Spatial patterns and environmental factors affecting the presence of *Melampsorella caryophyllacearum* infections in an *Abies alba* forest in NE Spain

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Summary

The presence of trunk swellings caused by the rust fungus *Melampsorella caryophyllacearum* was systematically surveyed in an *Abies alba* forest (Irati, NE Spain), using 1237 circular plots (diameter = 18 m). The relationship between fungal presence and several abiotic (aspect, elevation, distance to the nearest river and slope) and biotic factors (basal area of *A. alba* and/or *Fagus sylvatica*, shrub, fern and herb cover) was assessed through correlation and ordination analyses. Additionally, the spatial pattern of the presence of diseased trees was described using Ripley's *K* function. Southern-aspect plots with diseased trees were located at a significantly lower elevation, and at a shorter distance to the river than plots without infections. Plots with diseased trees had almost twice the average *A. alba* basal area, and less average *F. sylvatica* basal area than plots without diseased trees. However, similar mean values of slope and shrub, fern and herb cover were found in both types of plots. The disease showed spatial aggregation in patches with a mean radius of ca. 900 m. The implications of the results for diseased.

1 Introduction

Melampsorella caryophyllacearum Schroet. [=M. cerastii (Pers.)] causes an important rust disease of Abies spp. throughout the range of that genus in the Northern Hemisphere. It has been reported on Abies alba Mill. in Europe (TEGGLI et al. 1993; NICOLOTTI et al. 1995), on A. balsamea (L.) Mill., A. fraseri (Pursh) Poir., A. grandis (Dougl.) Lindl. and A. lasiocarpa (Hook.) Nutt. in the US (LUNDQUIST 1993; MERRILL et al. 1993), on A. balsamea in East Canada (SINGH 1978), and on A. sibirica Ledeb., A. homolepis Sieb. & Zucc., and A. cilicica Carr. in Asia (DRACHKOV 1976; PUPAVKIN 1982; HAMA 1987; SARIKAYA and AVCI 2002). In Spain, it was first reported on A. alba in the Pyrenees by MONTOYA et al. (2002). The most conspicuous symptoms of the disease are yellowishgreen witches' brooms and spherical swellings on the trunk. Damage includes radial growth loss, xylem rot by decay fungi, windbreak at the site of the swelling, and mortality (ZILLER 1974; SINGH 1978; SOLLA et al. 2006).

Melampsorella caryophyllacearum needs two hosts and at least 2 years to complete its life cycle. In the spring or early summer, spermogonia develop in two rows of small orange-yellow blisters on both surfaces of fir needles on a broom (MYREN 1994). By midsummer, aecia develop on the underside of needles, and produce aeciospores that are dispersed by wind to infect foliage of chickweeds (*Cerastium* and *Stellaria* spp.), the alternate hosts (STEIDLEY and BUCHANAN 1971). After a few weeks, urediniospores are

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produced on chickweeds, which result in an intensification of infection on this host. At the end of the summer or in the early fall, white to pale reddish telia appear on the chickweed leaves, and a perennial mycelium is formed (PADY 1946). During the following spring, teliospores germinate and release basidiospores, which infect fir shoots. Swellings usually are evident by the end of the first summer, and the mycelium of the fungus persists in the woody tissue (PADY 1946). The following spring, new shoots arise from the swellings, forming new witches' brooms and completing the life cycle (MYREN 1994).

No fungicide is registered for the use in controlling M. carvothyllacearum. If one was available, it probably would not be feasible to apply it to a forest stand. Removal of alternate hosts should reduce rust incidence (PUPAVKIN 1982), but this measure has not been tested, and would require removal of chickweed over long distances around the group of trees to be protected. A similar method has not been successful with other rust diseases, and given the size of most forest stands, this approach would be economically impractical (MYREN 1994). More research has to be conducted to study the spatial distribution of *M. caryophyllacearum* in order to reduce the impact of the disease on host populations by using information concerning factors favouring disease presence and the spread of fungal infection. Although spatial structures of disease outbreaks have received little attention in forest pathology, they can reveal processes affecting the ecological and evolutionary dynamics in host-pathogen systems (HOLDENRIEDER et al. 2004). The main objectives of the study were to determine which environmental and biotic factors (aspect, elevation, distance to the nearest river, slope and basal area) were related to the presence of *M. caryophyllacearum*, and to describe the spatial pattern of the fungal infection in an extensively affected A. alba stand.

