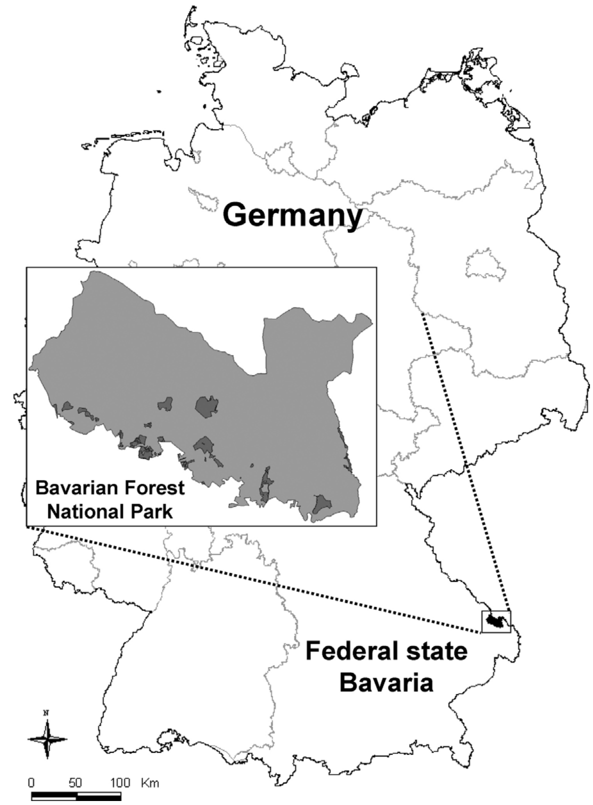

Fig. 1. Location of the study area – The Rachel-Lusen Area of the Bavarian Forest National Park, Germany.

National Park, from approx. 700 m above sea level to approx. 1450 m. The Bavarian Forest National Park was established in 1970 and has boasted a relatively natural state since 1972. Outbreaks of *I. typographus* (L.) have occurred from 1992, initially at higher elevations and peaking around 1996 and 1997 but continuing to this day. From 1988 to 2010 a total of 5800 ha of the naturally occurring Norway spruce stands died off because of *I. typographus* infestations (Fig. 1).

2.2. Collecting presence/absence data on I. typographus

To document the extent and the impacts of bark beetle dispersal, flight campaigns have been carried out in the National Park since 1988. The methodology behind taking, processing and interpreting the aerial images has been described in detail by the Bavarian Forest National Park administration (2002). Every year 267 CIR aerial images were taken per flight campaign with a geometrical resolution of 20 cm, corresponding to a total of 147 gigabytes of data. Two CIR flight campaigns were conducted every year with the first campaign in June/July of every year. Trees infested by bark beetle can only be recognised from the beginning of August, therefore conducting campaigns in June/July enables a documentation of any additional dead wood that has occurred since the previous year. The second campaign is then carried out in September/October of every year. With the help of these aerial images the current status of how much dead wood has accumulated can be documented in the year of investigation. Colour infrared stereo aerial images were taken at scales between 1:10,000 and 1:15,000. Up to the year 2000 the images were mapped using a stereoscope and transparent slides, drawn onto maps and finally digitalised (Nüsslein et al., 1999). From the year 2001 onwards, aerial images were scanned with a photogrammetric scanner at a

