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Predictability of the Spatiotemporal Pattern of Wild Boar (*Sus scrofa*) Rooting Influenced by Acorn Availability

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Abstract: The natural regeneration of the temperate oak forests is often insufficient. Acorns of the oak serve as the basis of the recruitment and key food resources in these ecosystems, thus the crop size, the germination success and seed predators have crucial roles in the process. Wild boar (*Sus scrofa*) is often considered as one of the main mitigating agents in oak regeneration. Therefore, in our study we analyzed and compared the spatial patterns of the acorn density and the patches rooted by wild boar within and among the different examined time intervals in a 28 ha Turkey-sessile oak (*Quercus cerris*, *Q. petraea*) forest stand. Data were collected between 2016 October and 2019 December. In the acorn density patterns, intra-annual similarities were recognized mainly, regardless of the crop size. Meanwhile, rooting patterns showed inter- and intra-annual similarities in mast years and intra-annual overlaps in non-mast years, indicating that masting is a fundamental driver of wild boar foraging behavior. However, a direct local connection between the rooting intensity and the acorn density could not be shown, as wild boars never fully depleted the acorns, even in intensively used patches. This study can help in predicting the intensively rooted forest patches, providing opportunities to manage wildlife conflicts.

Keywords: forest regeneration; hot spot analysis; masting; oak; *Quercus* spp.; ungulate impact

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1. Introduction

Throughout the temperate zone in the Northern Hemisphere, oaks (*Quercus* spp.) are among the most important tree species culturally, economically [1,2] and ecologically [3–5]. Many of the red-listed forest species are closely associated with the genus *Quercus*, thus the conservation aspect of oaks is also very important [6]. However, the natural regeneration of oaks has been regularly missing or deficient [7–13]. Therefore, the regeneration of oaks is often in the focus of interest of forest and wildlife managers or conservationists, and game species like wild boar (*Sus scrofa*) are often considered the main mitigating factors in oak regeneration.

Several factors and their interactions can affect the habitat use of ungulate species, including the abiotic and biotic heterogeneity of the environment, like distribution of foraging places or the proximity of water sources but also the risk posed by predators through the "landscape of fear", thus the availability of hiding places (the vegetation cover) [14–17]. Available food resources clearly have an outstanding effect on the space use and selection of patches [18,19].

White and Cerris oaks are characterized almost exclusively by sexual reproduction, and their acorns are the basis of the natural regeneration in an oak-dominated forest. Therefore, the crop size and germination success have a crucial effect on the successful recruitment [20–22]. Oak acorns have high nutritional values [23–26] and provide favored, fundamental resources for wildlife in oak forest ecosystems [27–31].

Oaks and their acorns are not unarmed against the impacts of seed predators. Generally, acorns contain digestion-inhibiting secondary compounds called tannins [32,33]. Oak species also typically show mast seeding (a synchronous intermittent production of large seed crops by a plant population), which is often considered to be a defensive strategy in reproduction to satiate predators in mast years and starve them in the intervening periods [28,29,34–37]. As a keystone resource, these episodic pulses in acorn availability have crucial and far-reaching multitrophic effects in these ecosystems and can directly influence the behavior of the consumer populations [28,38–42] and vice versa—seed predators can have a serious impact on oak recruitment and regeneration as mitigating agents [20,43,44].

Typically, the trophic generalist species are the ones that show the strongest response to these masting events [28], but some authors consider the masting as an ineffective defensive strategy against trophic generalist post-dispersal seed predators [34,36]. The wild boar is such generalist; it is one of the most controversial and widely distributed large mammal species, whose strong responses to these resource pulses have already been revealed [29,39,45,46]. Wild boars occur throughout the world in a wide range of habitat types, and their populations grow steadily and simultaneously with the number of conflicts generated by their activities [22].

As a generalist and opportunistic omnivore, the wild boar has a very plastic diet that is mainly determined by the availability and abundance of food items; studies show that 90% of its diet consists of plant materials in most cases [47–50]. However, one of the most important components in their diet are the large seeds and fruits with high energy content, such as the always-favored acorns of the *Quercus* genus throughout the temperate zone [30,48,49,51].

Wild boars can have a profound effect on the environment through their disturbances [38,47]; they can affect biodiversity [52–54], the properties of soil [55,56] and the regeneration of tree species [44,57–59]. These impacts occur mainly through their rooting behavior [60,61]. Therefore, wild boars are often considered one of the main reasons for the lack of oak regeneration through acorn depletion [18,50,62].

However, our knowledge and understanding of the spatiotemporal pattern of wild boar rooting and its relationship with the variabilities in acorn availability are still limited. Therefore, our main aim was to reveal the variability in the spatial distribution of wild boar disturbances on the forest floor and predict them based on acorn density patterns to make adequate practical interventions possible. Our questions were:

1. What is the general pattern of the acorn density in our studied temperate oak forest?
2. What is the general pattern of the patches rooted by wild boar and how does it overlap with the acorn density patterns?
3. Are there any patches used more frequently during the acorn-fall, acorn-rich or mast periods?
4. Does the acorn density decrease more intensively in patches disturbed more by wild boar than in the other parts of the forest?