2 Materials and methods

2.1 Study area

The study site is located in the Irati forest (1°10'-0°58'E, 42°56'-43°00'N), extending to the south of the axial Pyrenees, ca. 50 km north-east of Pamplona (Navarra, NE Spain) (Fig. 1). This natural forest has an area of 17 195 ha, at elevations ranging from 772 to 2021 m a.s.l. Soils are well drained Eutric Podzoluvisols above a chalk bedrock of Paleocene origin. The climate is Atlantic with some continental influence. Rainfall has a summer minimum from June to August, and a maximum from October to December, with a mean annual precipitation of 777 mm (observation period 1940–2002, Yesa station, 42°37'N, 1°11'W, 487 m a.s.l.). Monthly mean maximum temperatures occur from July to September (19–22°C), whereas mean minimum temperatures are observed from December to January (5–6°C). The mean annual temperature is 13.1°C. In the study area, the dominant tree species are *A. alba, Fagus sylvatica* L., and *Pinus sylvestris* L., and the main understorey plant species are *Vaccinium myrtillus* L., and *Daphne laureola* L. Phytosociologically, the area is defined as *Festuco altissima-Abieteto albae sigmetum*.

2.2 Extensive field sampling

An extensive survey of the disease was conducted from January to December 1996. The survey included a rectangular area of 10 500 × 7500 m with its (x,y) = (0,0) co-ordinates located at 42°56'30"N, 1°10'20"W. Circular plots, 18 m in diameter, were established at 150-m intervals along a regular grid. Only plots containing at least one *A. alba* tree were considered for data sampling (n = 1237). In every plot, fir trees were carefully examined for the presence (1) or absence (0) of *M. caryophyllacearum* symptoms (i.e. witches' brooms, and swellings on trunk or on branches). In each plot, d.b.h. of all trees was



Fig. 1. Distribution of *Abies alba* in Europe (upper graph), and location of Navarra and the study area in the Irati forest (lower left graph). The scatter (lower right graph) shows the circular plots with *A. alba* presence within the sampled rectangular area (10 500 × 7500 m)

recorded, and absolute percentage of understorey plants, fern [*Pteridium aquilinum* (L.) Kuhn], and herb cover was estimated. Finally, additional environmental measurements of each plot included the aspect (N, S, E, W), elevation, distance to the nearest river and slope. In the Navarra region, the following chickweed species have been cited (CASTROVIEJO et al. 1990): *Stellaria graminea* L., *S. holostea* L., *S. nemorum* L., *S. media* (L.) Vill., *Cerastium arvense* L., *C. cerastoides* (L.), *C. fontanum* Baumg., and *C. pumilum* Curtis. Although *S. graminea* and *S. media* are present within the Irati forest (FERNÁNDEZ and SÁNCHEZ DE LOS Ríos, unpublished data), the presence of these two chickweeds was not surveyed.

2.3 Intensive field sampling

Detailed examination of the severity of the disease was completed in July 2003 for three plots located within the central area. This area was selected because of the great abundance of swellings caused by *M. caryophyllacearum* and the absence of any other serious disease

and/or insect problems on *A. alba.* The identity of the fungus was confirmed by the symptoms (SINGH 1978), xylem anatomical changes at the point of swelling (SOLLA et al. 2006), and size of aeciospores produced on the infected needles. Xylem anatomical changes were observed on samples obtained from each of the three plots, and included eccentric growth increments and the presence of traumatic resin ducts. Aeciospores collected from needles of one witches' broom measured 14–17 μ m wide and 18–27 μ m in length, coinciding with previous descriptions of the species (ZILLER 1974). The plots were selected because of their similar elevation, slope and stand height (Table 1). The survey was conducted in nine sample points per plot (SINGH 1978), and each sample point occupied 181 m². The following observations and data were recorded in ca. 100 *A. alba* trees per plot: height and d.b.h. of the tree, number of swellings and brooms per tree, and height and aspect of each swelling. The percentage of affected trees (incidence) and the mean number of swellings and brooms per symptomatic tree (intensity) were also calculated.

2.4 Statistical and spatial analyses

The data from the intensive field sampling were arcsine transformed to follow normality, and analysed using unifactorial ANOVA, considering the plot as a factor. Tukey's multiple-range test was applied to compare mean values ($p \leq 0.05$).