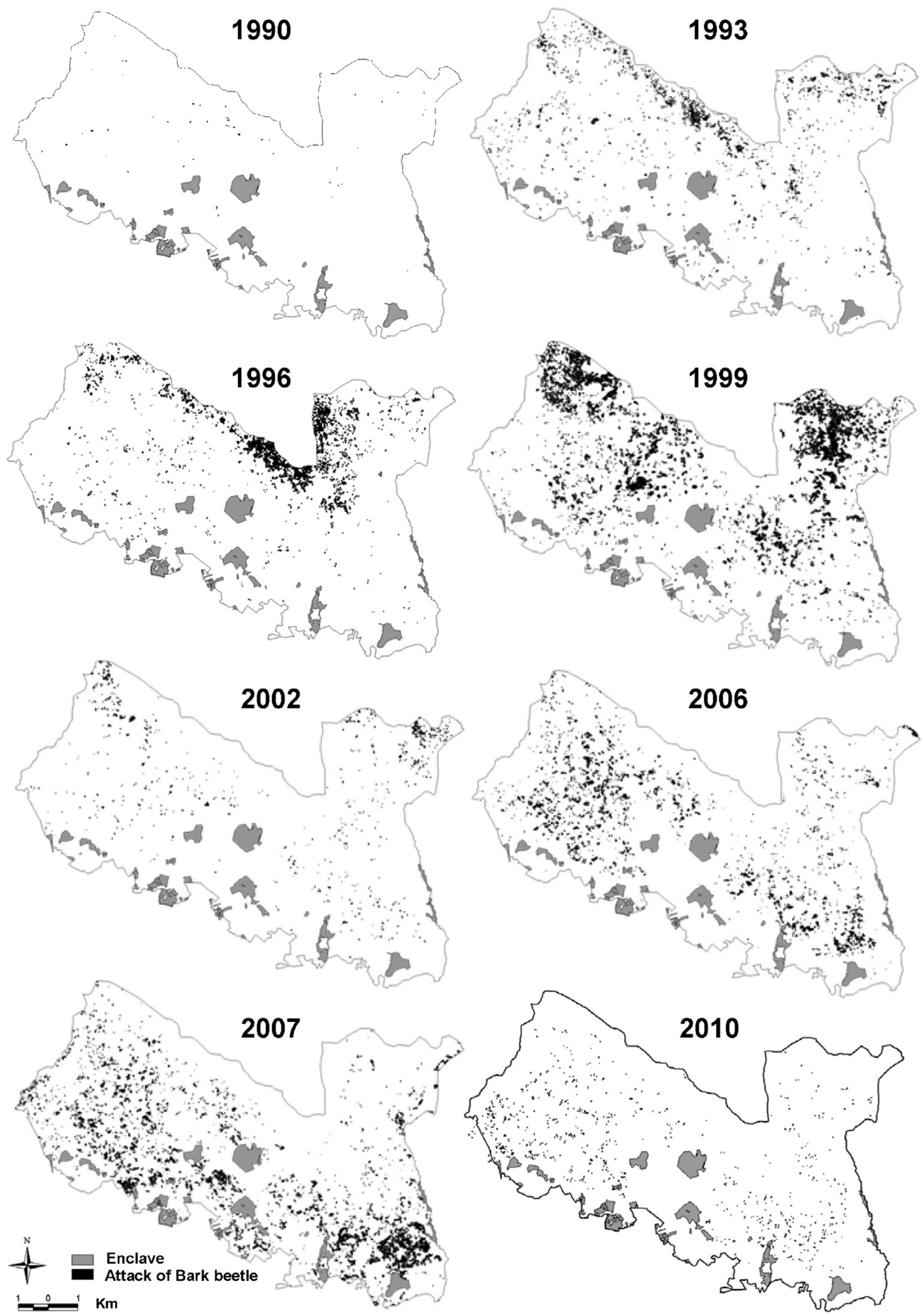

Fig. 2. Bark beetle outbreak in the Rachel Lusen Area ("old part") of the Bavarian Forest National Park, Germany (1990–2010). An enclave is a region without forest (e.g. settlement, rocks), changed according to Lausch et al. (2010).

resolution of between 15 and 20 μm. Based on these scans, a block triangulation and an ortho-image calculation was then carried out. The assessment of dead wood patches was conducted visually with ERDAS StereoAnalyst, which enables a 3D-view of forest stands. Using the StereoAnalyst, results of analyses from the previous year are overlapped with current aerial images. This enables any changes from the previous year to be directly delineated on the screen stereoscopically (Rall and Martin, 2002). To minimise time and effort, areas of less than 5 trees were not mapped (Fig. 2).

2.3. *Quantification of spatio-temporal infestation patterns of I. typographus*

2.3.1. *Analysing the centroids of infestation patterns*

The pattern of the spatio-temporal change to the focal area (centroid) of the bark beetle infestation is investigated by means of spatial statistics. Here, first of all, the focal area (centroid) for every deadwood patch of the year under investigation is calculated. Subsequently, based on the calculated centroids of the individually infested patches, the geostatistical variables (unweighted spatial mean or mean centre) are calculated for every year of infestation (Arc/GIS Desktop 9.3, Mean Center). The calculation of the centroid as well as the resulting mean centre is conducted in the same way for all years of bark beetle infestation under investigation.

2.3.2. Quantification of the spatio-temporal patterns of infestation

For a further characterisation and description of the spatio-temporal change to the pattern of dead wood patches from 1988 to 2010, meaningful variables for the spatial arrangement of the patches were ascertained. The dead wood patches available as vector data based on aerial image interpretation were transformed to raster data with a cell size of 4 m × 4 m. This cell size was selected because the average distance between spruce trees in the forest is ca. 4 m. Moreover, the selected cell size also generates a realistic data size, whereby calculations of structural parameters are still possible. Transforming the dead wood patches to raster data has the advantage that these can then be directly compared with the results from the spatially explicit simulation models. Variables considered to be meaningful for structure and pattern were then calculated using the structural analysis program FRAGSTATS (Vers. 3.3; McGarigal and Marks, 1995; McGarigal et al., 2002).

2.3.3. Spatially explicit simulation model

The agent-based simulation model (SAMBIA) integrated numerous biological processes (Fahse and Heurich, 2011). This spatially explicit simulation model (developed in C++) generates the spatial patterns of infested spruces in a stand, using a 128 × 128 grid, whereby each grid cell represents one spruce tree in reality. Due to the fact that in the upper section of the National Park spruce trees are approx. 4.5 m apart on average, the grid can be seen to represent a spruce stand that is equal to approx. 33 ha in the landscape. The model not only incorporates the bark beetles dispersing through the forest and trying to colonise spruces in order to reproduce but also the spruces attempting to avoid successful attacks. In the model, beetles are defined as the number of beetles in a grid cell, i.e. on or in a spruce tree. In their dispersal phase, bark beetles look for a new breeding site where they will attempt to colonise a spruce in order to reproduce. During this phase bark beetles communicate using pheromones that indicate suitable and unsuitable breeding trees. During the larval phase there might also be a direct interaction between bark beetles in the form of intraspecific competition, which can reduce breeding success considerably. A spruce is defined (a) by its position on the two-dimensional grid, (b) by one of the variables that describes its present status or fitness (i.e. healthy, weakened, infested or dead), (c) by a quantity that indicates its potential as a breeding habitat for bark beetles (breeding capacity), and (d) by the specific threshold value showing the minimum number of attacking beetles that are required to overcome the defence mechanisms of the tree. This defence threshold is then taken to be correlated with a spruce tree's fitness. In the model spruces do not interact and their characteristics only change after being damaged by non-biotic disturbances or after they have been successfully attacked by a sufficient number of beetles. Influences from natural antagonists and forest management on the bark beetles are included as mortality probabilities in the model with stochasticity playing a major role. Because single model simulations are realisations of random processes, several simulations must take place in order to gain reliable estimates for mean output quantities. Generally speaking, simulations were over a 5-year period and repeated 100 times. In particular, the temporal dynamics of the number of trees killed during the simulations were taken into account. For more detailed information about the model see Fahse and Heurich (2011).