2. Materials and Methods

2.1. Study Area

The study area was designated in Hungary, on the north of the lake Balaton, in Veszprém county, in the region of Zánka village (46°52′32.8′′ N 17°38′57.4′′ E). The area is in the dryer parts of the humid continental climatic region, with an average annual temperature between 10.2 and 10.5 °C. The annual average rainfall is between 600 and 640 mm, but it is not uncommon that only dry air arrives to the area. The bedrock of the forest is dominated by new red sandstone; meanwhile, the soil can mainly be characterized as red clay rendzina. The soil in the forest was quite shallow. The O horizon was generally 4 cm deep. Below that, the undisturbed hummus rich topsoil (A) was dark brown and around 3 cm deep, followed by transitional horizons. There was a darker, reddish AB_1

horizon from 3 to 14 cm and a paler AB_2 horizon between 14 to 24 cm deep. The proportion of inorganic matter (the stones (1–2 cm) and rock fragments (2–40 cm)) was high in both horizons. The BC horizon was from 24 to 38 cm with an even higher share of stones and rocks than the layer above. The C horizon was below 38 cm, but we were not able to reveal this layer due the high proportion of inorganic matter, which was composed mainly of large rocks.

Our investigation was carried out in a 157 ha private dry Turkey-sessile oak forest (*Fraxino orno-Quercetum cerridis*) [63] owned by Hercegerdő Forest Corporation and managed by Forestry Corporation of Bálint-hegy. The study area was a 28 ha forest unit surrounded directly by similar oak forests. This forest section represented the vegetation and the management of the surrounding forested areas well, and the oak regeneration was observed to be strongly affected by wild boar. In the examined area, the highest point was approximately 195 m above sea level, while the lowest was around 175 m. Generally, the higher area was the southwestern part of the study area, while the lower was the northeastern part, but the area also showed an uprising elevation from the northern boundaries to the southern ones. The slope was around 9% on average. Agricultural fields dominated by vineyards could be found in less than 500 m away from the study site in the north-northeast neighborhood. The forest unit had a quite even Turkey-sessile oak abundance (ca. 48% and 52% among oak trees, respectively). The forest stand was fairly mixed, and ca. 30% of the tree population was subdominant tree species, such as flowering ash (*Fraxinus ornus*), field maple (*Acer campestre*) and checker tree (*Sorbus torminalis*). Hornbeam (*Carpinus betulus*) was also sporadically present in patches, but it is generally declining in the area. The forest has been managed via single tree selection and group selection patch cuts since 1994. Generally, dead wood equivalent to 5%–10% of the living wood stock is left behind in the forest. The first private forest reserve in Hungary was also established here in 2011, near our study area. The main product of the area is firewood. Mitigation of the oak regeneration due to acorn predation by wild boar is considered a serious problem by the local forest managers, reflected in the fencing of small gaps established by previous timber utilization to enhance the development of acorns and defend the emerging saplings. The game population was managed by Káli-Medence Hunting Association until 2017 and then Csobánc Landowner Hunting Association since. Salt-licking places and baiting sites are prohibited to establish in the area by mutual agreement between the forest and game managers. We could not obtain precise data on the large, ungulate game species in the study area, but red (*Cervus elaphus*), roe (*Capreolus capreolus*) and fallow deer (*Dama dama*) are also occurring species. The population density estimation for every study year for every occurring game species on the county level is shown in Table 1.

Table 1. Population density estimation of game species in Veszprém county based on hunting bag data available from the National Game Management Database [64–68].

Species	Population Density (ind./km^2)			
	2016	**2017**	**2018**	**2019**
Red deer	1.3	1.4	1.7	1.8
Fallow deer	0.2	0.2	0.2	0.2
Roe deer	1.1	1.1	1.2	1.2
Wild boar	2.2	2.8	2.7	2.8

2.2. Field Data Collection

We designated our study area by recording several border points with a GPS device (GARMIN eTrex 20) around the examined forest stand. The data on acorn and wild boar rooting were collected once in about every 35 days between 2016 October and 2019 December. We designated 12 transects parallel with each other and the southern border of the area. All the transects were about 2 m wide, 500 to 1400 m long and 20 m from each other. On these transects, one sampling point per every 100 m was appointed; altogether, we obtained 118 sampling points (except in 2016 October, when there were 122, and in 2017 September, when there were 71 due to bad weather conditions) (Figure 1).

