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# Factors affecting the spatio-temporal dispersion of *Ips typographus* (L.) in Bavarian Forest National Park: A long-term quantitative landscape-level analysis

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ABSTRACT

The relationship between abiotic and biotic factors and the spread of the European spruce bark beetle, *Ips typographus* (L.), was investigated at a landscape level over a model period of 18 years in the Bavarian Forest National Park in Germany. Deadwood areas – where *I. typographus* – caused tree mortality of 100% – were photographed annually using Color-infrared aerial photography and digitally recorded in vector form. Thirty-two static and dynamic habitat variables were quantitatively determined using spatial pattern analysis and geostatistics from 1990 to 2007 at the landscape scale. The importance of the presence of deadwood areas for thirty-two habitat variables for the occurrence of the bark beetle was quantitatively recorded using an Ecological Niche Factor Analysis (ENFA).

It was shown over a long model period that the intensity of the bark beetle infestation went through different phases over the 18-year study period. No mono-causal correlations could be found between individual habitat factors and the spread of the bark beetle over the entire model period. On the one hand, these findings underline the complexity of the system, on the other hand, this could be interpreted as a possible explanation for conclusions drawn by previous studies that differ from each other.

The importance of individual habitat variables and the combinations of variables varied to different extents within these phases. An examination of the cumulative importance of the habitat demonstrated that the biological structural variables such as the distance from the site of the previous year's infestation, the area and the perimeter of the infested areas from the previous year are of great importance for the incidence of the bark beetle, but not across all years. Of equal significance for assessing the size of the area and the distance of the deadwood areas from the sites of the previous year's infestation are the size of the areas, the perimeter of the deadwood areas and the proximity index. An evaluation of the stages of forest succession showed that cumulatively, a short distance between the infested areas and the forest areas with conifers in the early stages of growth was an equally important habitat factor from 1990 to 2007. By quantitatively recording habitat factors that are significant for the spread of the bark beetle it may help predict areas that are at risk and thus to develop suitable management strategies to minimise or stop the spread and the effect of the bark beetle.

## 1. Introduction

The bark beetle (Scolytinae) is one of the most dangerous pests in forestry. In Europe there are approximately 154 species, with the bark beetle infesting different types of trees. The most important bark beetles in the Bavarian Forest National Park is the European (or eight-spined) spruce bark beetle *Ips typographus* which infest spruces *Picea abies* (L.).

Adult *I. typographus* range from 4.2 to 5.5 mm in length. They are cylindrical and reddish or dark brown to completely black. The male *I. typographus* initiates a nuptial chamber. After manifold copulation with attracted females, each female gnaws a maternal gallery with egg-pockets along the sides of the gallery. Approximately 50 eggs are laid on each side of the egg gallery. Larvae from the laid eggs gnaw right-angled to the maternal galleries larval tunnels, which end in a pupal chamber. The pupae change into hairy, brown juveniles. After maturation, grub juveniles change into dark-brown, mature adults. The whole generation development from the copulation to the adult has a duration of 7–11 weeks. Adults finish maturation in the spring prior to their dispersal flight. These flights are initiated in response to air temperatures of 20 °C. The number of generations per year is dependent upon temperature. In the northern part of its range, it has one generation a year, but it can complete two generations per year further south. In Central

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European lowlands it frequently completes two generations per year and has been reported to reach three generations in recent climatically favourable years. A first generation having a high rate of reproduction means the beginning of a large second generation, which will produce many offspring flying in the next season.

*I. typographus* is considered as secondary pests, i.e. he find favourable conditions to thrive in only in damaged and dying host trees. Storms and windthrow (Coulson et al., 1999; Schroeder et al., 1999), snow damage, emissions from environmental pollutants, or water shortage as a result of extreme weather conditions all lead to damaged spruce trees that can serve as the ideal breeding grounds for them but which can easily favour an outbreak given the right weather conditions. Once they have reached high population levels, the *I. typographus* are even able to attack and kill healthy trees. Some *I. typographus* (e.g. mountain pine beetle) are capable of causing the mortality of apparently-healthy trees over extensive areas (>ten million ha).

The forests between Bavaria and Bohemia form one of the largest continuous forest regions in Central Europe. The Bavarian National Park is 240 km$^2$ with an area of over 97% forest (Heurich and Neufanger, 2005). The National Park's principle is to protect both the natural succession of symbiotic communities and the natural processes in a region of Germany with outstanding natural beauty. In 1983–1984 severe thunderstorms caused a huge windthrow of old spruce (*P. abies* (L.) stands in the Bavarian Forest National Park within a matter of minutes that triggered off a chain reaction of *I. typographus* (L.) infestations which still continue to this day and which killed off spruce stands covering approximately 5370 ha between 1990 and 2007. The incident provided a unique opportunity to examine the spatio-temporal pattern of the spread of the *I. typographus* on a landscape scale as well as the habitat factors that were imperative for a spread of that extent (13722 ha) from 1990 to 2007. Therefore, this site provides excellent conditions to study to study factors influencing outbreaks dynamics.

Comparable studies on the spatial distribution and patterns of the spread of *I. typographus* populations have been carried out for different species in North America (Powers et al., 1999; Negron et al., 2000; Klutsch et al., 2009) and in Canada (Aukema et al., 2006; Wulder et al., 2006; Aukema et al., 2008; Coops et al., 2009). Other recent studies also relate to European species such as *I. typographus* and Pityogens chalcographus in Slovenia (Jurc et al., 2006), the Czech Republic (Svoboda and Pouska, 2008), Poland and the Slovak Republic (Grodzki et al., 2003), France (Gilbert et al., 2005; Rossi et al., 2009) as well as Germany (Heurich, 2001; Heurich et al., 2003; Müller et al., 2009).

There is a broad consensus that global warming is changing both the temporal and spatial dynamics, and the pattern, frequency and population dynamics of *I. typographus* (Parmesan, 2006; Hillstrom and Lindroth, 2008; Netherer and Schopf, 2009): rises in temperature are leading to changes in the number of generations per year and their survival through winter periods, as well as an increase in the susceptibility of the host vegetation. Baier et al. (2007) and Aukema et al. (2008) detected a change in both flight activity and dispersal in *I. typographus* and *Dendroctonus ponderosae*. Changes in the development and reproduction rate (Jönsson et al., 2009), and the diapause and winter mortality (Bale et al., 2002) of *I. typographus* have also been investigated. Currently, however, only little is known about the direct interactions between the different factors involved: different environmental and climatic parameters, plant resistance and stress, state of vitality, the nutrient supply, the structure of antagonists, the distribution pattern and the spread of the *I. typographus* (Netherer and Schopf, 2009).

In each of the previously available studies different population and habitat factors from the fine scale, through the meso-scale and up to the landscape level were examined in relation to the spatial spread of the *I. typographus*. However, they allow sometimes only for limited conclusions about the triggering effects. In the studies conducted by Powers et al. (1999) and Gilbert et al. (2005) only one year in the spread of the *I. typographus* was included, making a comparison of the importance of different habitat variables for a potential spatio-temporal spread only possible to a limited degree. While a larger period of *I. typographus* infestation – seven and eleven years respectively – was examined for a particular region in the studies by Grodzki et al. (2003) and Jurc et al. (2006), only very selective habitat variables on the fine scale to the meso-scale were included over the whole period. It is therefore difficult to compare the studies, or to detect causal inferences between the habitat factors and the spread of the *I. typographus* at the landscape level over a longer model period. The aim of this study was to close this gap.

The main aims of this project were as follows. (I) The examination of the relationship between the spread of the *I. typographus* and the spatio-temporal site conditions (abiotic-biotic factors, spatio-temporal pattern) for a long eighteen years model period at the landscape level. (II) The determination of the critical factors for the spread of the *I. typographus* as a basis for modelling the spread of the *I. typographus* (more objective models, model parameterisation, model calibration)

## 2. Data and methods

### 2.1. Study area

The study area known as the Rachel-Lusen-Region (Lat. 13.23°E, Long. 48.53°N) covers approximately 37 km$^2$ of Bavarian National Park, rising from about 700 m above sea level to about 1450 m. Bavarian Forest National Park, established in 1970, is the oldest national park in Germany boasting a relatively natural state since 1972. This basic principle underlying the National Park's concept of leaving nature to itself, was adhered to even after the severe thunderstorms in 1983–1984, which blew down many old stands within the borders of the National Park and it is a principle that is still strictly observed today.

An outbreak of *I. typographus* occurred from about 1992, initially at higher elevations, reaching a peak in 1996 and 1997 but continuing to this day. By 2007 a total of 5370 ha of the naturally occurring Norway spruce stands had died because of the *I. typographus* infestation.