Concerning the extensive sampling, univariate non-parametric tests were used to compare mean values of selected variables for plots with presence or absence of symptomatic trees (Mann–Whitney test). Then, correlation analyses were performed using the non-parametric Spearman's correlation coefficient (SOKAL and ROHLF 1995). Multivariate analyses were carried out to quantify the relationships among the selected environmental (aspect, distance to the nearest river, elevation and slope) and biotic (*A. alba* basal area, *F. sylvatica* basal area and total basal area) variables and the presence of *M. caryophyllacearum* symptomatic trees. Principal component analysis (PCA) was performed after converting the binary variable 'presence of symptomatic trees' to two variables 'presence' and 'absence'. This procedure allowed the use of these two new variables as quantitative descriptors, which is a requisite for PCA (LEGENDRE and LEGENDRE 1998). Statistical analyses were performed using sPSS ver. 6.1.2 (SPSS Inc. 1989–1995, Chicago, IL, USA).

	Plot 1	Plot 2	Plot 3				
Location (latitude N, longitude W)	42°59′ 1°03′	43°00′ 1°04′	42°58′ 1°03′				
Elevation (m a.s.l.)	1030	1005	1010				
Aspect	Ν	Ν	S				
Slope (°)	32	37	31				
A. alba density (stems ha^{-1})	716	584	595				
A. alba average height (m)	21.0	22.3	22.9				
A. alba basal area $(m^2 ha^{-1})$	47.8	66.4	58.1				
Trees examined	117	95	97				
Trees with swellings (%)	39.3	45.3	43.3				
Swellings per symptomatic tree	$1.6 (1-5)^1$	2.1 (0-5)	1.4 (0-4)				
Swellings on trunk (%)	76	86	54				
Swellings on branches (%)	24	14	46				
Mean height of swellings on trunk (m)	7.9 (1-16)	7.2 (1-18)	7.7 (0.5-22)				
Mean height of swellings on branches (m)	12.2 (4-20)	11.8 (4-20)	11.0 (4–21)				
¹ Values within parenthesis are the range of the variable.							

Table 1. Site specifications, severity, position and mean height of swellings caused by *Melampso*rella caryopbyllacearum on Abies alba trees located in Irati forest (Navarra, NE Spain)

The spatial pattern of the presence of the disease was described using Ripley's K(t). To avoid problems related with the possible heterogeneity of data, only an homogeneous subarea delimited by co-ordinates (x,y) = (3000,1500) - (9000,6000) was analysed. The variable 'presence of symptomatic trees' was obtained by transforming into spatial coordinates (x,y), the raw 'matrix' data selecting only those plots where the presence of the diseased was recorded within the defined homogeneous subarea. Then, Ripley's K secondorder analysis, which considers the distances between all pairs of points, was calculated (RIPLEY 1981). The original K(t) statistic is calculated for several distances (t) to detect the relevant scale of the spatial pattern (e.g. the scale of maximum aggregation), and is usually represented as $L(t) = [K(t)/\pi]^{0.5}$ to stabilize the variance (HAASE 1995). As we were interested in the detection of patches of symptomatic trees, we analysed the spatial pattern using a distance t = 300 m up to a maximum t = 2100 m. In the case of complete spatial randomness, L(t) - t = 0, whereas values above or below 95% CI, obtained through 10 000 permutation tests, will indicate the aggregated or regular patterns, respectively. We performed this analysis using ADE-4 software (THIOULOUSE et al. 1997).

3 Results

3.1 Intensive field sampling

The mean incidence of *M. caryophyllacearum* infections on *A. alba* trees was about 40%, with no significant differences among the three plots (p > 0.10; Table 1). However, the highest intensity, i.e. the greatest number of swellings per symptomatic tree, was observed in plot 2 (p = 0.07). In all plots, more swellings were observed on trunks than on branches. Mean height of swellings on trunk, and on branches, was about 7.5 and 12.5 m respectively, not differing significantly among plots. In the north-oriented plots 1 and 2, most trunk swellings were observed in the southern position on *A. alba* main stems (Fig. 2). However, in plot 3, which showed a southern aspect, trunk swellings were more frequently observed in the northern position on *A. alba* main stems.

3.2 Extensive field sampling

In the Irati forest, from 1232 sampled plots containing *A. alba* trees, 246 plots showed trunk swellings caused by *M. caryophyllacearum*. The number of plots oriented to the N (n = 543), S (n = 196), E (n = 168) and W (n = 325) directions in which trunk swellings were observed were 125, 19, 40 and 62, respectively. Southern-aspect plots showed a significantly ($p \le 0.01$) lower presence of trunk swellings than plots oriented N, E or W (Mann–Whitney test, Fig. 3).