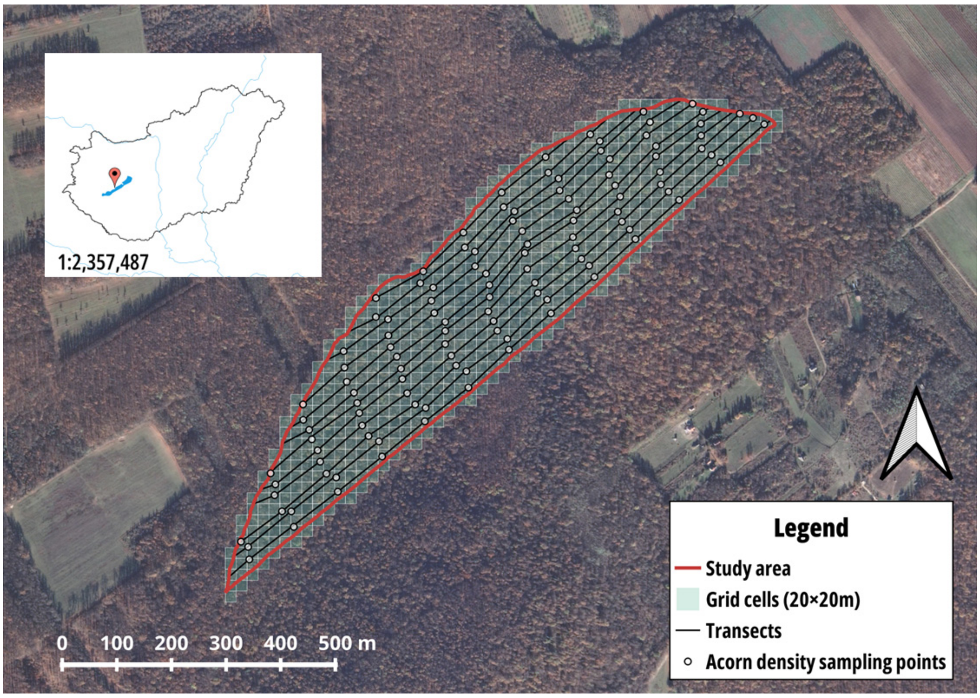

Figure 1. Location of the study area (top left), grid cells and the design of the acorn density sampling points and transects.

On all these sampling points, we measured the density of acorns of the two oak species in a 1 m × 1 m quadrant. During this examination, we moved over the litter at the sampling points to find and count all the acorns on the ground. Then, we arranged the litter back to decrease our disturbing effect. Along the full length of the transects, we also used the GPS device to record the locations of all patches rooted by wild boar. When our transects crossed a rooted area, we recorded an entry and an exit point. We considered a patch as rooted by wild boar when the disturbed site heavily differed from the undisturbed surroundings. Wild boar rooting often means the disturbance of the top of the soil layer, thereby litter and soil can mingle. The size of the rooted patch usually varies between 1 and 100 m^2, and the disturbed soil layer can be up to 20 to 40 cm deep.

2.3. Data Analysis

The data were processed and analyzed in Microsoft Office Excel 365, StatSoft Statistica 12 (Tulsa, OK, USA) and ESRI ArcGIS 10.4 (Redlands, CA, USA) (in the HD72/EOV (EPSG: 23700) coordinate reference system).

We drew the borders of our study area from the collected points, and then we converted them to a polygon to geolocate the study area as precisely as possible. A new layer was added that was divided into 20 m by 20 m (400 m^2) cells. We kept the cells that were on our polygon; therefore, within the borderline of the study area, that gave us 702 cells of 400 m^2, altogether 28.08 ha. The location points that we recorded whenever we entered and left a rooted patch were connected with a line. We split these lines at the borders of the grid cells, then we measured and summarized the total length of lines (m) in each cell. In this way, we were able to determine how many linear meters of rooting we found along the transects each time for every cell.

We divided the study into different temporal sample units. We appointed the acorn-fall period, when oak acorns fall from the trees, as between September and November, except in 2016, when we began our data collection in October, and in 2019, when acorns had already begun to fall in August. We also appointed an acorn-rich period; these were between October and April in every study year, when acorns should be available on the ground for the post-dispersal seed predators before germinating and becoming a seedling.

We determined the average acorn density for every interval in every study year per sampling points, and we did the same for the total recorded lengths of rooted patches along the transects per grid cells.

2.4. Statistical Analysis

The acorn density values of the annual intervals were compared to specify the characteristics of the study years regarding the availability of the acorns (mast and non-mast years). The acorn density values (n = 118) were significantly different from the normal distribution during the acorn-fall (Shapiro–Wilk test: $p < 0.001$) and acorn-rich periods (Shapiro–Wilk test: $p < 0.001$) as well. Therefore, we used a non-parametric Kruskal–Wallis test with Dunn's post hoc test for the comparison.

We used spatial autocorrelation (Global Moran's I) to analyze the spatial patterns of rooting and acorn densities during the above-mentioned intervals to reveal any significant pattern (clustering, random, or dispersed) among the features with similar values, where features meant the individual points (low/high acorn density) or the cells (avoided/intensively rooted cells). If the features showed clustering, we performed a hot spot analysis (Getis–Ord Gi*) to determine the exact locations of these features.