### 2.2. Presence/absence data

In order to record the spread of the *I. typographus* and the resulting dead wood area of the Bavarian Forest National Park as a vector representation, CIR aerial photographs were taken every year from 1988 at a scale of 1:15.000 for the entire Rachel-Lusen area (Fig. 1). For the first time ever, this enabled a digital vector representation of extensive changes to forest structures caused by *I. typographus*. The high sensitivity in the infrared range of the image data provided us with reliable information on the forests' state of vitality, thereby making it possible to distinguish between living and dead trees. Up until 2000 the image data was mapped out using a stereoscope and transparent slides, and then drawn onto maps, that were then digitalised. From 2001 the aerial pictures were scanned using a photogrammetric scanner with a resolution of between 15 and 20 $\mu$m. From 2004 the images were produced by digital cameras that enabled the image data to be stored in digital form. A block triangulation and orthoimage calculation were carried out based on the scans and the digital images. The interpretation of the dead wood areas was carried out visually using the StereoAnalyst manufactured by ERDAS. This enables forest stands to be depicted in 3D, a process, which superimposes the evaluation result from the

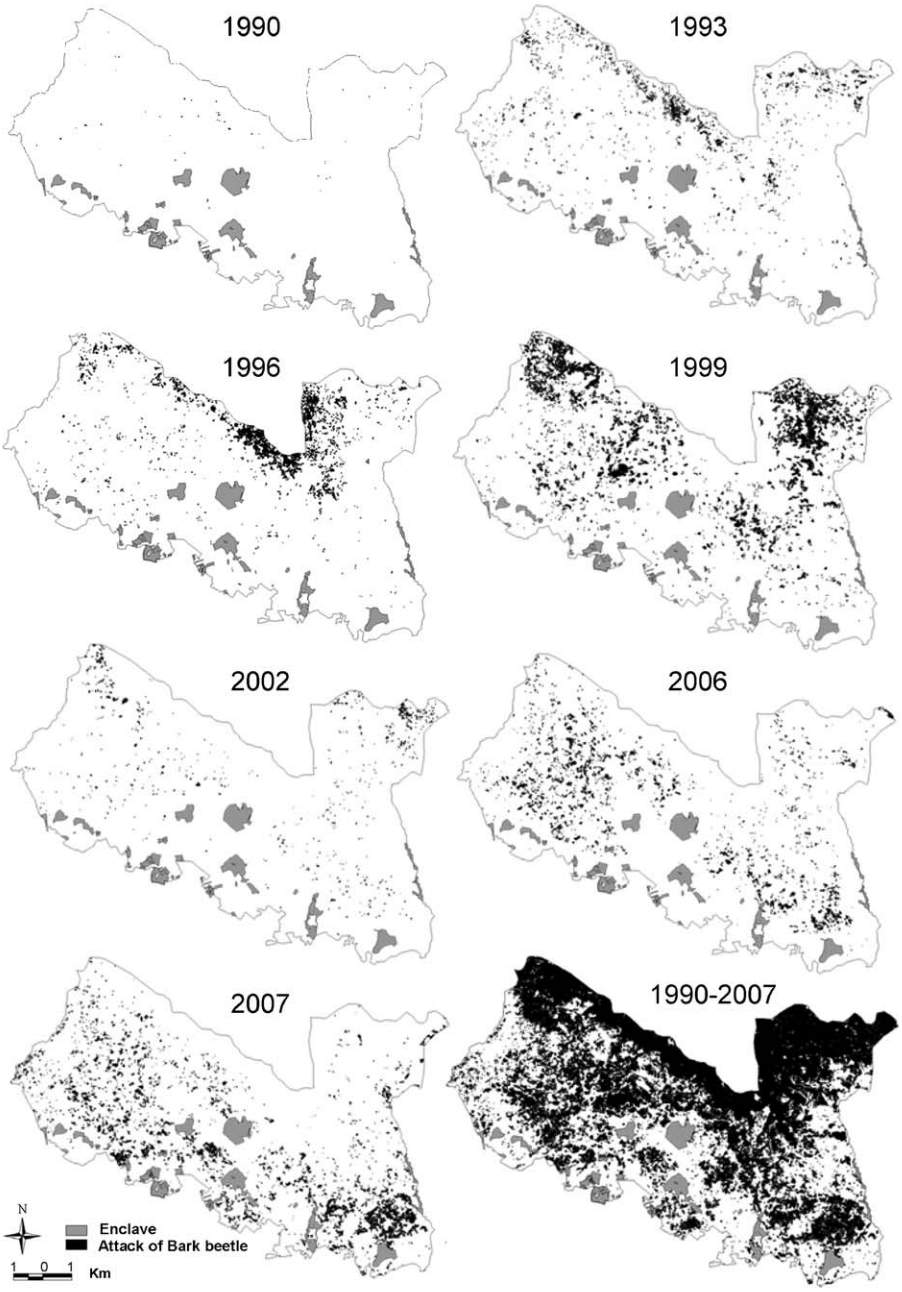

**Fig. 1.** Bark beetle outbreak in the Rachel-Lusen-Area ("old part") of the Bavarian Forest National Park (1990–2007). Enclave is a region without forest (e.g. settlement, rocks).

previous year over the current aerial photos in the StereoAnalyst. In this way any changes from the previous year can be stereoscopically digitalised directly on the screen. The limit of detection for the definition of a source of infestation was set to a minimum of five dead trees.

The processes referred to above enable an up-to-date digital recording of the annual dead wood areas from 1988 to 2007 (Heurich and Rall, 2002; Heurich et al., 2010). The annually recorded vector data stored in digital form of the dead wood areas forms the basis of the habitat modelling conducted for the Bavarian Forest National Park from 1990 to 2007.

### 2.3. *Environmental indicators of I. typographus*

The hypotheses for the habitat preferences of the bark beetle form the basis for modelling potential habitats of the bark beetle (*I. typographus*). The quantification and conversion of the hypotheses to biotic and abiotic habitat factors into variables or eco-geographical variables (EGVs) was carried out using geographic information systems, ArcInfo, Erdas Imagine and the structural analysis program Fragstats 3.3 (Herzog and Lausch, 2001; Mc Garigal, 2001; FragStats, 2006). The study area – the Bavarian Forest National Park (13.700 ha) – was modelled as a raster map (400 $m^2$ per pixel, $n = 647\,408$ cells). We used different types of environmental factors to describe every 20 m × 20 m unit grid of the study area – topographic characteristics, climate forecasts, soil conditions, forest succession and biological and structural variables. Depending on the change in variables, both static and dynamic variables were generated for the respective habitat parameters (Table 1). The variables with a resolution of 20 m × 20 m were then continuously converted into the data format as described in (Hirzel and Hausser, 2004). The least problems arose in calculating the overall model with the data format selected according to Hirzel and Hausser (2004). The variables used in the model were subsequently

**Table 1**
Environmental descriptors retained for the habitat analysis of the bark beetle from 1990 to 2007 (EGV = ecogeographical variables), static – no changes to variables, variables used for every model (1990–2007), dynamic – variables are recalculated every year (1990–2007).

| Variable category | Variable description ecogeographical Variables (EGV) | Variable static/ dynamic (1990–2007) | Unit | Data source | EGV code |
|---|---|---|---|---|---|
| Topography | Distance to aspect – north (315.01–360°) | Static | m | DEM 50 m[a] | dist-asp1 |
| | Distance to aspect – east (45.01–135°) | Static | m | DEM 50 m[a] | dist-asp2 |
| | Distance to aspect – south (135.01–225°) | Static | m | DEM 50 m[a] | dist-asp3 |
| | Distance to aspect – west (225.01–315°) | Static | m | DEM 50 m[a] | dist-asp4 |
| | Slope | Static | % | DEM 50 m[a] | slope |
| | Digital elevation model (DEM) | Static | m | DEM 50 m[a] | dem |
| | Relief energy (hights difference/unit) | Static | Number | DEM 50 m[a] | dem-class |
| Climate | Temperature – mean temperature – interpolation over digital elevation model | Dynamic | °C | DEM[a] | temperature |
| | Potential sunshine duration (April–September) | Static | h | DEM, SAGA-gis model | soldur |
| | Potential solar radiation (April–September) | Static | $kWh/m^2$ | DEM, SAGA-gis model | solrad |
| | NDVI (band 4 – band 3)/(band 4 + band 3) from Landsat-TM5 | Static | Metric | Landsat-TM 5 (07.08.1991) | ndvi |
| Soil type | Distance to different soil types, according to potential to support suitable forest types (spruce) | | | | |
| | Distance to soil – intermediate clay over compacted rubble | Static | m | Soil-map[a] | soil1 |
| | Distance to soil – deep clay over compacted rubble | Static | m | Soil-map[a] | soil2 |
| | Distance to soil – clay | Static | m | Soil-map[a] | soil3 |
| | Distance to soil – boulder clay mosaic | Static | m | Soil-map[a] | soil4 |
| | Distance to soil – mineral hydromorphic soil | Static | m | Soil-map[a] | soil5 |
| Stages of forest | Distance to different stages of forest development | | | | |
| | Distance to young phase – coniferous wood | Static | m | Forest classification 1993[a] | dist-ys-conif |
| | Distance to pole phase – coniferous wood | Static | m | Forest classification 1993[a] | dist-ws-conif |
| | Distance to late pole phase – coniferous wood | Static | m | Forest classification 1993[a] | dist-rs-conif |
| | Distance to regeneration stage – coniferous wood | Static | m | Forest classification 1993[a] | dist-vs-conif |
| | Distance to optimal phase – coniferous wood | Static | m | Forest classification 1993[a] | dist-ps-conif |
| | Distance to disturbance phase | Static | m | Forest classification 1993[a] | dist-ms |
| | Distance to terminal phase | Static | m | Forest classification 1993[a] | dist-zs |
| | Distance to unstocked areas | Static | m | Forest classification 1993[a] | dist-u-area |
| Biological/structural data | Percentage of spruce from previous year | Dynamic | cm | Forest mapping 1991/2001[a] | %-spruce-prevyr |
| | diameter at breast-height (DBH at 1.30 m above ground) for spruce | Dynamic | cm | Forest mapping 1991/2001[a] | dbh-prevyr |
| | Distance to areas of bark beetle from previous year | Dynamic | m | Bark beetle detection per year (1990–2007)[a] | dist-infest-prevyr |
| | Percentage of area of deadwood (spruce)[b] | Dynamic | % | Bark beetle detection per year (1990–2007)[a] | area-deadwd |
| | Perimeter of deadwood areas (spruce)[b] | Dynamic | m | Bark beetle detection per year (1990–2007)[a] | perim-deadwd |
| | Perimeter-Area-Ratio (para) of deadwood areas (spruce)[b] | Dynamic | None | Bark beetle detection per year (1990–2007)[a] | paratio–deadwd |
| | Proximity index of areas with deadwood (spruce)[b] | Dynamic | Metric | Bark beetle detection per year (1990–2007)[a] | prox-deadwd |
| | Distance to windthrow | Static | m | Classification of windthrow (1984)[a] | dist-winthr |