3. Results

3.1. Analysis of the centroids of infestation patterns

The goal of the investigation was to ascertain the spatio-temporal changes ("migration") and the extent of the change to dead wood focal points from 1988 to 2010. An important indicator for the spatial shift in the sites is the non-weighted spatial mean or the mean centre (MC). The results of the MC for *I. typographus* in the Bavarian Forest National Park from 1988 to 2010 showed that the focal point (or centroid) of the dead wood patches "moves" annually (cf. Fig. 3). It can be clearly seen that the shift of the dead wood focal point from 1988 to 2001 was not in a specific direction (i.e. it was undirectional). From 2001 to 2007 however the shift of the MC occurred in a specific direction (i.e. it was directional) from the Northeast to the Southwest.

The results of the change of the MC between individual years show that the greatest shifts take place in the focal points (centroids) of the infested patterns of *I. typographus* in the years 1991–1993 as well as 2000–2001 (cf. Fig. 4).

Investigations of the relative change in the distance of the individual infested patterns show for the period from 1992 to 1993 a

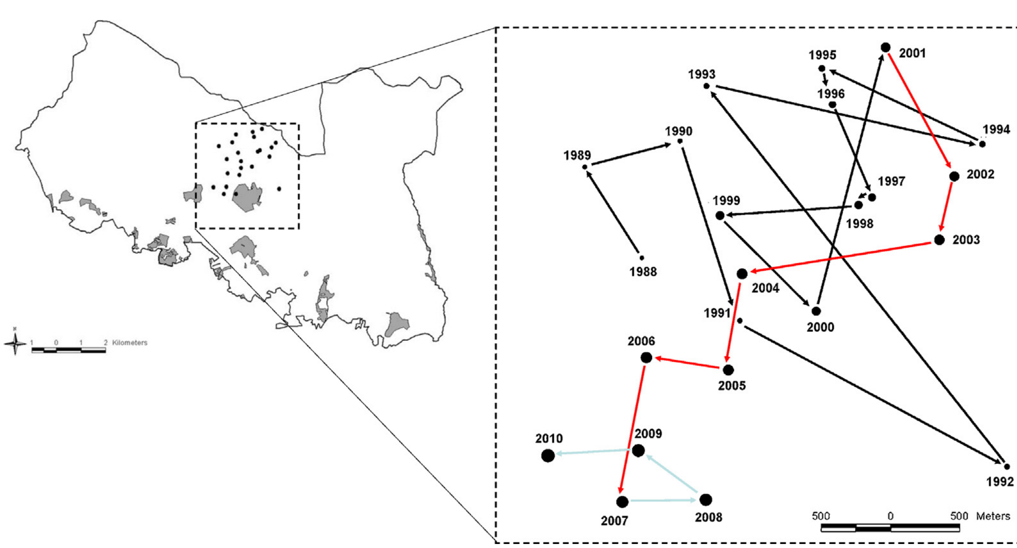

Fig. 3. Location and movement of the mean centre of the infestation pattern of *Ips typographus* (L.) in the Bavarian Forest National Park, Germany from 1988 to 2010.

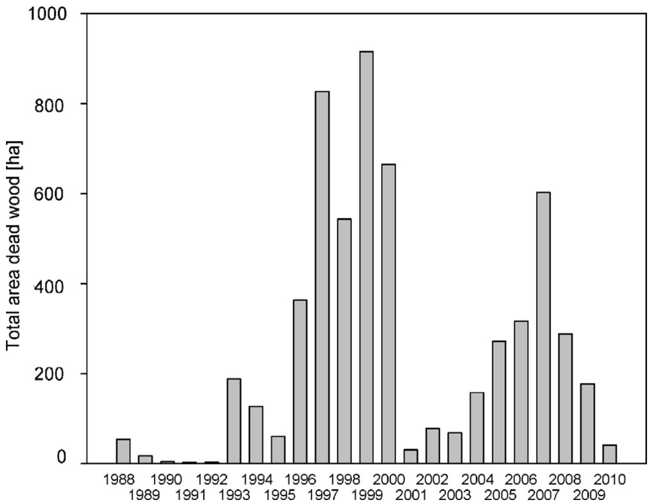

Fig. 5. Annual acquisition of total area of dead wood as a result of bark beetle infestation in the Bavarian Forest National Park, Germany from 1988 until 2010.