We conceptualized that all the acorn density sampling points were neighbors of each other since masting was occurring synchronously in vast areas. When considering the modifier effects of post-dispersal seed predators or even the varying local environmental conditions (soil characteristics, light availability, etc.), we also considered an inverse distance effect on the acorn density; thus, we assumed that the closer two features (acorn density sampling points) were in space, the more likely they influenced each other. When analyzing the patterns of the rooting and disturbance regime by the wild boars, we conceptualized that the entire study area was accessible to the individuals of the species. Therefore, we expected that the disturbances caused by the wild boar rooting would appear cell by cell as the wild boars were searching for food on the forest floor. As there were no landscape factors (rifts, gaps, watercourses, etc.) preventing the shortest route from being taken between two locations in our study area, we used Euclidean distances when analyzing the rooting distribution. There, we considered those cells as neighbors that shared their edges and corners (Queen's case).

During the hot spot analysis, we defined every sampling point as hot or cold point, and every grid cell hot or cold spot if the confidence interval was at least 90%.

We also examined how the results of the analysis for the two variables (acorn density, wild boar rooting) showed inter- and intra-annual matches and differences between the different time intervals, i.e., if there was any change in their category from hot spot to cold spot or vice versa. We also determined the proportion of overlapping spatial arrangement results for the two variables.

3. Results

3.1. Acorn Density Results

3.1.1. Acorn-Fall Periods

The average acorn density during the acorn-fall periods was 5.61 ± 9.2 pcs/m^2 (median (mdn): 2 pcs/m^2; interquartile range (IQR): 7.67), although the acorn densities in these periods were not uniform interannually (KW = 123.25; $p < 0.001$). The median densities were the following (in chronological order): 2016: 2.5 pcs/m^2 (IQR: 7); 2017: 8.33 pcs/m^2 (IQR: 10.63); 2018: 0 pcs/m^2 (IQR: 1.58); and 2019: 0 pcs/m^2 (IQR: 3.33). In 2016 and 2017, the density of the acorns was significantly higher on the sampling points compared to the other two examined acorn-fall periods ($p < 0.001$). However, there was also a significant difference between 2016 and 2017; in 2017, we observed a significantly higher acorn density

($p < 0.001$). When comparing 2018 and 2019, there was no significant difference between them ($p = 1$), which also was indicated by their identical median values (Figure 2).

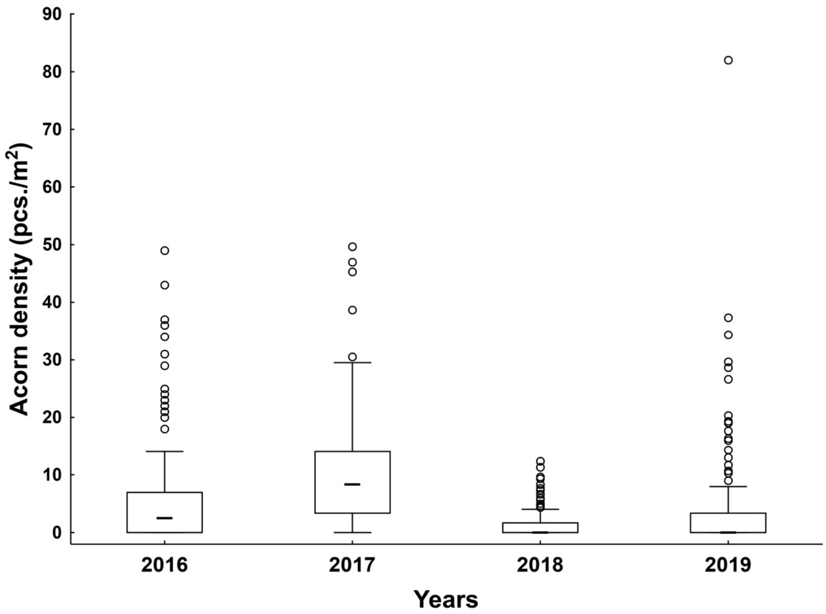

Figure 2. Acorn density in the acorn-fall periods during the entire study interval.

3.1.2. Acorn-Rich Periods

We examined altogether three acorn-rich periods during our entire study interval. The average acorn density at the study site in these periods was 2.93 ± 4.33 pcs/m^2 (mdn: 1.46 db/m^2; IQR: 3.76). The median densities were the following during the acorn-rich periods (in chronological order): 2016–2017: 2.00 pcs/m^2 (IQR: 3.12); 2017–2018: 3.75 pcs/m^2 (IQR: 4.5); and 2018–2019: 0.14 pcs/m^2 (IQR: 3.76). The interannual difference was significant when we compared these periods (KW = 120.73, $p < 0.001$). We observed the highest acorn density during the second examined period; it was significantly higher than in the third ($p < 0.001$) or even the first acorn-rich period ($p < 0.05$). The acorn density was the lowest during the third acorn-rich period, and the difference was significant compared to the other two ($p < 0.001$) (Figure 3).