[a] Bavarian Forest National Park, Germany.
[b] Computed with GIS and the landscape pattern analysis program FRAGSTATS 3.3 (Mc Garigal, 2001).

standardised using a Box-Cox Transformation (Box and Cox, 1964; Sokal and Rohlf, 1981). Statistical habitat modelling was carried out using the GIS-toolkit to model ecological niche and habitat suitability – Biomapper, Vers. 4.0 (Hirzel and Hausser, 2004). A description of the statistical basis follows in the next section.

EGVs (Table 1) were generated based on the following assumptions:

1. Climatic factors affect the mobility, larval development, proliferation and the spread of the *I. typographus* – *Variables*: temperature, potential duration of sunshine, potential solar radiation.
2. The topography of the terrain plays an important role in the spread of the *I. typographus* – *Variables*: aspect, slope, elevation, relief energy (hights differences/unit).

3. Abiotic factors affect the vitality of the spruces, leading to an increase in *I. typographus* infestation – *Variables*: soil type, aspect, slope, elevation, relief energy
4. The structure and composition of the forests affect *I. typographus* infestation – *Variables*: distance to young phase of coniferous wood, distance to pole phase of coniferous wood, distance to late pole phase of coniferous wood, distance to regeneration phase of coniferous wood, distance to optimum phase of coniferous wood, distance to disturbance phase of forest, distance to unstocked areas without dead wood, percentage of spruces in the previous year, diameter breast height of spruce.
5. The spatial composition and configuration (structuring within a species) of the *I. typographus* infestation from the previous year plays a crucial role in the spread of the *I. typographus* – *Variables*: distance to areas with *I. typographus* from the previous year, percentage of area of dead wood (spruce), perimeter of dead wood areas (spruce), perimeter-area-ratio (para) of dead wood areas (spruce), proximity index of dead wood areas (spruce), distance to windthrow.

## 3. Statistical habitat analysis

### 3.1. Habitat suitability modelling (ENFA)

The ecological niche factor analysis (ENFA; Hirzel et al., 2002; Hirzel and Le Lay, 2008) is based on Hutchinson's concept (Hutchinson, 1957) of the ecological niche. According to Hutchinson's concept, the spread and frequency of organisms is not linked to just one individual environmental factor, but rather the organism has tolerances to a multiplicity of habitat parameters. The niche is therefore an *n*-dimensional structure that is made up of different environmental factors. According to this assumption the occurrence of the species under investigation is limited to an area within the multidimensional area investigated with specific ecological properties or parameters (Hirzel et al., 2002). The ecological niche compares the conditions of those sites with proven species presence against the conditions of the whole study area, requiring only presence data. The habitat of a species can be characterized by the marginality and the specialization.

The marginality ($M$) is defined as the absolute difference between the global mean (average value of the global distribution, $m_G$) and the mean of the species ($m_S$), divided by 1.96 standard deviations ($\sigma_G$) the global distribution (Fig. 2, Hirzel et al., 2002):

$$M = \frac{|m_G - m_S|}{1.96\sigma_G} \quad (1)$$

Large values for marginality means that the species lives in a very specific habitat with specific conditions or habitat factors relative to the total study area of the species. The absolute value of the marginality provides information about the importance of the habitat factor for the species. The higher the absolute value of the coefficient, the further the species are from the mean available habitat regarding the corresponding variable or habitat factors. The relative value of the marginality means that positive coefficients indicate preference for higher-than-mean values, while negative coefficients indicate that the species prefers values that are lower than the mean with respect to the total study area (Hirzel et al., 2002).

The specialization ($S$) is defined as the ratio of the standard deviation of the global distribution and the standard deviation of the studied species (Fig. 2, Hirzel et al., 2002):

$$S = \frac{\sigma_G}{\sigma_S} \quad (2)$$

The specialization explains how selective the species is by comparing the variance of the species distribution to the variance found within the investigation area. Values that are closer to 1 indicate that the species occurs in a range of conditions similar to the investigation area as a whole.

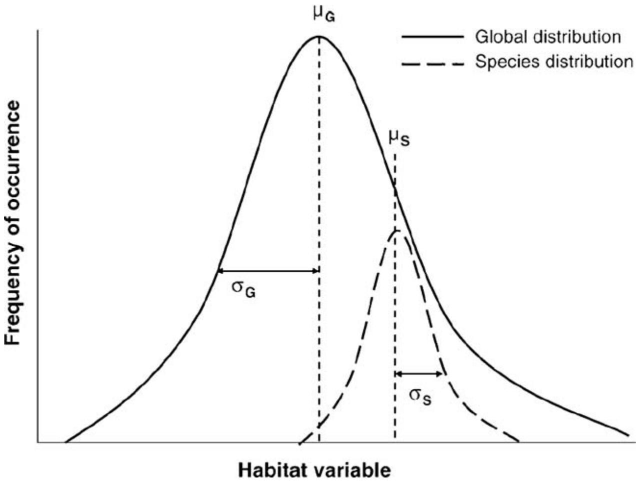

**Fig. 2.** Concept of the ecological niche factor analysis. The model is based on distributions of a habitat variable for both the global area (test sites) and for the area within the investigation area where presence is known (species distribution). The difference between the global and species means ($\mu$) and standard deviations ($\sigma$) defines the marginality and specialization factors, respectively. The figure was modified from Hirzel, 2002.

The ENFA is geared towards determining the EGVs, which make the greatest contribution to the characterisation of the ecological niche of the species under investigation (here the *I. typographus*). The factor analysis therefore reduces the relatively large number of EGVs originally introduced to just a small number of factors. Using the score matrix (Hirzel et al., 2002), the most important factors are listed with their associated coefficients, which, when classified according to their significance, show the ecological importance of the EGVs introduced for the species under investigation. For each of the study years (1990–2007), a separate ENFA-Model was calculated which led to 18 different models.

### 3.2. Model evaluation

The quality of all 18 models was quantified using two indices respectively. The absolute validation index (AVI) calculates the proportion of validation points (validation points are those observation left out during the cross-validation process) occurring in the predicted core habitats. The contrast validation index (CVI), which compares this value with the value that could be expected from a random model (Boyce et al., 2002; Hirzel and Arlettaz, 2003; Hirzel and Hausser, 2004) gives an indication of how well the model distinguishes poor from good habitat. For the calculation of AVI and CVI we applied a 10-fold area adjusted frequency cross validation (Manly, 1991; Fielding and Bell, 1997). This process allowed the computation of confidence intervals, where the observation data set was partitioned into 100 subsets with a set of 99 for calibration and 1 for a validation set. Furthermore, the number of factors required for the model calculation and the level of explanatory information can be obtained. The absolute validation index (AVI) varies from 0 to 1. The contrast validation index (CVI) varies from 0 to AVI, very good model → $\text{AVI} \geq 0.75/\text{CVI} \geq 0.3$, bad model → $\text{AVI} \leq 0.5/\text{CVI} \leq 0.2$. The evaluation showed that the ENFA analysis can be considered good models for the 18 different years as shown in Table 2.