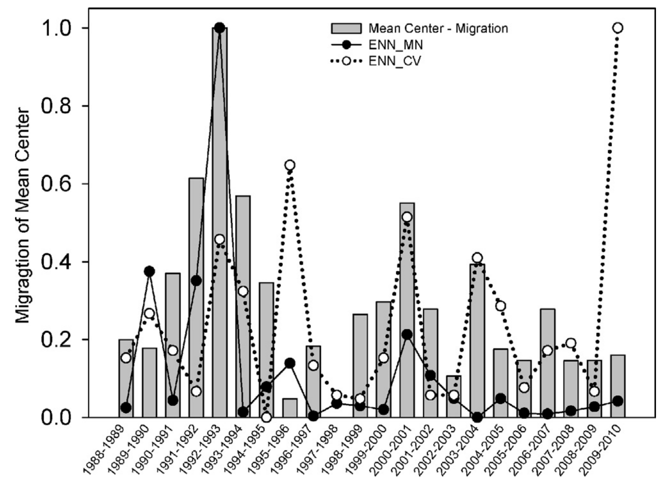

Fig. 4. The extent of the shift of the mean centre, the relative change of the Mean Center of the infestation pattern *of Ips typographus* (L.) in the Bavarian Forest National Park, Germany from 1988 to 2010, ΔENN_MN (Delta Euclidean Nearest-Neighbour Distance of Dead wood Patches), ΔENN_CV (Delta Covariance of Variation of the Euclidean Nearest-Neighbour Distance of Dead wood Patches), all values were normed between 0 and 1.

high mean distance (ENN) of the infested pattern of the total area for the same low variation of distance between the individual infested patches. Furthermore, in the years 2000–2001 there was another great spatial shift in the dead wood patches. Here the individual patches of the total area were closer to each other, although there was a higher variability of ENN of the infestation pattern over the total area (cf. Fig. 4).

3.2. *Quantification of spatio-temporal patterns of infestations*

The spatio-temporal changes to the pattern of dead wood patches from 1988 until 2010, meaningful parameters were ascertained for the spatial arrangement and spatial distribution of infested areas. As can be seen from Fig. 5, the absolute area of dead wood increased constantly from 1988 until 1999, reached its peak in the infestation year of 1999 and then fell until 2001 to the same level as in 1992. From 2001 until 2007 a new phase emerged with an increase in dead wood patches, which reached its peak in 2007. Consequently the population did not collapse completely as it did in 2001, more so the tree population decreased systematically from 2008 to 2010.

During the first phase of outbreaks from 1988 until 2000 the mean size of dead wood patches from 1997 to 1999 was very high (cf. Fig. 6a). During the second period of outbreaks from 2001 to 2010 the infested areas reached approx. 600 ha in 2007, however the mean size of the infested areas was almost half the size of the infested areas during the first phase of infestations. Furthermore, the covariance of variation of deadwood patches (AREA_CV) and hence the variance of patch sizes was particularly high in the first phase of infestations from 1999 until 2001 (cf. Fig. 6a).

The largest infestation patches (LPI) were found in 1997. From 1998 to 2000 in spite of a very high proportion of dead wood area (cf. Fig. 4) there were only a few large individual patches. The number of deadwood patches (NP) over the entire period from 1988 to 2010 reached three peaks in the years 1994, 2000 and 2007 (cf. Fig. 6b). The edge density (ED) of dead wood patches coincided well with the TAD (total area of dead wood) over the entire period from 1988 until 2010 (cf. Fig. 6c). Furthermore, our investigations from 1988 to 2010 show that the minimum average size of the infested areas was approx. 0.04 ha while the maximum individual patch size was around 0.57 ha. The mean infested area was found to be approx. 0.18 ha (cf. Table 2).

The mean euclidean nearest-neighbour distance of dead wood patches increased from 1988 to its maximum value in 1992. Consequently, over the entire investigation period the infested patches were found to be at a maximum distance from one another in 1992. From 1993 until 2010 on the other hand the distance was much closer between the individual infested patches (cf. Fig. 7a). Our investigations from 1988 until 2010 showed that the minimum distance between the individual infested patches was around 45 m while the maximum distance was around 536 m. The mean distance between infested patches was found to be approx. 119 m (cf. Table 2).

The mean perimeter–area ratio of dead wood patches reached its first peak in 1991, falling to its lowest value in 1993. Starting from 1993 the ratio increased again until it reached a new peak in 2003. Until 2010 only lower values were obtained for the perimeter–area ratio of dead wood patches (cf. Fig. 7b). The covariance of the variation of perimeter–area ratio of dead wood patches from 1988 to 2010 indicates that from 1996 to 1999 there was a high variance of PARA of individual dead wood patches.

The fractality or self-similarity (FRAC) of the infestation patterns is already very high during the first years of the investigation in 1988 and 1989, falling to its lowest in 1994 and then increasing relatively systematically to its highest value in 2010 (cf. Fig. 6a). The covariance of the variation of the dimension index of dead wood patches does not differ considerably from the mean fractal of the dead wood patches. The self-similarity is only very low in 1991 to 1995, otherwise the dispersal pattern or the structure of infested patches are very similar.