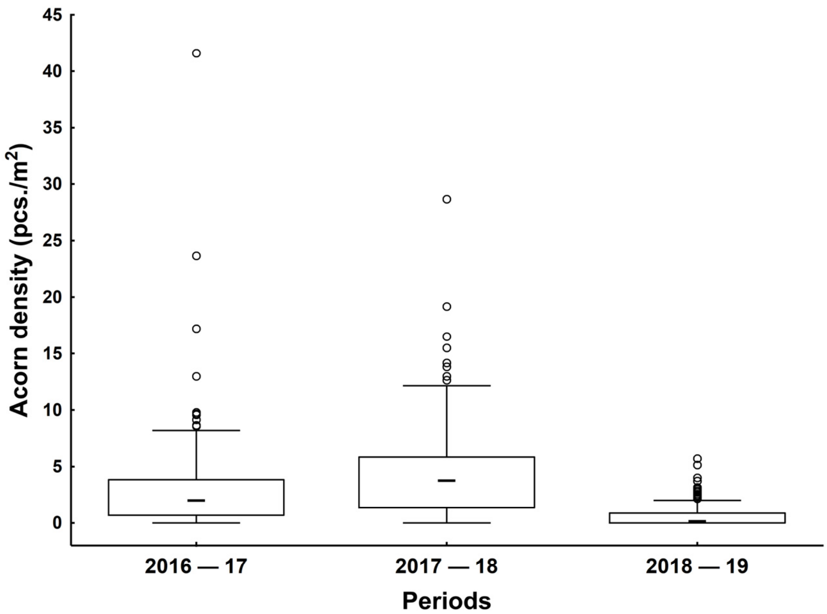

Figure 3. Acorn density in the acorn-rich periods during the entire study interval.

Based on these results, we recognized the first two years as mast years and the last two years as non-mast years.

3.2. Spatial Analysis Results

Spatial Autocorrelation

Based on our spatial autocorrelation analysis, the acorn density patterns were never random, neither in the acorn-fall (Table 2) nor the acorn-rich periods (Table 3).

Table 2. The results of the spatial autocorrelation analysis for the acorn density sampling points in the acorn-fall periods.

Year	Acorn Crop	Moran Index	z-Value	*p*-Value	Pattern
2016	Mast year	0.048	4.081	<0.001	Clustered
2017	Mast year	0.04	3.244	<0.01	Clustered
2018	Non-mast year	0.074	5.36	<0.001	Clustered
2019	Non-mast year	0.043	3.549	<0.001	Clustered

Table 3. The results of the spatial autocorrelation analysis for the acorn density sampling points in the acorn-rich periods.

Period	Acorn Crop	Moran Index	z-Value	*p*-Value	Pattern
2016–2017	Mast year	0.086	6.86	<0.001	Clustered
2017–2018	Mast year	0.032	2.676	<0.01	Clustered
2018–2019	Non-mast year	0.082	5.858	<0.001	Clustered

The results were quite similar regarding the wild-boar-caused disturbances on the ground. The cells rooted with similar intensity also showed clustered patterns in every study year. The results are presented in the Table 4 for the acorn-fall period and Table 5 for the acorn-rich period.

Table 4. The results of the spatial autocorrelation analysis for the wild boar rooting in the acorn-fall periods.

Year	Acorn Crop	Moran Index	z-Value	*p*-Value	Pattern
2016	Mast year	0.341	17.6	<0.001	Clustered
2017	Mast year	0.247	12.731	<0.001	Clustered
2018	Non-mast year	0.109	5.924	<0.001	Clustered
2019	Non-mast year	0.409	21.249	<0.001	Clustered

Table 5. The results of the spatial autocorrelation analysis for the wild boar rooting in the acorn-rich periods.

Period	Acorn Crop	Moran Index	z-Value	*p*-Value	Pattern
2016–2017	Mast year	0.277	14.294	<0.001	Clustered
2017–2018	Mast year	0.285	14.686	<0.001	Clustered
2018–2019	Non-mast year	0.253	13.205	<0.001	Clustered

3.3. Hot Spot Analysis

3.3.1. Acorn Density

When analyzing the acorn density sampling points, we could not identify any cold-point groups during the entire study interval. However, when examining the acorn-fall periods, only 9.02% of the sampling points were hot points in 2016, 5.08% in 2017, 8.47% in 2018 and 6.78% in 2019. The average acorn densities on these sampling points are shown in Table 6.

Table 6. Average acorn densities on the sampling points of different categories in the acorn-fall periods. "NS" means non-significant category (neither hot nor cold point).

Categories	Acorn Density (pcs/m^2)			
	2016	**2017**	**2018**	**2019**
Hot point	32.09 ± 8.71 (*n* = 11)	49.83 ± 11.75 (*n* = 6)	8.80 ± 2.01 (*n* = 10)	45.63 ± 19.6 (*n* = 8)
NS point	3.72 ± 4.54 (*n* = 111)	8.14 ± 6.78 (*n* = 112)	0.88 ± 1.54 (*n* = 108)	3.02 ± 5.96 (*n* = 110)
Cold point	---	---	---	---

During the acorn-rich periods, 4.24% in the first, 8.47% in the second and 11.02% of the points in the third period were identified as hot points. The average acorn densities on these sampling points are shown in Table 7.

Table 7. Average acorn densities on the sampling points of different categories in the acorn-rich periods. "NS" means non-significant category (neither hot nor cold point).