**Table 2**
Model evaluation indices for the habitat suitability maps (1990–2007) of *Ips typographus*, computed with 10-fold cross-validation. High mean values (AVI and CVI) indicate a high consistency with the evaluation data set. Absolute validation index (AVI) varies from 0 to 1. Contrast validation index (CVI) varies from 0 to AVI, very good model → AVI ≥ 0.75/CVI ≥ 0.3, bad model → AVI ≤ 0.5/CVI ≤ 0.2.

| Model-year | AVI mean | CVI mean | Number of factors | Explained Information | Model-year | AVI mean | CVI mean | Number of factors | Explained information |
|---|---|---|---|---|---|---|---|---|---|
| 1990 | 0.74 | 0.39 | 8 | 0.85 | 1999 | 0.66 | 0.31 | 8 | 0.70 |
| 1991 | 0.74 | 0.47 | 6 | 0.84 | 2000 | 0.67 | 0.27 | 10 | 0.72 |
| 1992 | 0.77 | 0.20 | 3 | 0.76 | 2001 | 0.66 | 0.28 | 3 | 0.67 |
| 1993 | 0.67 | 0.40 | 11 | 0.76 | 2002 | 0.70 | 0.27 | 9 | 0.75 |
| 1994 | 0.62 | 0.38 | 10 | 0.79 | 2003 | 0.66 | 0.30 | 11 | 0.76 |
| 1995 | 0.70 | 0.41 | 8 | 0.73 | 2004 | 0.69 | 0.26 | 11 | 0.76 |
| 1996 | 0.67 | 0.51 | 6 | 0.74 | 2005 | 0.63 | 0.28 | 9 | 0.71 |
| 1997 | 0.71 | 0.50 | 6 | 0.69 | 2006 | 0.70 | 0.33 | 10 | 0.74 |
| 1998 | 0.62 | 0.32 | 6 | 0.68 | 2007 | 0.65 | 0.25 | 11 | 0.74 |

## 4. Results

The distribution of dead wood areas in the Bavarian Forest National Park from 1990 to 2007 (Figs. 1 and 3) shows that there was no uniform spread of the *I. typographus* population over the years of the study. Depending on the strength of the *I. typographus* outbreak (Fig. 3, total area deadwood), five periods of spread can be identified:

- *Period I (1990–1993)*: Latent infestation, post-storm-fall after storm (1983–1984).
- *Period II (1993–1996):* Medium-perennial gradation.
- *Period III (1996–2000):* Strong-perennial gradation.
- *Period IV (2000–2004):* Post-collapse-period (heat wave summer 2003).
- *Period V (2004–2007):* Perennial gradation, steeply (after heat wave summer 2003).

These time segments (periods) were then used as a basis for interpreting all of the habitat variables examined in the habitat model.

An initial characterisation of the systematic behaviour of the spread of the *I. typographus* was carried out by determining the global marginality, the global specialisation and the global tolerance (cf. Section 3.1, Fig. 2 of the EGVs examined.

In the following, we shortly describe the findings as presented in Fig. 3.

*Period I (1990–1993)*: Latent infestation, post-storm-fall after storm 1983/1984 Over this investigation period there was a great variation in global marginality. There was still no clear trend identifiable, i.e. there was no selection of highly specific habitats compared to the habitat selection for the entire study area from 1990 to 1993. Selectivity (global specialisation) fell sharply after a brief rise, reaching its lowest point in 1993. From 1990 to 1993 there was only a small proportion of dead wood areas, with a sharp increase in 1993 to 195 ha (Fig. 3).

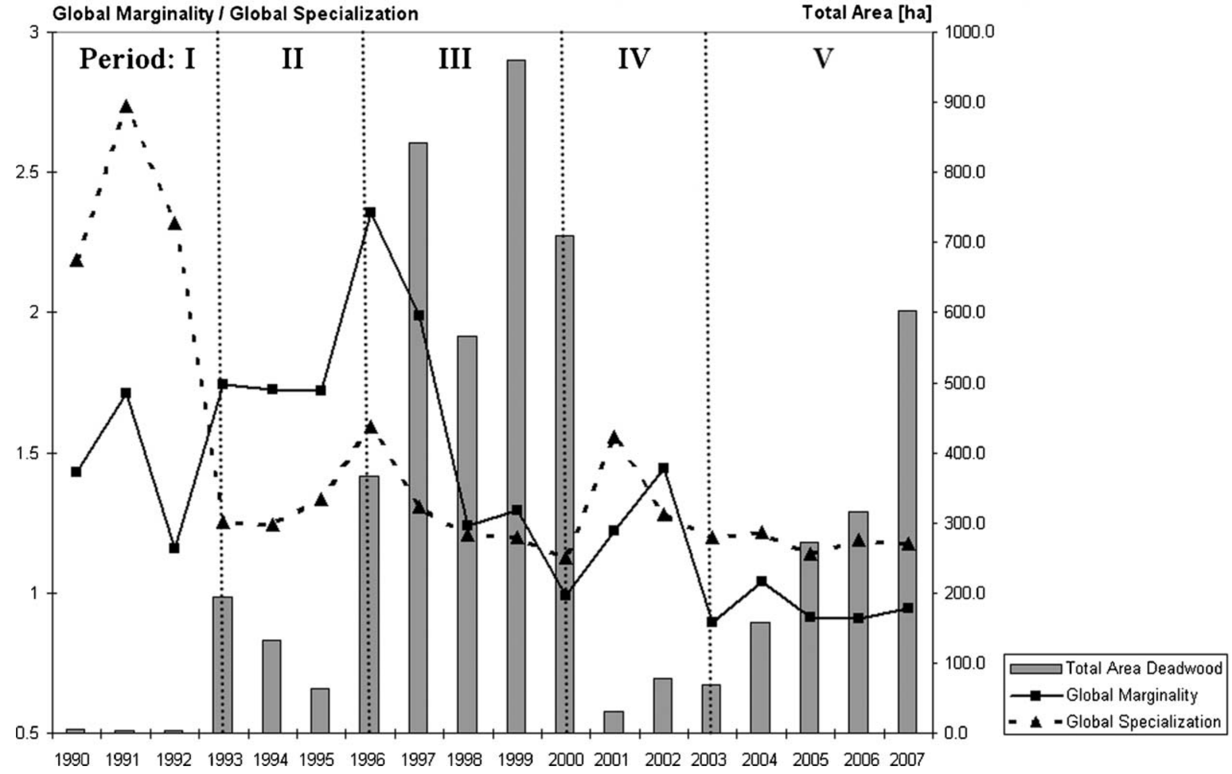

**Fig. 3.** Total area of deadwood in the Bavarian Forest National Park (1990–2007), global marginality and global specialization (1990–2007). Global marginality explains the difference between the average conditions within areas with species presence and those in the entire study area. Global specialization explains how selective the species is by comparing the variance of the species distribution to the variance found within the study area.

*Period II (1993–1996)*: Medium-perennial gradation. This period showed an increase in global marginality, i.e. a selection of highly specific habitats compared to the overall habitat area from 1993 to 1996, reaching its peak in 1996. Selectivity (global specialisation) was still very low, although this had increased again slightly by 1996. The proportion of dead wood fell from 1993, reaching a dead wood proportion of 63 ha in 1995 (Fig. 3).

*Period III (1996–2000)*: Strong-perennial gradation. Over this period there was a sharp reduction in global marginality (a decrease in specific habitat use) with relatively low selectivity (global specialisation). There was an explosive increase in dead wood areas in the study year 1996, reaching a maximum extent of 960 ha in 1999. Subsequently, the dead wood proportion decreased slightly but steadily until 2000 (Fig. 3).

*Period IV (2000–2004)*: Post-collapse-period (heat wave 2003). Over the model years 2000–2002 global marginality and global specialisation increased only slightly, whereas there was a fall in marginality and specialisation from 2002 to 2004. This means that comparable conditions existed between the habitats used by the *I. typographus* and the habitat quality of the entire study area with only a small degree of specialisation. The *I. typographus* population collapsed almost completely in 2000, with the resulting proportion of deadwood shrinking in 2001 to 31 ha. However, in the subsequent years up to 2004 there was a new infestation of more extensive *I. typographus* populations (cf. Fig. 3).

*Period V (2004–2007)*: Perennial gradation, steeply (after heat wave 2003). Over this period there was only a very low degree of global marginality and global specialisation, i.e. the conditions of the habitats used by the *I. typographus* were similar to the habitat quality of the entire study area. Up until 2007 the *I. typographus* population increased continuously again, covering a dead wood area of approximately 600 ha in 2007 (Fig. 3).

The factors (factor loadings) were determined from the EGVs that were incorporated in the model for every model year using ENFA. After the score matrix had been calculated (Table 3), the significance of the coefficients (EGVs) to the factor loading for each model year was determined. The coefficients were standardised between 0 and 1. In addition, the prefixes (−/+) were used to show whether the species has a low (−) or high (+) tendency/preference for the habitat variable being investigated. The coefficients that were determined and their tendency (+/−, relative marginality) were used to form the basis for interpreting the results and images (Figs. 4–7).

In the following we shortly describe characteristic results from the ENFA-analysis within the five different time periods.

### 4.1. *Period I (1990–1993)*

There was a very clear preference for only a few factors or EGVs over this period.

- An increase in temperature caused a spread of *I. typographus* (Fig. 4)
- Good is a short distance from the young stage of conifers (dist-ys-conif) (Fig. 6)
- A short distance to the areas affected by windthrow (dist-winthr, Fig. 7) was recorded.
- The distance from the infected areas of the previous year (dist-infest-prevyr) played a major role over the period from 1990 to 1993. The range of values showed that a very short distance from those areas infested in the previous year were sought (Fig. 7)

Only a few dominant environmental variables determined the spread of the *I. typographus* in the period from 1990 to 1993. What is striking is that the biological-structural EGVs in particular, such as the distance from infested areas in the previous year as well as the distance from areas affected by windthrow, account for a considerable proportion. Moreover abiotic EGVs have very little effect and their behaviour varies greatly over the investigation period.