The connectivity of dead wood patches (CONNECT_MN) indicates the number of functional connections between dead wood patches and the distribution of infected areas (cf. Table 1). In this respect, our results (cf. Fig. 8b) show a high degree of connectivity from 1988 to 1991. This falls dramatically in 1991 and reaches its lowest level in the year 2000. During the second infestation phase of bark beetle there is only a slight increase in connectivity. The percentage of similar adjacencies of dead wood patches (PLADJ) is the most important index for the dispersion of dead wood patches. From 1988 to 1995 an increase in connectivity and clustering with a simultaneous decrease in the scattering (PJADJ) of individual patches was observed. A low level of connectivity and a clustering with a simultaneously high total spatial dispersion of the infested patches (cf. Fig. 7b) was from 1995 to the year 2000. The same pattern reoccurs during the second infestation period from 2000 to 2010.

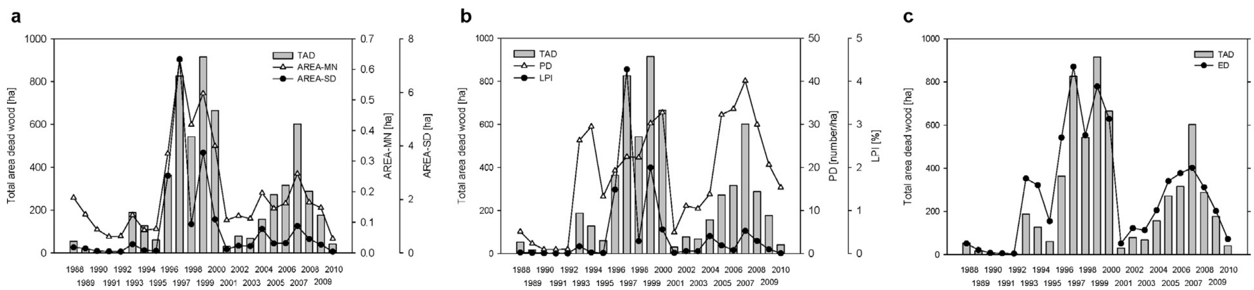

Fig. 6. Calculation of meaningful structural indicators of the dead wood patterns and their changes from 1988 until 2010, (a) TAD (total area of dead wood), AREA-MN (mean area of dead wood patches), AREA-SD (standard deviation of dead wood patch), (b) TAD (total area of dead wood), PD (patch density of dead wood patches), LPI (large dead wood patch index), (c) TAD (total area of dead wood), ED (edge density of dead wood patches).

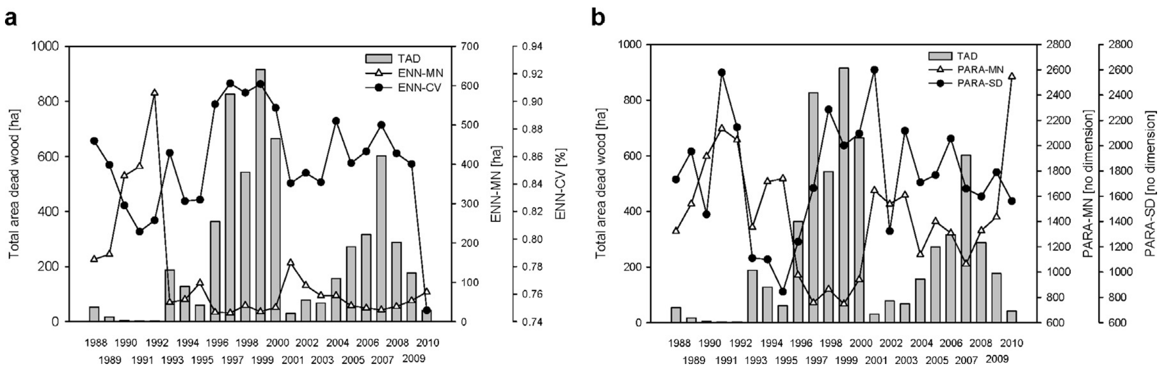

Fig. 7. Meaningful structural indicators of the dead wood patterns and their changes from 1988 to 2010, (a) TAD (total area of dead wood), ENN-MN (mean euclidean nearest neighbour distance of dead wood patches), ENN-CV (covariance of variation of euclidean nearest neighbour distance of dead wood patches), (b) TAD (total area of dead wood), PARA-MN (mean perimeter–area ratio of dead wood patches), PARA-SD (standard deviation of perimeter–area ratio of dead wood patches).