Plots with diseased trees were located at a significantly lower elevation, and at a shorter distance to the river than plots without disease (Table 2). Plots with diseased trees showed almost twice the average *A. alba* basal area, and less average *F. sylvatica* basal area than plots without diseased trees ($p \le 0.001$). However, both types of plots showed similar mean values of slope and of shrub, fern and herb cover (Table 2).

The first two axes of the PCA summarized 25% and 18% of the overall variance, respectively (Fig. 4). The first axis was positively related to the presence of diseased trees, to *A. alba* basal area, and to total basal area, but negatively related to elevation. The second PCA axis was positively related to elevation, to distance to the nearest river, and to *F. sylvatica* basal area.

The correlation values shown in Table 3 agree with the results presented in Table 2 and those obtained in the PCA (Fig. 4). The significant relationships between the presence of diseased trees and elevation and distance to the nearest river indicate that the disease is



Fig. 2. Wind rose of position frequency of infections caused by Melampsorella caryophyllacearum (n = 147) on A. alba main stems in three intensively sampled plots



Fig. 3. Mean frequency values for the presence of *M. caryophyllacearum* in plots (n = 1232) with different aspect. Vertical error bars represent SE, and different letters show significant differences among values ($p \le 0.01$, Mann–Whitney test)

Variable	Presence $(n = 246)$	Absence $(n = 986)$	Significance ¹				
Elevation (m)	1056.0 ± 6.4	1141.3 ± 3.4	**				
Distance to river (m)	8.4 ± 0.5	10.1 ± 0.3	*				
Slope (%)	41.3 ± 1.2	39.7 ± 0.5	ns				
A. alba basal area $(m^2 ha^{-1})$	23.0 ± 1.0	12.7 ± 0.5	**				
Fagus sylvatica basal area $(m^2 ha^{-1})$	18.6 ± 0.7	22.6 ± 0.4	**				
Total basal area (m ² ha ⁻¹)	41.6 ± 0.9	35.4 ± 0.5	**				
Shrub cover (%)	0.2 ± 0.2	0.4 ± 0.3	ns				
Fern cover (%)	0.2 ± 0.1	0.9 ± 0.2	ns				
Herb cover (%)	3.9 ± 0.5	6.3 ± 0.5	ns				
¹ Significance levels: ns, non-significant; * $p \le 0.05$; ** $p \le 0.001$.							

Table 2. Mean values (± SE) of variables measured in plots with *M. caryophyllacearum*-diseased trees (presence), and in plots without diseased trees (absence)



Fig. 4. Ordination diagram of the analysed variables in the first two axes of the principal component analysis. Abbreviations of the variables are: ASP, aspect; DIS, distance to the nearest river; ELE, elevation; SLO, slope; Aa, A. alba basal area; Fs, F. sylvatica basal area; Aa + Fs, total basal area; MC, presence of M. caryophyllacearum diseased trees

spatially structured. Indeed, plots showing diseased trees were significantly aggregated within the range 300-1800 m with a maximum clustering intensity at a distance of 900 m, i.e. the mean radius of a symptomatic *A. alba* patch in the studied forest was ca. 900 m (Fig. 5).

4 Discussion

The disease incidence reported here is only comparable with the one reported on *A. balsamea* in Newfoundland (SINGH 1978), where *M. caryophyllacearum* infected up to 40% of the trees. On *A. sibirica* in the Krasnoyar region (Russia), on *A. balsamea* in New England and on *A. alba* in the Apennine and Alpine areas of Italy, incidences were about 30%, 20%, 15% and 2%, respectively (PUPAVKIN 1982; TEGGLI et al. 1993; MERRILL et al. 1993).

The study reported here is the first to provide information on the spatial pattern and the abiotic and biotic variables that influence the presence of swellings caused by

	ELE	DIS	SLO	Aa	Fs	Aa + Fs
ELE DIS SLO Aa Fs Aa + Fs MC	0.37** ¹ 0.01 -0.31** 0.24** -0.10** -0.31**	-0.22** -0.16** 0.16** -0.01 -0.06*	0.07* -0.03 0.05 0.03	-0.50** 0.50** 0.31**	0.40** -0.14**	0.21**

Table 3. Spearman's correlation coefficients among variables for the extensive field sampling

¹Significance levels: * $p \le 0.05$, ** $p \le 0.001$.

Abbreviations of the variables: ELE, elevation; DIS, distance to the nearest river; SLO, slope; Aa, A. *alba* basal area; Fs, F. *sylvatica* basal area; Aa + Fs, total basal area; MC, presence of M. *caryophyllacearum* diseased trees.