### 4.2. *Periods II–IV (1993–2004)*

- Extreme elevations were used (dem Fig. 4).
- Higher temperatures were preferred from 1993 to 1997, which fell again sharply by 2004 (Fig. 4).
- A low vegetation index (NDVI) was preferred, although this correlates with the DEM (Fig. 4).
- Short distances to soil type 1 – (intermediate clay over compacted rubble), soil type 2 – (deep clay over compacted rubble), and soil type 4 – (boulder clay mosaic) were recorded (Fig. 5).
- Areas still at an early stage of growth (ys = Distance to young phase – coniferous wood, were used (Fig. 6).
- Areas suffering from the previous year's infestation (dist-infest-prevyr, Fig. 7) were still important.
- Distance from the areas affected by windthrow (dist-winthr) was no longer significant (Fig. 7).
- Areas with a high percentage of spruce from the previous year (%-spruce-prevyr) were preferred (Fig. 7).
- Dead wood areas with a high proximity index (prox-deadwd) were preferred, i.e. the *I. typographus* sought large and/or adjacent dead wood areas from the previous year (Fig. 8).
- Areas with a large perimeter and a smaller area were preferred giving high importance to the index ptchratio-deadwd, i.e. the ratio of the patch perimeter to area (Fig. 7).
- Extensive dead wood areas (area-deadwd) and dead wood areas with a large perimeter (perim-deadwd, Fig. 7) were important.

From 1993 to 2004 many EGVs displayed a relatively stable and constant behaviour, with the variable groups, topography, soil conditions, stage of forest succession in the period from 1993 to 2004 being roughly of equal importance, with the sole exception of temperature, which fell from 1997. There was, however, a greater variation in the importance of the factors regarding the biological structural data (cf. Fig. 8) from 1993 to 2004, although the tendency (whether positive or negative) remained unchanged.

### 4.3. *Period V (2004–2007)*

- Extreme elevations were used less (dem, Fig. 4).
- Constant, low temperatures were recorded (Fig. 4).
- Climatic factors such as temperature, duration of sunshine (sodur) and solar radiation (sorad) were of no importance (Fig. 4).
- There was a marked change in the preference of EGV soil conditions from 2004, with very clayey locations being preferred (Fig. 5).
- There was a preference for a short distance from areas pole phase (dist-rs-conif), forest areas at the regeneration stage (dist-vs-conif) and forest areas at the mortality stage (dist-ms, Fig. 6).
- The areas of infestation from the previous year were extremely important (dist-infest-prevyr, Fig. 7).
- There was a sharp increase in the importance of the size, perimeter, and proximity of dead wood areas from the previous year from 2004 to 2007 (Fig. 7).
- There was a dramatic increase in the importance of a high DBH from 2003 to 2007 (Fig. 7).

There was a drastic change in the trend concerning the spread of the species and its importance from 2004, particularly in terms of the abiotic EGVs. However, the trend and importance of the EGVs from the biological structural data for the spread of the species remained constant.

**Table 3**
Score-matrix for *Ips typographus* from 1990–2007. Displaying only factor 1 (marginality) for every model year 1990–2007. Factor 1 explains 100% of the marginality.

| EGV | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| dist-asp1 | ++ | ++ | + | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | – | 0 | – | 0 | 0 | 0 | – |
| dist-asp2 | ++ | ++ | ++ | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | – | – | 0 | 0 | 0 | 0 | 0 |
| dist-asp3 | – | + | ++ | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | + | + | – | 0 | 0 | 0 | 0 |
| dist-asp4 | – | –– | ––– | – | 0 | 0 | 0 | 0 | 0 | + | 0 | + | 0 | 0 | 0 | 0 | + | 0 |
| slope | + | + | 0 | + | + | 0 | + | + | + | + | + | + | 0 | –– | 0 | – | 0 | – |
| dem | + | + | 0 | ++ | +++ | +++ | +++ | +++ | ++ | +++ | +++ | ++ | ++ | 0 | + | – | – | ––– |
| dem-class | + | + | 0 | + | + | 0 | 0 | + | + | + | + | + | 0 | –– | 0 | 0 | 0 | – |
| temperature | – | – | 0 | –– | ––– | ––– | ––– | ––– | –– | ––– | ––– | –– | –– | 0 | – | + | + | +++ |
| soldur | – | – | 0 | 0 | 0 | 0 | 0 | 0 | – | – | – | ––– | – | 0 | 0 | 0 | 0 | + |
| solrad | + | + | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | –– | – | – | 0 | 0 | 0 | – |
| ndvi | –– | – | – | –– | –– | –– | –– | –– | –– | –– | –– | –– | –– | ––– | –– | 0 | 0 | – |
| soil1 | – | – | 0 | –– | ––– | ––– | ––– | ––– | ––– | ––– | ––– | ––– | –– | – | –– | + | + | +++ |
| soil2 | –– | – | – | –– | – | – | – | –– | –– | –– | –– | –– | –– | 0 | – | – | – | ++ |
| soil3 | –– | – | – | –– | –– | –– | –– | –– | ––– | ––– | ––– | ––– | –– | – | –– | 0 | + | ++ |
| soil4 | – | –– | ––– | 0 | + | + | + | + | 0 | 0 | 0 | 0 | 0 | –– | – | – | – | – |
| soil5 | + | + | 0 | +++ | +++ | +++ | +++ | ++ | ++ | ++ | ++ | ++ | ++ | +++ | + | –– | – | –– |
| dist-js-conif | –– | –– | –– | ––– | ––– | ––– | ––– | ––– | ––– | ––– | –––– | –– | –– | ––– | – | 0 | + | ++ |
| dist-ws-conif | + | 0 | – | ++ | + | ++ | + | + | + | ++ | ++ | ++ | ++ | + | ++ | 0 | 0 | – |
| dist-rs-conif | + | 0 | + | + | ++ | ++ | ++ | ++ | ++ | ++ | + | 0 | 0 | –– | –– | ––– | ––– | ––– |
| dist-zs | – | 0 | 0 | – | 0 | – | 0 | 0 | – | –– | –– | –– | –– | – | –– | – | – | + |
| dist-vs-conif | 0 | 0 | 0 | ++ | ++ | ++ | ++ | ++ | ++ | ++ | ++ | + | ++ | 0 | 0 | –– | –– | ––– |
| dist-ps-conif | + | + | ++ | + | ++ | ++ | ++ | ++ | ++ | ++ | + | + | 0 | 0 | 0 | 0 | – | –– |
| dist-ms | – | – | 0 | 0 | + | 0 | 0 | + | 0 | + | + | + | + | + | + | – | –– | – |
| dist-u | + | + | + | ++ | ++ | ++ | ++ | ++ | ++ | ++ | + | 0 | + | + | + | 0 | 0 | –– |
| %-spruce-prevyr | 0 | ––– | 0 | ++ | ++ | ++ | + | + | + | + | + | ++ | ++ | +++ | + | + | + | +++ |
| dbh-prevyr | – | ––– | + | – | 0 | 0 | –– | –– | –– | –– | – | 0 | 0 | – | 0 | + | ++ | +++ |
| dist-infest-prevyr | –––– | ––– | –––– | –– | –– | ––– | ––– | ––– | ––– | –– | ––– | ––– | ––– | ––– | ––––– | ––––– | ––––– | – |
| area-deadwd | ++ | +++ | ++ | ++ | + | ++ | +++ | ++ | + | ++ | + | +++ | +++ | ++ | ++++ | +++ | +++ | + |
| perim-deadwd | +++ | ++ | ++ | ++ | + | + | ++ | + | ++ | + | + | – | +++ | ++ | 0 | +++ | +++ | + |
| para-toth | +++ | ++ | ++ | ++ | + | 0 | 0 | + | ++ | ++ | + | 0 | 0 | ++ | +++ | ++ | ++ | + |
| prox-deadwd | + | ++++ | ++ | ++ | 0 | ++ | ++ | + | ++ | 0 | + | ++ | +++ | ++ | ++++ | +++ | +++ | 0 |
| dist-winthr | –– | – | –––– | –– | 0 | 0 | 0 | 0 | 0 | 0 | – | 0 | 0 | – | 0 | 0 | 0 | – |

[1] Marginality factor. A + symbol means that the species was found in locations with higher values than average. A – symbol means the opposite. The greater the number of symbols, the higher the correlation. 0 indicates a very weak or no significant correlation.