Categories	Acorn Density (pcs/m^2)		
	2016–17	**2017–18**	**2018–19**
Hot point	22.53 ± 11.32 (*n* = 5)	15.78 ± 5.03 (*n* = 10)	3.74 ± 0.99 (*n* = 13)
NS point	2.58 ± 2.57 (*n* = 113)	3.63 ± 2.64 (*n* = 108)	0.37 ± 0.64 (*n* = 105)
Cold point	---	---	---

The sampling design was slightly different in 2016, thus we were not able to compare this dataset with the rest. However, following the acorn-fall period in 2017, 83.3% of the identified six hot points fell into the same category in the upcoming acorn-rich period as well. In 2018, in the case of the 10 identified hot points during the acorn-fall period, this proportion was 100%, meaning that all these points were identified again as hot points during the 2018–19 acorn-rich period.

When comparing the same periods interannually, there was no match between the acorn-rich periods of 2017 and 2018, while there was only 1 sampling point out of 10 in 2018 that was identified as a hot point again in 2019 (a 10% match). In 2017, of six of the identified hot points, two showed the same characteristic again in 2019 (a 33.3% match).

Regarding the acorn-rich periods, when comparing the first (2016–17) and second (2017–18) intervals, there were no matching hot points. However, when comparing the second and the third (2018–19) period, among 10 hot points, 1 remained a hot point again. When comparing the first and the last examined acorn-rich periods, we could not reveal any match among the hot points.

3.3.2. Wild Boar Rooting

When analyzing the disturbance patterns of the wild boars in our study site, during the acorn-fall periods, we were only able to identify cold spots in 2017; the proportion of these cells was 10.4%. The proportions of hot spots in the acorn-fall periods were 17.66% in 2016, 16.81% in 2017, 9.12% in 2018 and 11.97% in 2019.

When analyzing the acorn-rich periods, cold spots were always detected during these intervals except in the last examined period. The proportions of the cold spots were 12.82% in the first and 13.96% in the second acorn-rich period. Meanwhile the proportion of the hot spots in chronological order were 14.96%, 18.66% and 13.11% during the same interval of 2017–2019, respectively.

The locations of hot spots were quite similar between the periods, both inter- and intra-annually. The results are shown in Figure 4. During the mast years, these similarities were more emphasized, and it was quite rare that a hot spot became a cold spot. On the contrary, during the non-mast interval, there were some occasions when this transition between the categories occurred: 16.3% of the cold spots in the second acorn-rich period became hot spots in the last examined period.