Fig. 5. Spatial point pattern analysis of *M. caryophyllacearum* presence using Ripley's K(t). The different symbols correspond to the calculated L(t) - t (filled circles), and the upper and lower 95% CI (empty circles). The upper inset graph shows the study site (black squares indicate plots showing trunk swellings) and the analysed homogeneous subarea within the sampled rectangular area (10 500 × 7500 m; see Fig. 1)

M. caryophyllacearum on *A. alba*. The presence of the disease increased at lower elevations, shorter distances to the nearest river and higher total basal area. Other factors such as slope, shrub, fern and herb cover did not show any significant relationship with the disease presence. In previous studies, disease incidence has been reported to be higher at wet than at dry sites (NICOLOTTI et al. 1995), and wet-spring weather favoured the disease (PUPAVKIN 1982). At a national scale in Italy, NICOLOTTI et al. (1995) showed that *M. caryophyllacearum* incidence was greater in the mesic Alpine forests than in the more xeric southern forests. These authors also found a negative correlation between the incidence of the fungus and the distance from infected trees to the nearest river.

Our results support the hypothesis that *M. caryophyllacearum* infections are more intense on *A. alba* trees located in sites where moist conditions prevail (Figs 3 and 4). In fact, in the north-oriented plots 1 and 2, the number of swellings per tree was significantly higher than in the south-oriented plot 3. The range of air moisture content

optimal for *M. caryophyllacearum* basidiospore germination or mycelium growth warrants further investigation, but probably low moisture conditions or extremely high moisture conditions will not lead to the swelling formation. Microenvironmental conditions with low or with high moisture and water-filled xylem are inhospitable to most fungi. However, conditions in a humid and aerated tissue are favourable for fungal growth and spore germination (BODDY 1992). According to Fig. 2, the north part of the stem of trees grown in north-oriented slopes (plots 1 and 2) developed fewer infections than the south part of the stem, probably as a consequence of extreme moisture conditions. The contrary trend was observed on trees grown in the south-oriented plot. The possible role of light and its interaction with moisture in favouring the swelling formation should not be ruled out. Observations made on *A. sibirica* in the Archangel region and the Komi ASSR suggested that trees more exposed to light were more severely attacked (DRACHKOV 1976).

In Irati, plots with diseased trees had an average basal area of both *A. alba* and *F. sylvatica* 17% higher than plots showing no disease. This is not in agreement with the observations made in pure and mixed stands in the Siberian Archangel region and the Komi ASSR, which showed that the incidence of *M. caryophyllacearum* was not affected by the abundance of *A. sibirica* in the stand (DRACHKOV 1976). In these stands, *A. sibirica* reaches its northern limit of distribution in European Russia, in contrast with Irati forest, near the south-western limit of distribution of *A. alba* in Europe (Fig. 1). Therefore, care must be taken in comparing different species and environments, which may represent limiting autoecological conditions for each fir species. Into this complex equation including the host density and microenvironment factors on fungal development, could be added yet another two variables to explain differences in disease incidence – the presence of chickweeds and conditions for basidiospore release from chickweed leaves.

We also detected that *M. caryophyllacearum* infection formed patches of maximum aggregation with a mean radius of ca. 900 m (Fig. 5). Spatial analyses have proved useful for investigating the spread of plant pathogens and the incidence and/or severity of tree diseases (e.g. COULSTON and RIITTERS 2003). Landscape pathology is developing as a subdiscipline at the interface between forest pathology and landscape ecology (HOLDEN-RIEDER et al. 2004). In this line, a pathoregion could be identified by the presence of a particular pathogen population and/or by a significant reduction in disease incidence at its borders (HOLDENRIEDER et al. 2004). In the Irati forest, the pathoregion found for *M. caryophyllacearum* on *A. alba* was about 2.5 km², coinciding with the mean area of a typical deep and narrow 2-km long valley in this site.