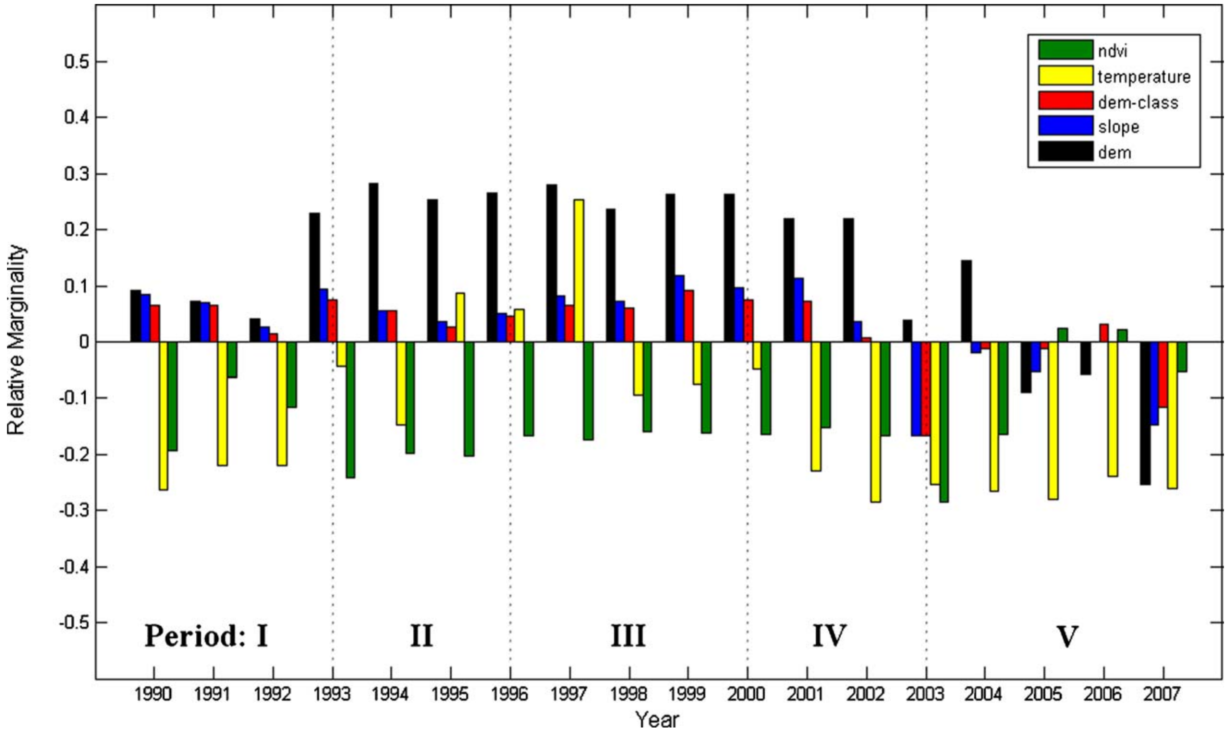

**Fig. 4.** Relative marginality of EGVs topography and climate (1990–2007). The value of marginality of the EGVs for topography and climate provides information about the importance of these factors calculated every year. The relative value means that positive coefficients indicate a preference for higher-than-mean values, while negative coefficients indicate that the species prefers values that are lower than the mean with respect to the total study area.

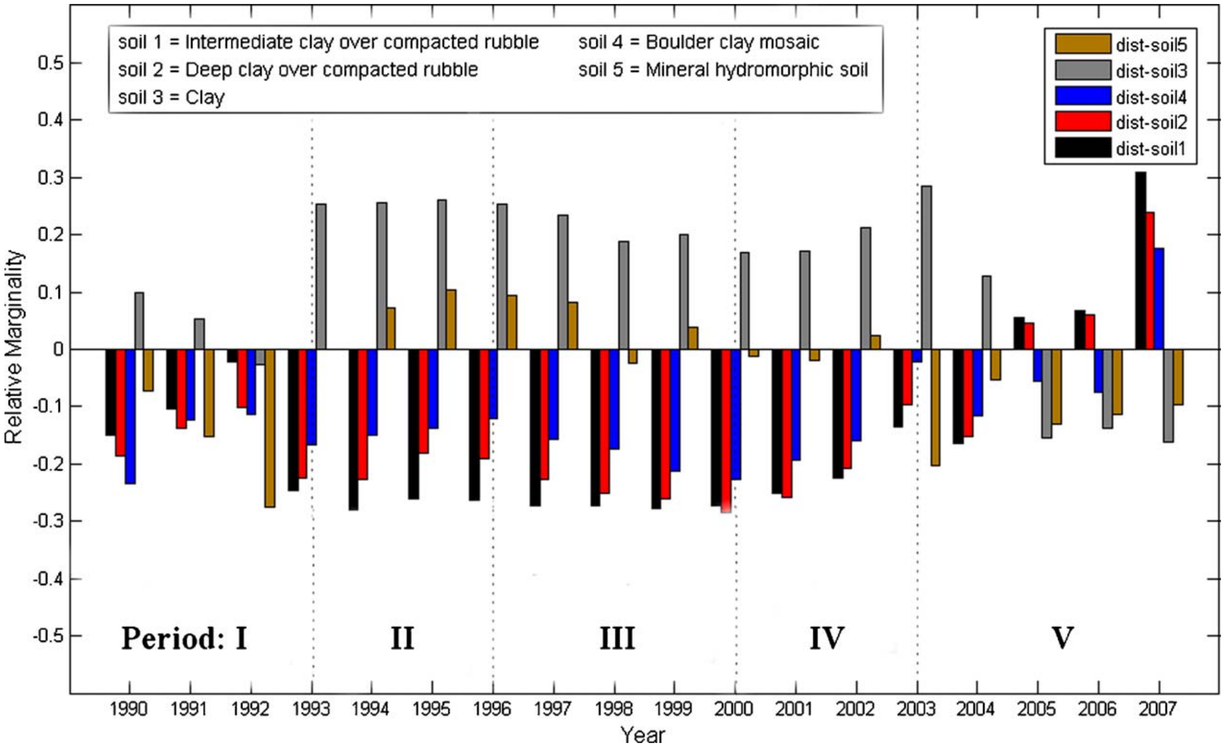

**Fig. 5.** Relative marginality of the EGV 'Distance to different soil conditions' (1990–2007). The value of marginality for the EGV – 'Distance to different soil conditions' provides information about the importance of these factors calculated every year. The relative value means that positive coefficients indicate a preference for higher-than-mean values, while negative coefficients indicate that the species prefers values that are lower than the mean with respect to the total study area.

The relative marginality of the individual EGVs for the model from years 1990 to 2007 was then used to determine the cumulative importance over all years as factors for the spread of the *I. typographus*. The results of which can be seen in Fig. 8.

A comparison of all the factors examined with their cumulative importance and specific tendency from 1990 to 2007 shows that the EGVs of the biological structural data in particular are of greatest importance as well as having the most stable spe-

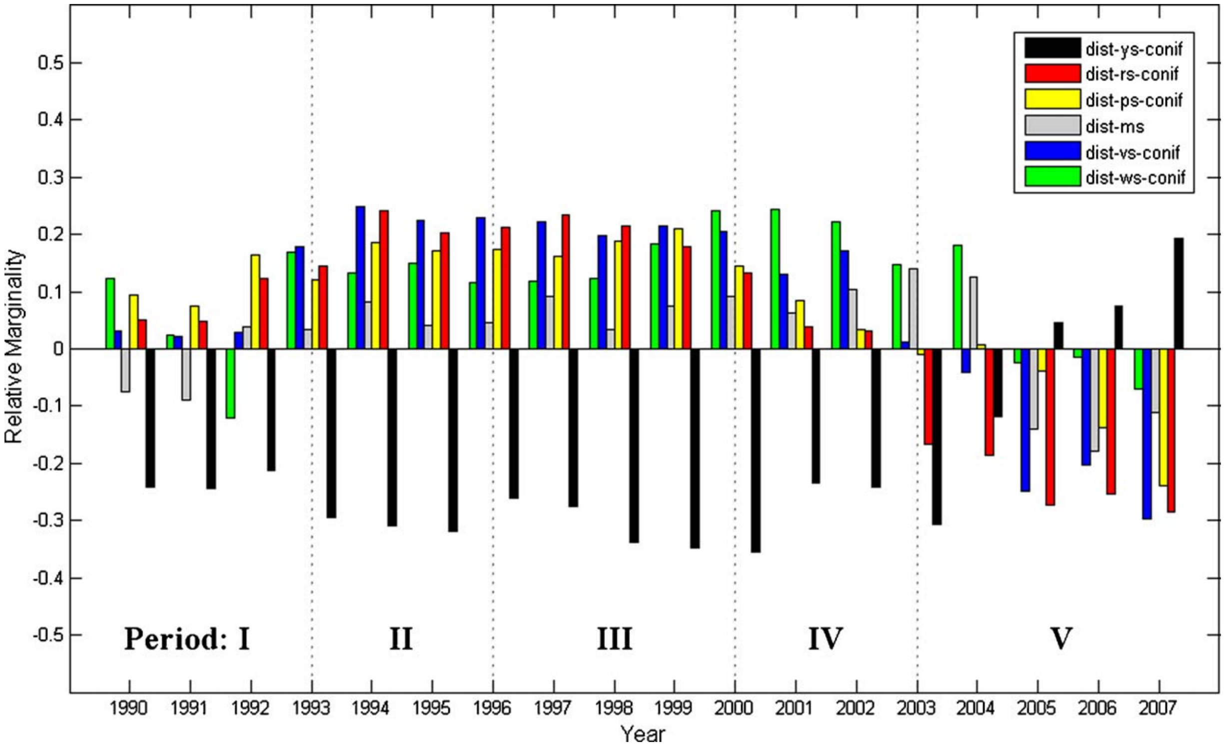

**Fig. 6.** Relative marginality of the EGV 'Distance to different stages of forest' (1990–2007). The value of the relative marginality for the EGV 'Distance to different stages of forest' provides information about the importance of these factors calculated every year. The relative value means that positive coefficients indicate a preference for higher-than-mean values, while negative coefficients indicate that the species prefers values that are lower than the mean with respect to the total study area.