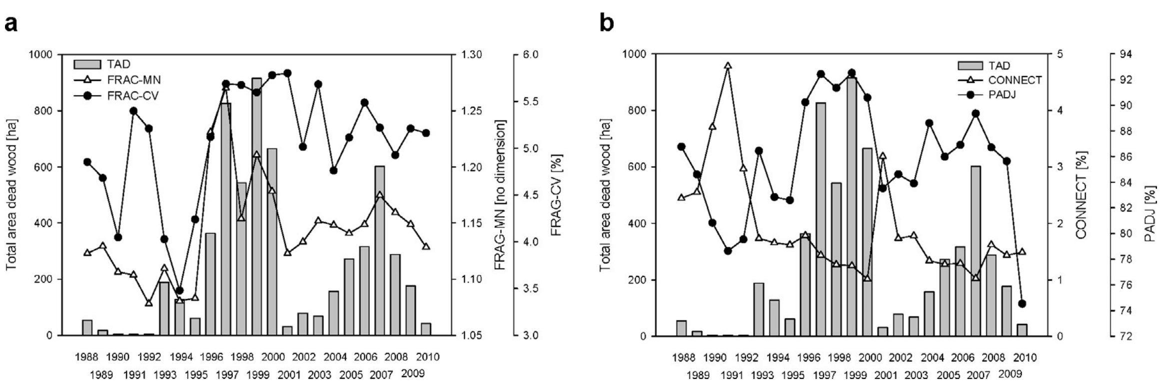

Fig. 8. Calculation of meaningful structural indicators for the pattern of dead wood and its changes from 1988 to 2010, (a) TAD (total area of dead wood), FRAG-MN (mean fractal dimension index of dead wood patches), FRAG-CV (covariance of variation of fractal dimension index of dead wood patches), (b) TAD (total area of deadwood), CONNECT (connectivity index of dead wood patches), PADJ (percentage of like adjacencies of dead wood patches).

Table 1
FRAGSTATS – spatial pattern metrics chosen to quantify the attributes of dead wood patterns of *Ips typographus* (L.), with their acronyms, names and units. For a description of the spatial pattern metrics see McGarigal et al. (2002).

Acronym	Spatial pattern metric	Unit
TAD	Total area of dead wood	ha
AREA_MN	Mean area of dead wood patches	ha
AREA_DS	Covariance of variation of dead wood patches	ha
PD	Patch density of dead wood patches	number/ha
LPI	Large dead wood patch index	percent
ED	Edge density of dead wood patches	m/ha
ENN_MN	Mean euclidean nearest neighbour distance of dead wood patches	m
ENN_CV	Covariance of variation of euclidean nearest-neighbour distance of dead wood patches	percent
PARA_MN	Mean perimeter–area ratio of dead wood patches	None
PARA_SV	Covariance of variation of fractal dimension index of dead wood patches	None
FRAG_MN	Mean fractal dimension index of dead wood patches	None
FRAG_CV	Fractal dimension index – coefficient of variation	None
CONNECT	Connectivity index of dead wood patches	percent
PLADJ	Percentage of like adjacencies of dead wood patches	percent

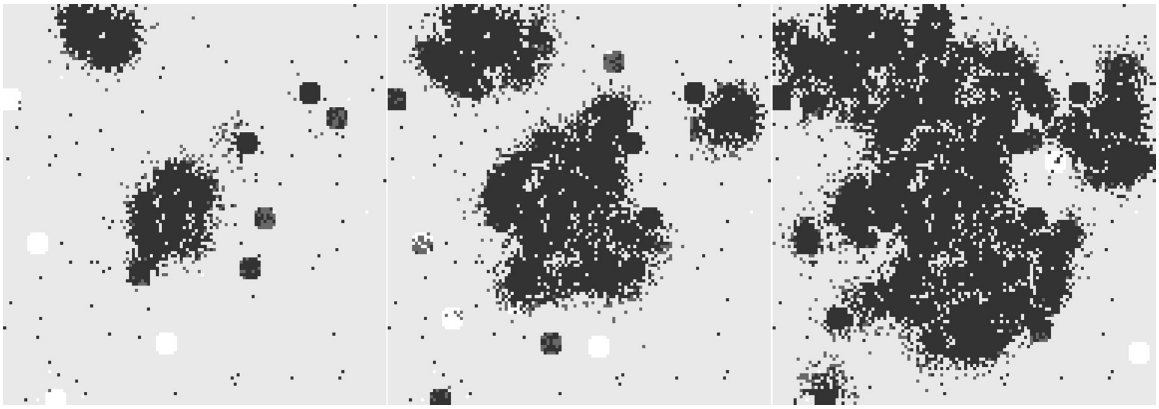

Fig. 9. Typical temporal dynamics of dead wood patches, generated using the simulation model. Light grey: healthy spruces; black and dark gray: dead wood and currently infested spruces, white: points of disturbance (i.e. damaged by windfall).

Altered from Heurich et al. (2003).