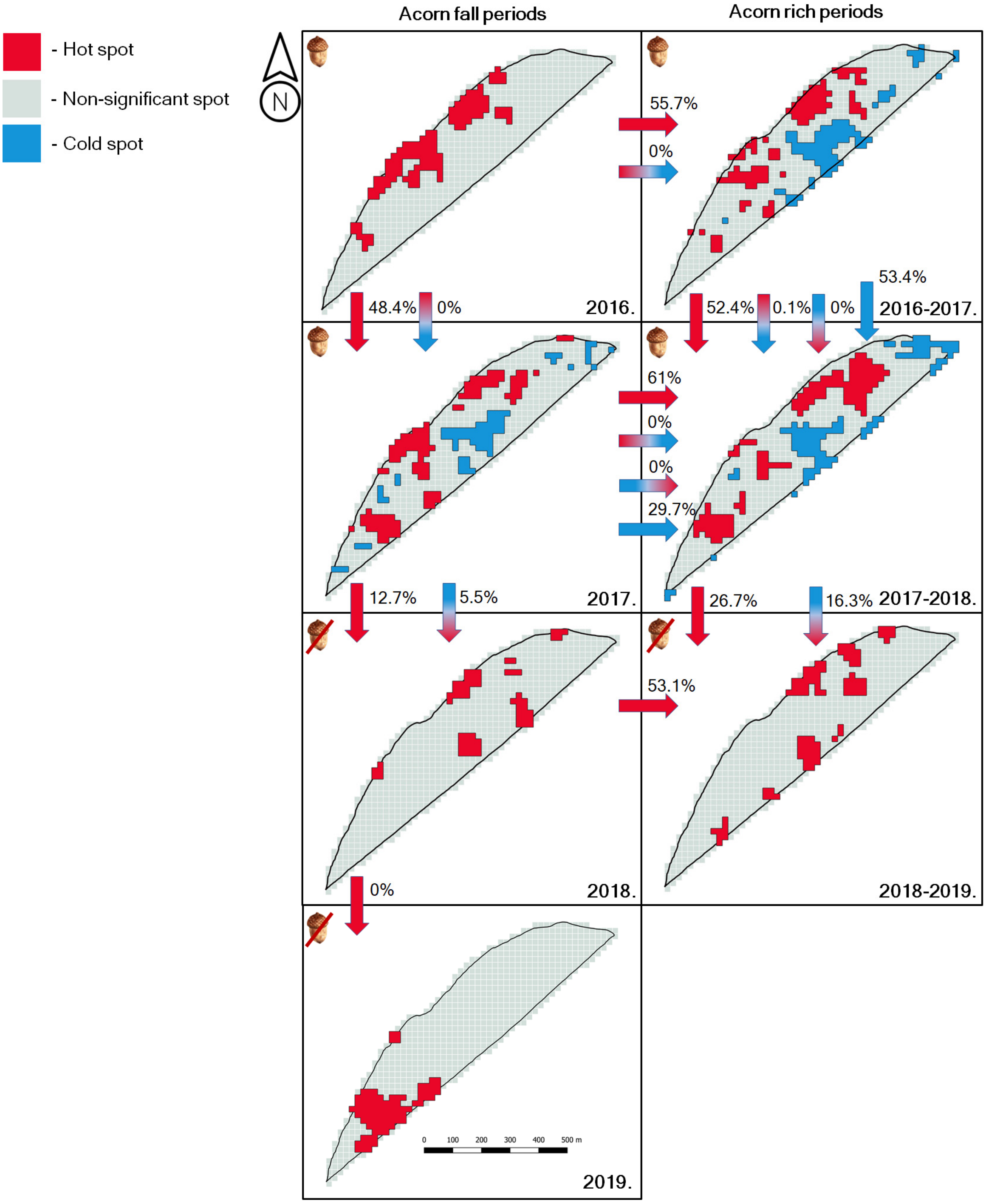

Figure 4. Wild boar disturbances in the study area during the different inter- and intra-annual time intervals. Colors of the arrows indicate the constancy of and the category changes between the hot and cold spots, while the percentages indicate the proportion of the change while always using the earlier phase as the basis. The acorn symbols indicate the mast years, while the strike-through acorn symbols indicate the non-mast years.

3.3.3. Interactions among the Acorn Densities and the Wild Boar Rooting

The overlapping of the acorn density sampling points and the level of disturbance by wild boars belonging to different categories are shown in Table 8. In the acorn-fall periods, during our entire study interval, hot points in hot spots—in other words, locations with a relatively high acorn density impacted by intensive wild boar rooting—were only found in 2016 (a mast year) and 2019 (a non-mast year). However, regarding the cold spots in wild boar rooting disturbances, they only appeared during the acorn-fall period of 2017, and there were no acorn density hot points in those patches, i.e., there were no acorn density peaks in places without rooting.

Table 8. The distribution of the acorn density sampling points of different categories among the varyingly rooted areas during the acorn-fall periods. The values in brackets indicate the average acorn density at the sampling points, while the "---" indicates there was no intersection among those categories. "NS" means non-significant category (neither hot nor cold point/spot), and "ND" means no data.

	Acorn-Fall Period	**Cell-Use Intensity in Rooting by the Wild Boars**		
	2016 (N = 122)	***Hot Spot***	***NS Spot***	***Cold Spot***
Categories	***Hot point (n = 11)***	9.1% (31)	90.9% (32)	---
	NS point (n = 111)	18% (4.2)	82% (3.6)	---
	Cold point (n = 0)	---	---	---
	2017 (N = 118)	***Hot spot***	***NS spot***	***Cold spot***
Categories	***Hot point (n = 6)***	0% (ND)	100% (49.8)	0% (ND)
	NS point (n = 112)	21.4% (5.9)	69.6% (8.6)	8.9% (9.7)
	Cold point (n = 0)	---	----	---
	2018 (N = 118)	***Hot spot***	***NS spot***	***Cold spot***
Categories	***Hot point (n = 10)***	0% (ND)	100% (8.8)	---
	NS point (n = 108)	9.3% (1)	90.7% (0.9)	---
	Cold point (n = 0)	---	---	---
	2019 (N = 118)	***Hot spot***	***NS spot***	***Cold spot***
Categories	***Hot point (n = 8)***	25% (36.3)	75% (48.8)	---
	NS point (n = 110)	10.9% (4.9)	89.1% (2.8)	---
	Cold point (n = 0)	---	---	---

Our results revealed the distribution of wild boar rooting disturbances of an "average" level across the area, with some more intensively used patches (hot spots) but with the scarcity of the patches avoided by wild boar relative to other places (there were few or no cold spots) during the acorn-fall period. Nevertheless, they did not deplete those foraging places entirely, meaning that we were able to find acorns at sampling points within each rooting spot category (even in the hot spots) regardless if it was a mast or non-mast year.

We also examined this potential overlapping pattern during the acorn-rich periods (Table 9). Acorn density hot points only appeared in rooting hot spots in the last, non-masting acorn-rich period. The proportion of rooting cold spots became higher compared to the acorn-fall period, and even in these longer periods after the acorn fall, they did not consume all the acorns in those foraging places.

Table 9. The distribution of the acorn density sampling points of different categories among the varyingly rooted areas during the acorn-rich periods. The values in brackets indicate the average acorn density at the sampling points, while the "---" indicates there was no intersection among those categories. "NS" means non-significant category (neither hot nor cold point/spot), and "ND" means no data.