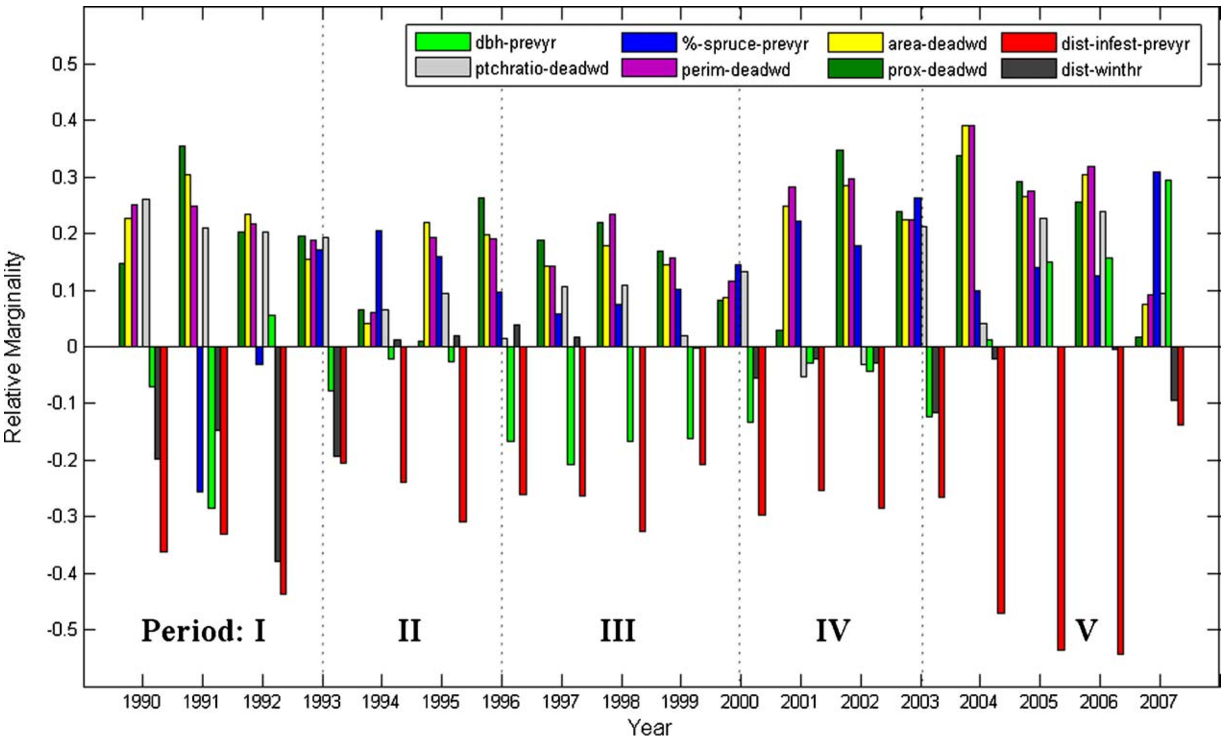

**Fig. 7.** Relative marginality of the EGV 'biological/structural data' (1990–2007). The value of relative marginality for the EGV 'biological/structural data' provides information about the importance of these factors calculated every year. The relative value means that positive coefficients indicate a preference for higher-than-mean values, while negative coefficients indicate that the species prefers values that are lower than the mean with respect to the total study area.

cific tendency (positive/negative). The factor regarding the distance from the areas of infestation from the previous year (dist-infest-prevyr) is of particular importance here. However, a relatively short distance between the current areas of infestation and the old sites of infestation from the previous year outweighs all other factors. Equally as crucial in assessing the size of the area and the distance of the deadwood areas (prox-deadwd) from the sites of the infestation from the previous year in one parameter are the size of the areas (area-deadwd), the perimeter (perim-deadwd) of the dead wood areas and the proximity index.

An evaluation of the stages of forest succession revealed that a short distance between the areas of infestation and the areas of conifers still at an early stage of growth stage (dist-ys-conif) was cumulatively an equally important EGV from 1990 to 2007. We suspect that old trees are repeatedly being blown down, especially on the edges of stands in the early growth stage, which can in turn stimulate the *I. typographus* infestation.

With regards to the importance of the abiotic EGVs such as topography, climate and soil conditions, it was shown from the DEM that elevation in particular is of high importance and has a constant specific tendency, with particular preference being shown for locations in the upper regions of the Bavarian Forest National Park in the model over the years. Vice versa – a predilection for lower temperatures is also closely correlated with elevation. The great significance of both factors – higher elevation and low temperatures – seems to contradict previously held assumptions about the trends in the spread of the *I. typographus* and its preferred areas (but see Section 5.2). It had previously been assumed that the *I. typographus* could not spread effectively at an elevation to 900 m.

Particular preference was also shown in the model over all years investigated from 1990 to 2007 for areas that were only a short distance from areas with intermediate or deep clay over compacted rubble (dist-soil1 and dist. soil 2), which happens to be a typical soil type at high elevation.

## 5. Discussion

### 5.1. Data base and model approach

The formulation of hypotheses about the habitat use of the *I. typographus* is a crucial step in making the correct choice in data collection, and the type of data calculation. This step in preparing the model is often either underestimated or undervalued and neglected. One source of errors lies in the fact that not all habitat variables defined in hypotheses about the spread of the *I. typographus* can be converted into relevant GIS data sets. An integration of habitat factors is simplified by using the GIS data format in the habitat modelling tool Biomapper.

Because of the absence of monitoring networks (e.g. sufficient climate data weather stations) for specific study periods, some important parameters, which are of great importance for the spread of the *I. typographus* have not been included in the habitat model.

Furthermore, not all variables have been integrated into the model as dynamic data because of the absence of information, and this may lead to errors and inaccuracies in the model.

A problem of the model approach ENVA is also that it can be only calculated for each survey year a model. Hence this static modelling approach (ENFA-model) does not allow for the calculation of spatial and temporal autocorrelations, which may lead to a distortion of the importance of the predictors for each model year.

### 5.2. Interpretation of habitat variables

From the abiotic factors the absolute elevation is the most important factor. The importance of absolute elevation for *I. typographus* also supports the results from Logan and Powell (2001) and Wulder et al. (2006), who found the absolute elevation to be a decisive key factor in the occurrence of *I. typographus*. Recently, Coops et al. (2009) analyzed new mountain pine beetle (*D. ponderosae*) infestations in an area of northern British Columbia, with

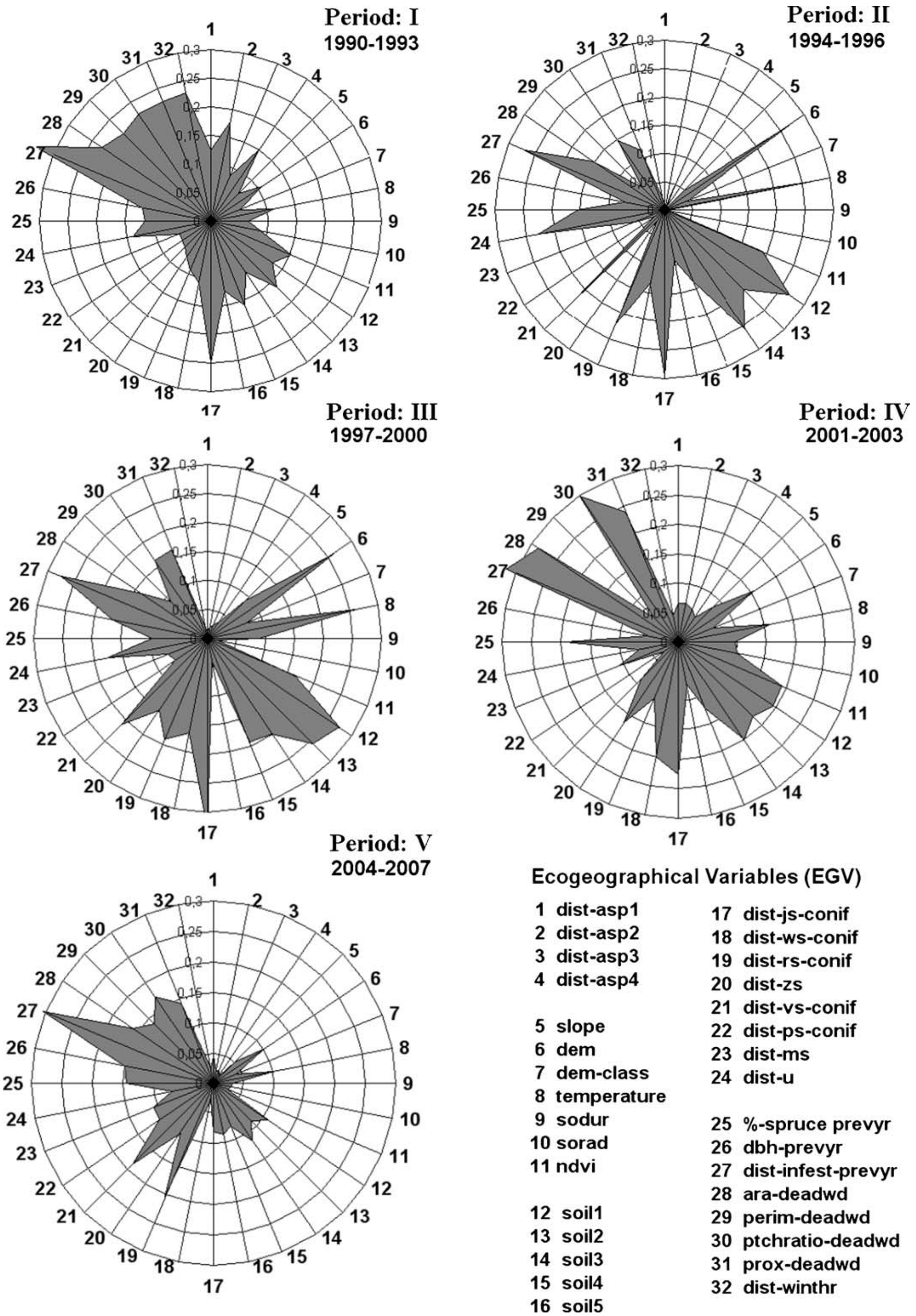

**Fig. 8.** Cumulative absolute marginality for space and time of the EGVs for the bark beetle. The value of marginality for the EGVs provides information about the importance of these factors calculated in space and time.