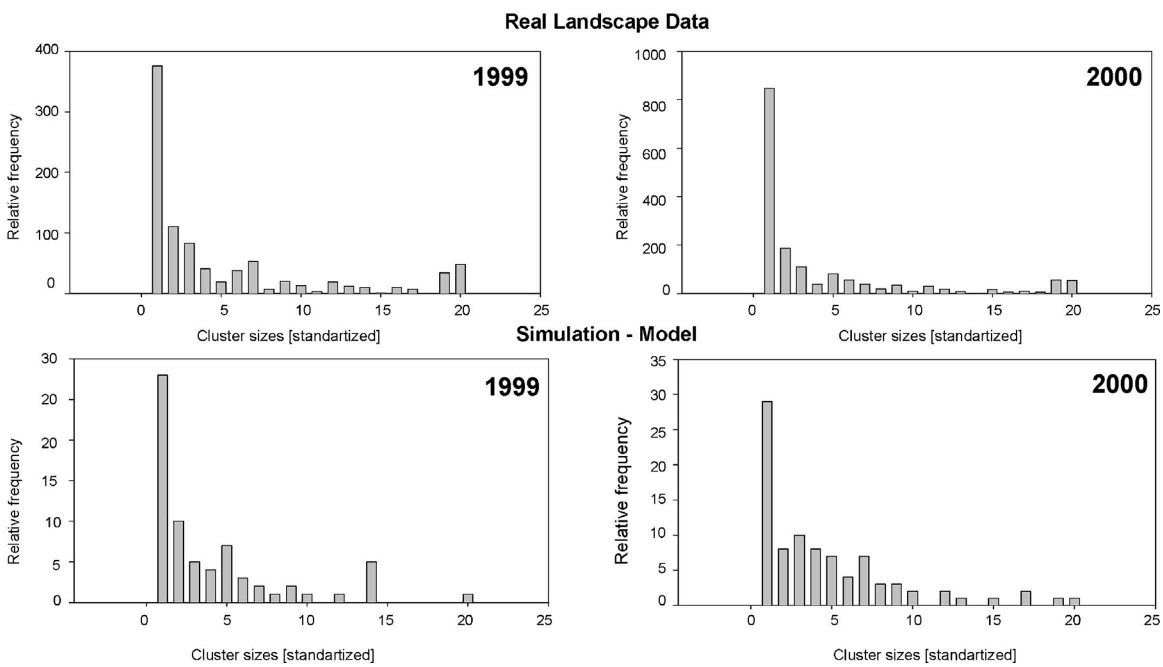

Fig. 10. A comparison of the frequency distribution trends of dead wood patches from two consecutive years. (a and b) Real data; (c and d) simulation data for 1999 and 2000.

Altered from Heurich et al. (2003).

Table 2
Structural information on dead wood patterns of *Ips typographus* (L.) from 1988 to 2010. The FRAGSTATS spatial pattern metrics chosen to quantify attributes of severity of fire with their acronyms and units (McGarigal et al., 2002).

Acronym	Unit	Min	Max	Mean	Median	Std. dev.	C.V. of mean
TAD	ha	2.92	915.40	252.13	156.81	275.88	119.30
AREA-MN	ha	0.05	0.63	0.20	0.15	0.16	0.07
AREA-SD	percent	0.05	7.24	0.93	0.31	1.66	0.72
PD	number/ha	0.95	40.11	18.21	19.30	12.25	5.30
LPI	percent	0.00	4.28	0.46	0.08	0.97	0.42
ED	m/ha	0.45	87.05	28.23	20.57	25.40	10.98
ENN-MN	m	22.29	581.38	116.45	56.34	142.61	61.67
ENN-CV	percent	0.75	0.91	0.86	0.86	0.04	0.02
PARA-MN	None	747.98	2546.15	1437.96	1400.89	456.13	197.25
PARA-SD	None	845.36	2600.65	1756.58	1733.38	455.32	196.90
FRAC-MN	None	1.08	1.27	1.14	1.14	0.05	0.02
FRAC-CV	percent	3.48	5.80	5.05	5.16	0.62	0.27
CONNECT	percent	1.01	4.78	1.93	1.62	0.94	0.41
PADJ	percent	74.54	92.52	85.62	85.99	4.56	1.97

3.3. Comparison and incorporation with a simulation model

The results from the analysis of focal patches of infestation patterns as well as the results of the spatio-temporal patterns of infestation form the basis for the spatially explicit agent-based simulation model (SAMBIA) designed by Fahse and Heurich (2011). Various analyses were conducted using the SAMBIA model (cf. Fig. 9). The exact configurations and model parameters of the simulation model can be taken from the work of Fahse and Heurich (2011).

Fig. 10 illustrates a comparison between the model results from SAMBIA and the real data from spatio-temporal changes to the infestation patterns of *I. typographus*. Here the frequency distributions of patch sizes were recorded respectively. Due to the fact that the SAMBIA-model runs on a larger scale (a 128×128 grid with cells $4.5\,m \times 4.5\,m$ represents 33 ha in the landscape, Fahse and Heurich, 2011) than the data collected for *I. typographus* (cells of $4\,m \times 4\,m$, total study area of 13,722 ha), a relative class division took place in order to be able to make a comparison, i.e. the 20 size classes each arose from an equidistant division between the minimum and maximum patch size of dead wood. Furthermore, in the model analysis (analogous to the aerial image interpretation) only those patches with a minimum size of 5 trees were taken into consideration. The qualitative distribution trends from the graphics are very consistent (cf. Fig. 10). Both the real data as well as the simulation results show an almost exponentially distributed dead wood patch size.