	Acorn-Rich Periods	Cell-Use Intensity in Rooting by the Wild Boars		
	2016–17 (N = 118)	*Hot Spot*	*NS Spot*	*Cold Spot*
Categories	*Hot point (n = 5)*	0% (ND)	80% (24.9)	20% (13)
	NS point (n = 113)	16.8% (2.7)	69.9% (2.6)	13.3% (2.1)
	Cold point (n = 0)	---	---	---
	2017–18 (N = 118)	*Hot spot*	*NS spot*	*Cold spot*
Categories	*Hot point (n = 10)*	0% (ND)	90% (16)	10% (14,1)
	NS point (n = 108)	25.9% (3.3)	63% (4)	11.1% (2)
	Cold point (n = 0)	---	---	---
	2018–19 (N = 118)	*Hot spot*	*NS spot*	*Cold spot*
Categories	*Hot point (n = 13)*	7.7% (2.7)	92.3% (3.5)	0% (ND)
	NS point (n = 105)	17.1% (0.7)	82.9% (0.3)	0% (ND)
	Cold point (n = 0)	---	---	---

4. Discussion

Based on our results, the quantity of the acorn crop—in the mast and non-mast years—and therefore the availability of the acorns can have a fundamental effect on the habitat use of wild boars [29,39,69]. Simultaneously, wild boars can have a substantial effect on their surroundings, and their rooting behavior can affect certain places more intensively than others [50,60].

We did not find cold-point groups in any of the study intervals; the explanation for this could be that the acorn density was probably uniform and often low through the entire study area. Contrary to what we expected, the proportion of hot points matching interannually among the same intervals was quite low. This can indicate the variable performance in crop production of the different trees and tree groups from year to year [36,70,71]. However, acorn density hot points were mostly identical intra-annually (between the acorn-fall and acorn-rich periods), which was also unexpected, thus we would assume that those will be the ones that would be depleted first by the seed predators. Even so, the proportion of hot points increased from the acorn-fall to the acorn rich-period, probably due the effects of post-dispersal seed predators like wild boars [72]. The acorn density, irrespective of the category, decreased with a similar order of magnitude between the consecutive periods.

The patterns of wild boar rooting behavior showed during the acorn-fall period that the much less used patches, i.e., the cold spots, only appeared in 2017, which was a mast year. But during the acorn-rich periods, cold spots were only missing in the third, non-mast interval. This suggests that the crop size of the oaks had a fundamental effect on the habitat use of the wild boars, the patterns of the wild boar rooting expressed in the locations of hot and cold spots, and the expansion of the disturbances. During the mast years, we could identify similar patterns of wild boar disturbances inter- and intra-annually, while during the non-mast years, these patterns were only present on an intra-annual scale regarding the hot spots.

The results regarding the overlapping of the two features of different categories showed hot points in hot spots only in the first and last acorn-fall periods. Interestingly, during the mast acorn-rich periods, acorn density hot points never appeared in rooting hot spots.

In the acorn-rich period, we also found higher acorn densities on sampling points that were located in the non-significant spots than in the cold spots. Moreover, we were able to find acorns at sampling points in hot and non-significant rooting spots during both acorn-fall and acorn-rich periods or mast and non-mast years. Therefore, we can conclude that wild boars used both the hot and non-significant spots, but they never fully depleted the acorns.

In summary, although the patterns showed that certain places were used intensively by wild boars in given time intervals depending on the acorn crop availability (mast or non-mast year), we were not able to reveal a direct local connection on a much finer scale between the rooting intensity and the acorn density, as favorable high-density acorn sampling point groups and more intensively used rooted patches did not show obvious overlapping. The cause behind this is probably a more complex relationship than just the presence or the absence of the food resource, in this case the acorn [73,74].

5. Conclusions

Negative human–ungulate interactions have become increasingly common in Europe in recent years [75–77], while inadequate natural oak regeneration means an ever-growing pressure and concern for the forest sector [78–80]. The seed predator wild boar is often considered the main mitigating agent in the regeneration of oaks, causing heated debates among stakeholders. Therefore, to be able to successfully manage these conflicts, we have to have a better understanding of the species and its impact on ecosystems in which it is involved. As we increasingly recognize and utilize the resources and services that ecosystems such as oak forests provide, and as there is increasing pressure on these systems, there is a growing expectation that has also emerged that ecological research should be able to predict the outcomes and effects of certain events in these complex systems. Our results showed that the crop size of the oaks fundamentally drove the habitat use of wild boars, but we were unable to show a tight connection on a finer scale between the exact location of high-density acorn spots and the intensively rooted areas, suggesting that the interplay of several other factors probably affects the rooting behavior of the species apart from the acorns, including soil properties, vegetation structure and composition, and predator avoidance [14]. However, our results also showed that it might be possible to forecast the locations more intensively disturbed by wild boars based on previous datasets. In this way, the identification of more intensively used forest patches might offer a good opportunity to intervene and mitigate the wild-boar-related conflicts to a tolerable level for forest managers [57,81–83] by applying methods such as increasing the hunting pressure at certain locations to invigorate fear through the landscape of fear effect [84] or temporarily fencing the vulnerable areas. We advocate further research on other temperate oak forests, especially in less dry conditions, to analyze the predictability of the general patterns of wild boar rooting.

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