an elevation ranging from 221 to 2945 m. They also demonstrated the importance of elevation and slope in their studies.

In our investigation the habitat variables of slope and aspect did not play a crucial role for the dispersal of *I. typographus*. This does not support the findings of Wulder et al. (2006), who were able to improve the model using the slope variable. Jurc et al. (2006) calculated a strong correlation between a high population density of *I. typographus* and a North East (NE) exposure. Similarly, a study conducted by Jurc et al. (2006) found a greater catch of *I. typographus* particularly on western and eastern exposures, compared to catches for southern and northern exposures that were minimal. Slopes that are exposed to the west are generally warmer and it is more likely that a stronger (greater spatial spread) infestation should take place here. The mountains in our study area are relatively low, so that the effects from the heat are probably less apparent. Furthermore, there is an unequal distribution of exposures in our study area, which tends more to a westerly exposure.

The NDVI derived from the Landsat TM data is an indicator for the 'greenness' and the stage of the phenology of the vegetation (greenness index, index for active biomass). The results of our analysis display a high degree of marginality for the NDVI factor over the entire modelling period. Hence one could conclude that most *I. typographus* prefer areas with a low degree of greenness. In a similar way to the NDVI Wulder et al. (2006) calculated moisture differences (Enhanced Wetness Difference index – EWDI) derived from the Landsat-TM data. This proved to be a crucial factor. If one only considers the NDVI and the absolute elevation of the occurrence of *I. typographus*, it is clear that the NDVI and the EWDI here do not represent a small amount of greenness (low vitality or green vegetation). Both indicators were derived from the Landsat TM data with a geometrical resolution of 30 m × 30 m. With a geometric resolution of 30 m, the spectral signal represents a mixture of dead wood, soil and rock in a high absolute elevation. Because of the mixed pixel information from the satellite sensor, Landsat-TM (30 m × 30 m) is not ideal for deriving factors that affect the spread of *I. typographus*. Factors regarding greenness and for characterizing the vegetation water content should be derived from remote sensors with a high geometric and spectral resolution, i.e. hyperspectral sensors such as Quickbird or HyMap and AISA. Furthermore the temporal resolution of the Landsat TM data is also a problem when deriving factors affecting the spread of the *I. typographus*.

In our study, we still calculated the potential duration of sunshine (so-major) as well as the potential solar radiation. However, neither of these factors contributed a significant improvement to the model's performance.

The analysis of the climate variable temperature (Fig. 5) does not display a consistent picture of preferred temperature ranges. Hence, in the time periods 1990–1994 and 2001–2007 lower temperatures were preferred, whereas from 1995 to 1998 the *I. typographus* preferred warmer temperatures. Our statements contradict the results of Rolland and Lemperiere (2004) and Aukema et al. (2008). They found in their analyses that increasing temperatures contributed to explaining outbreak probabilities over a 15-year outbreak. In fact it is possible that *I. typographus* invade areas with a lower than average annual temperature when the food supply is short.

Areas with windthrow damage have been found to be crucial for the spread of the *I. typographus* (Gilbert et al., 2005; Eriksson et al., 2005). Therefore, in our investigations, we also calculated the distance to areas with windthrow damage (dist-winthr). Between 1992 and 1993 we could see that a short distance to areas with windthrow damage was important, but this became less important over the course of time. This result has also been confirmed by investigations conducted by Bourget and Duelli (2004) and Eriksson et al. (2005). In our study area, the areas with windthrow damage were mapped in 1983–1984. Areas of windthrow provide large quantities of suitable host material that allow for rapid population. Subsequently, it attacks the trees surrounding the areas with windthrow damage and the infestation continues to spread, then as the duration of the infestation increases it moves out of the areas with windthrow damage.

Further, we took up the question as to whether the spatial arrangement of forest structure influences the distribution of *I. typographus*. Coulson et al. (1999), Grodzki et al. (2003) and Fettig et al. (2007) collected various forest structural parameters. They showed that different forest structures have an influence on the occurrence and spread of *I. typographus*. In our study, we created a number of distance parameters on the basis of different stages of forest. The results showed that a short distance to the juvenile stage of conifers (dist-js-config) is preferred, compared to all other forest structure classes, where a high distance was recorded. We suppose that this could be due to the lack of available GIS data on forest structure. This could be obtained however through a forest growth model, which would include an image of a real space-time structure of the forest into the calculated model.

We analyzed tree characteristics such as DBH. The percentage of spruce was characteristic of the previous year and the spatial patterns of distribution for its potential role in the mechanism for the spread of the *I. typographus* population. In agreement with the analysis from Grodzki et al. (2003) the tree stand characteristics (DBH and the increment of trees) show no important differences in our analysis that might affect *I. typographus* preferences.

Furthermore, we also investigated whether the structure of deadwood from the previous year would have an influence on the occurrence and spread of *I. typographus*. One noticeable influence was the distance to the deadwood from the previous year.

Through our investigations we were able to establish that the area and the perimeter of deadwood from the previous year have an important effect on the distribution and dispersal of *I. typographus*. Gilbert et al. (2005) and Eriksson et al. (2006) came to similar conclusions in their research. Their studies showed that the number and size of damaged trees affect the number of *I. typographus* that end up colonizing.

An obvious preference was also shown over all years investigated in the model from 1990 to 2007 for areas that were a short distance away from those areas with intermediate and deep clay over compacted rubble – a soil type typically found in high elevation areas (dist-soil1and dist. soil 2). According to Reif and Przybilla (1995) while the compacted rubble constitutes an obstacle that can only be penetrated with difficulty by spruces, this does not impair the growth of spruces, according to Reif and Przybilla (1995). In our opinion the rubble makes it difficult for the trees to root and at the same time their water retention ability is restricted. In good years the water supply of the spruces would not present a problem, however in drought years both factors can lead to water stress for the trees. This could have been the case in the exceptional year of 1993.

### *5.3. Monocausally versus multi-causal relation*

From all the factors examined over the period from 1990 to 2007, the ecological variables relating to population such as the distance from the site of infestation from the previous year (dist-infest-prevyr) and the area and perimeter of the areas infested in the previous year are of greatest importance for the incidence of *I. typographus* in subsequent years. From a cumulative point of view, all the other factors play a subordinate role. In the period from 1993 to 2004 the importance of and preference for certain habitat variables (dem, soil-condition, successional stages of forest and biological structural data) were found to be relatively constant. The biological structural data show greater variance here and greater fluctuations in its importance in each of the individual model years.

The difficulty in determining the governing factors lies in the fact that the spread of the I. typographus is determined on the one hand by habitat-forming factors and on the other hand by purely population-specific factors. On this basis it may be assumed that the factors do not only act individually but that rather a combination of the factors, which might change annually, determines the spread of the bark beetle. *It remains possible that, in addition to the examined variables, further environmental factors influence the spread of* I. typographus *on the local and regional level (e.g. extreme drought conditions 2003 in Germany).*

## 6. Conclusions

This study has proven – to our knowledge – for the first time over a long period that the intensity of the *I. typographus* infestation over an 18-year study period goes through different phases where the importance of individual habitat variables and the combinations of these variables vary to different extents. Our results show that over the entire modelling period there is no single habitat factor that is of crucial importance for the occurrence and the spread of *I. typographus*.

We conclude from this that there are no monocausal correlations between individual habitat factors and the spread of the *I. typographus* over the entire eighteen years 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 importance at individual phases. This revealed the complexity of processes and variables could make it nearly impossible to predict future outbreaks or the dynamics of present infestation patterns.

The habitat modelling refers to the investigation and the input of the habitat factors for the entire area of the National Park Bavarian Forest. The conclusions about the importance of the variables are therefore based on the scale of the entire study area (landscape level). The *I. typographus* has a dispersal range of to 500 m. This limits the spatial and time-limited spread of *I. typographus*. Further studies may show whether the factors examined at the local level or scale would lead to the same conclusions about their importance for the spread of the *I. typographus*.

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