4. Discussion

The investigations on the spatio-temporal change or the “shift” in the focal point of infested patterns of *I. typographus* from 1988 to 2010 show that this is undirectional from 1988 to 2001 i.e. not in a specific direction. From 2001 to 2007 however the shift of the MC was directional i.e. in a specific direction from the North east to the South west. So far the literature has primarily reported results of an undirectional shift in the focal point of infestation. Incidentally, Heurich et al. (2003) found no undirectional infestation pattern when they investigated a shift in the dead wood focal point from 1992 to 2001 in the Bavarian Forest National Park in Germany. Sauvard (2004) and Williams and Robertson (2008) indicate that a high variability in the dispersal abilities among individuals can either be caused by genetic predisposition or by different energy reservoirs formed by different extents of competition during the larval phase. Our current results of the spatio-temporal change of the focal point of dead wood patches over a period of 23 years indicate that the infestation pattern of *I. typographus* shows an anisotrophic shift in the first 13 years from 1988 to 2001. This was a period that saw the first massive increase in dead wood. In the years from 2000 to 2001 the bark beetle population collapsed completely, because all the available food resources for the bark beetle had been exhausted. In the period from 2001 to 2007 the specific direction of the infestation pattern of bark beetle shifted from the North east to the South west. From 2008 on the bark beetle population collapsed again. A shift then occurred from 2008 to 2010 from West to East. So far with the results at hand we were only able to ascertain the spatio-temporal change in the focal point of infestation with *I. typographus* in the National Park. Byers (2000) and Meyer and Norris (1973) showed in their investigations that the wind regime can have an influence on the direction and the shift in the focal point of the bark beetle. For our period of investigation further analyses will be conducted to test this hypothesis on the wind regime.

Different aspects of the dispersal patterns and movements of various bark beetle species have been quantitatively measured and simulated (Duelli et al., 1997; Byers, 2000; Cronin et al., 2000; Lausch et al., 2011). Due to technical, financial and methodological limitations of the experimental design of mark-recapture methods for the bark beetle, many studies only relate to small-scale surveys and frequently to data from point counts. To the best of our knowledge there have been no investigations on the spatio-temporal dispersion pattern of *I. typographus* on the landscape scale that have been quantitatively analysed and quantitatively described over such a long period of 23 years.

Although the SAMBIA simulation model is intended to be a generic model at its heart, it is orientated towards the conditions in the Bavarian Forest National Park. We used this site with more than 20 years of data on the *I. typographus* (*Picea abies*) infestation patterns as a reference for the parameterisation of the model. This site therefore provides a unique opportunity to study the dynamics of bark beetle outbreaks in Central Europe and to validate the model’s outcome.

In addition to finding those management strategies that are most appropriate to prevent bark beetle outbreaks, the model was also used to investigate the extent to which the dispersion pattern on the landscape level can be understood as emerging characteristics of system components. Several comparable analyses on the relationship between the results from aerial image interpretations and model simulations only slightly match. Here it can be seen very clearly that the dynamics of the infestation patterns are not only influenced by coincidental but also by spatially heterogeneous factors. Particularly in this context, patch-related parameters emerge, which influence the competitiveness of the bark beetle to act as a key factor. There is still a need to conduct further analyses with the specific goal of investigating the influence of spatial structural parameters as well as site-specific factors on the dispersal patterns of the bark beetle population.

5. Conclusions and outlook

Many case studies and research on the bark beetle are in progress, but it is difficult to find data on dispersal and infestation patterns on the landscape scale or in particular on physiological processes and interactions with antagonists of the behaviour of the bark beetle (Biesinger et al., 2000; Fahse and Heurich, 2011). In spite of its devastating economic impacts, the bark beetle remains one of those species for which still very little is known about its dispersal and dispersion patterns. This is not so much because of a lack of interest in the beetle species but more so due to a lack of investment in research on the biology and the dispersal of the bark beetle. Current research approaches for the bark beetle using mark-recapture methods can only be applied in a limited context, because it is very time-consuming (Wermelinger, 2004; Trzcinsky and Reid, 2008). Therefore spatially explicit studies on dispersal and habitat use have until now primarily concentrated on local regions.

The current study is therefore an important contribution to understanding presence/absence data, dispersal as well as the spatio-temporal use of important habitat resources of *I. typographus* on the landscape scale over a period of 23 years. The assessment and quantification of structures and patterns of infestation with *I. typographus* (L.) provides a sound basis for understanding the dispersion pattern of the bark beetle.

The results of the structure analysis show that the structure and pattern of presence/absence data and the dispersal of *I. typographus* over the entire period from 1988 to 2010 does not occur according to strictly defined patterns and sequences but is rather influenced by a number of unknown factors. The study by Lausch et al. (2011) already proved that there are no monocausal correlations between individual habitat factors and the spread of *I. typographus* over the entire 18-year model period. The spread of the bark beetle can therefore be said to be affected by a complex interplay between on the one hand active population factors and on the other hand habitat factors with varying degrees of significance at individual phases. This reveals that the complexity of processes and variables could make it difficult to predict future outbreaks or the dynamics of present infestation patterns.

The quantification of presence/absence and dispersion patterns of *I. typographus* in the Bavarian Forest National Park, Germany provides a unique opportunity to gain a better understanding of the dispersion pattern of the bark beetle on the landscape scale. The patterns and structures of infestation found for *I. typographus* therefore serve as: (a) a basis for the criteria that are significant for generating spatio-temporal simulation models, (b) a better understanding between bark beetle patterns and existing processes such as predator–prey ratios as well as disturbance or damage patterns in the food chain e.g. the susceptibility of spruces to drought due to climate change, (c) a test of the hypotheses on correlations between bark beetle presence and significant habitat variables as well as (d) a basis for generating forecast models on the dispersal of the bark beetle. These predictions can then be used to implement management strategies specifically targeted at preventing the dispersal of the bark beetle.

The analysis of landscapes and species dispersal patterns allows the assimilation of results in further complex species-landscape models for predicting the optimal configuration and composition of landscape elements, pattern and land-use structures for species (Lausch and Herzog, 2002).

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