This study highlights several implications for disease management. To reduce the presence of *M. caryophyllacearum* swellings, it can be suggested to favour plantations of A. alba at higher elevations and distances to the river. This measure, combined with thinning or gap opening, would reduce the moisture conditions for potential swelling formation. In addition, the opening of small gaps would avoid evolving towards an undesirable stand uniformity and single stratum (SCHÜTZ 1997), with the consequent progressive disappearance of the lower-strata individuals caused by a lack of light. That structural uniformity causes the loss of physical stability against natural disturbances such as strong wind and snow, and it affects biological diversity because of the low understorey development. In addition, this homogeneity is also associated with an undesirable overstock of timber, which is observed over the threshold of 400 m³ ha⁻¹ (BERNETTI 1985). This was the case with the three plots intensively surveyed. Only recently, researchers have realized that spatial plantation design influences the severity of some tree diseases (HUNTER et al. 2002). In the Irati forest, the M. caryophyllacearum incidence was lower in the mixed A. alba-F. sylvatica stands compared with the monospecific A. alba stand, which is consistent with previous studies and suggests an additional alternative for disease management. The use of mixed stands has been shown to be an extremely important strategy in reducing the impact of willow foliar rust without recourse to intervention with pesticides (see HUNTER et al. 2002). Mixed *A. alba–F. sylvatica* stands in the Pyrenees are extremely stable despite having been historically logged for centuries (CAMARERO 2001). To reduce the spread and incidence of *M. caryophyllacearum*, similar stands should be conserved and promoted where possible, taking into account the results presented here.

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Résumé

Structure spatiale et facteurs environnementaux affectant la présence des infections de Melampsorella caryophyllacearum dans une forêt d'Abies alba du Nord de l'Espagne

La présence de renflements sur les troncs causés par l'agent de la rouille, *Melampsorella caryophyllacearum*, a été étudiée de façon systématique dans une forêt d' *Abies alba* (Irati, NE Espagne), en utilizant 1237 placettes circulaires (diamètre de 18 m). Les relations entre la présence du champignon et divers facteurs abiotiques (orientation, altitude, distance à la rivière la plus proche, pente) et biotiques (surface terrière de *A. alba* et/ou *Fagus sylvatica*, abondance de la couverture herbacée et abondance d'arbustes et fougères) ont été étudiées par analyses de corrélation et d'ordination. D'autre part, la structure spatiale de la présence d'arbres infectés a été décrite en utilizant la fonction K de Ripley. Les placettes exposées au sud présentent moins fréquemment des arbres malades que celles exposées au nord, à l'est ou à l'ouest. Les placettes avec des arbres malades sont situées à une altitude significativement plus faible et à une distance plus faible d'une rivière que les placettes sans infections, et elles présentent une surface terrière 2 fois plus forte en moyenne pour *A. alba*, et plus faible pour *F. sylvatica*, que les placettes non-infectées. Toutefois, des valeurs moyennes équivalentes pour la pente, la couverture herbacée et l'abondance d'arbustes et fougères, sont observées pour les deux types de placettes. La maladie montre une agrégation spatiale en foyers d'un rayon moyen de 900 m. Les résultats sont discutés dans une perspective de gestion de la maladie.

Zusammenfassung

Melampsorella caryophyllacearum–Infektionen in einem Abies alba-Wald in Nordost-Spanien: Räumliche Verbreitung und Einfluss von Standortfaktoren

Das Vorkommen von durch den Rostpilz *Melampsorella caryophyllacearum* verursachten Stammdeformationen wurde in einem *Abies alba* - Wald (Irati, NO-Spanien) auf 1237 kreisförmigen Probeflächen (Durchmesser 18 m) systematisch erfasst. Die Beziehung zwischen dem Pilzvorkommen und mehreren abiotischen (Exposition, Meereshöhe, Distanz zum nächsten Fluss, Hangneigung) und biotischen Faktoren (Deckungsgrad von *A. alba* und/oder *Fagus sylvatica*, Strauch-, Farn- und Krautschicht) wurden durch Korrelations- und Ordinations-Analysen überprüft. Zudem wurden räumliche Muster der befallenen Bäume mit Hilfe von Ripley's K-Funktion beschrieben. In südexponierten Probeflächen kamen signifikant weniger erkrankte Bäume vor als in nach Norden, Osten und Westen orientierten Standorten. Flächen mit Befall lagen in signifikant geringerer Meereshöhe und kürzerer Distanz zum nächsten Fluss als solche ohne Befall. Zudem hatten sie beinahe die doppelte Basalfläche mit *A. alba* und eine durchschnittliche geringere Basalfläche mit *F. sylvatica*. Die durchschnittlichen Werte für die Strauch-, Farn- und Krautschicht sowie die Hangneigung unterschieden sich jedoch nicht in den Flächen mit und ohne Befall. Erkrankte Bäume waren räumlich aggregiert mit einem mittleren Radius von ca. 900 m. Die Bedeutung dieser Befunde für das Krankheitsmanagement wird diskutiert.

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