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The Role of Forest Stands Characteristics on Formation of Exterior Migratory Outbreak Spots by the Siberian Silk Moth *Dendrolimus sibiricus* (Tschetv.) during Population Collapse

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Abstract: The characteristics of *Abies sibirica* Ledeb.- and *Pinus sibirica* Du Tour dominated forests stands in outbreak spots formed during a *Dendrolimus sibiricus* outbreak in 2014–2017 were studied at the stage of population collapse (east of the West Siberian Plain and western foothills of the Yenisei Range). The research was based on the data obtained during ground surveys conducted in 2016 when stands characteristics, the Siberian silk moth population density, and defoliation level were recorded. We classified the studied stands using decision trees and random forest algorithms to identify the key characteristics that determine the formation of outbreak spots. The classification results showed that the characteristics of the detected outbreak spots differ significantly from those previously described for dark coniferous stands of the southern taiga in Siberia. The highest probability of the outbreak spot occurrence in the study area was revealed for stands with the following characteristics: moderately moist site; Siberian stone pine and Siberian fir take 40% or more of stem volume; age of less than 105 years. Another group of forest stands under threat are those sharing the following characteristics: large area (more than 60 ha); stand homogeneity; ground vegetation is dominated by feather mosses; age of more than 120 years; *Picea obovata* Ledeb. takes a significant share in a stem volume. Such characteristics indicate that during the population collapse, the Siberian silk moth forms outbreak spots in stands that either undergo an early successional stage after previous outbreak or have been slightly damaged during the previous outbreaks due to unfavorable habitat conditions.

Keywords: *Dendrolimus sibiricus*; outbreak; collapse of population; southern taiga; dark coniferous stands

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1. Introduction

Boreal forests are one of the world's largest land biomes in terms of area and above-ground biomass [1,2]. They contain 16% of the world's forests' above-ground biomass [2]. Russian boreal forests are currently a major net carbon sink as they compensate carbon emissions by tropical forests and North American boreal forests [3]. Thus, Russian boreal forests play a crucial role in maintaining global environmental sustainability.

Siberian forests mostly belong to the boreal forest zone, except for the narrow forest belt elongated in the latitudinal direction along the steppe border that belongs to the temperate forest zone [1]. Despite the fact that Siberian boreal forests occupy about 250 million ha, the diversity of their tree species is extremely low. Siberian boreal forests are mostly dominated by larch (*Larix* spp.), birch (*Betula* spp.), Scots pine *Pinus sylvestris* L., aspen *Populus tremula* L., Siberian stone pine *Pinus sibirica* Du Tour, Siberian fir *Abies sibirica* Ledeb., and Siberian spruce *Picea obovata* Ledeb. Siberian stone pine-/Siberian fir-/Siberian spruce-dominated forest stands occupy about 20% of Siberian forests [4]; they are united by the term "dark coniferous forests" due to the similarity of ecological preferences of these species.

The sustainability of boreal forest ecosystems in Siberia is being disturbed by a number of factors. The most hazardous of them after fires [5] are outbreaks of the Siberian silk moth *Dendrolimus sibiricus* (Tschetverikov, 1908) (=*superans* Butler) [6] (Lepdioptera, Lasiocampidae). The Siberian silk moth outbreaks have been observed in Siberia since the end of the 19th century; outbreaks recur approximately every 15 years and affect up to 10 million ha [7,8]. Each outbreak develops over several years, gradually increasing the covered area [8–10]. The Siberian silk moth's preferred host trees are *Larix* ssp., *P. sibirica*, and *A. sibirica* [11]. Moreover, the last two species are sensitive to defoliation; they die when they lose 25% or of more of their needles [12]. Therefore, in the absence of control measures, dark coniferous stands may lose several million ha during an outbreak [8].

Currently, the situation is being exacerbated by climate change. Air temperature has been increasing in Siberia at least since the 1970s [13] and is predicted to rise in the future [14]. Boreal biomes are the most vulnerable to such change [15]. Climate change-induced stress combined with defoliation can significantly amplify the negative consequences of tree damage by insects [16]. One of such consequences has already been observed: climate change increases the reproductive rates of forest pests [15,17]. As for the Siberian silk moth, the most likely warming-induced changes are: range expansion and outbreak spots (i.e., the stands where the population density of *D. sibiricus* is high and the defoliation is conspicuous) occurrence further northward than they have been previously observed [18].

The approach to reduce the economic and environmental damage caused by defoliation is to develop methods for the early detection of outbreak spots. Such methods will make it possible to timely implement control measures and reduce an area of damaged and dead stands [8]. Satellite images analysis after the onset of defoliation makes it possible to only detect the damage already caused by the Siberian silk moth. Notably, it is impossible to identify forest sites that were damage to low or mid extent (less than 50% defoliation) [18]. Thus, a field survey is necessary to detect stands where an increase in *D. sibiricus* population density has begun, but conspicuous defoliation has not yet occurred. In Siberia, forests cover a vast area and road infrastructure is poor, which makes it impossible to conduct field studies in all forests dominated by the pest host species. Therefore, it is advisable to conduct field studies of forest stands that are most likely to be damaged. It is possible to identify such forests both using forest inventory data and remote sensing [19].

The data about stands characteristics in dark-coniferous forests damaged by *D. sibiricus* are fragmentary and to some degree controversial. Brief but informative data for West Siberian Plain and mountains of Southern Siberia indicated the preference of this defoliator to mature stands of moderate density and moisture [8]. For the lower course of the Angara basin, the most intensive damage for mature and moderate dense stands was also shown [19]. Later for West Siberian Plane [20] and for North-Western Altai [21], similar conclusions were made, but the damaged stands were younger and denser in the early stage of the outbreaks. For Cisbaikalian forests, the priority defoliation by Siberian silk moth of the pole, mature, and old-growth stands with low density was mentioned [22]. All these investigations were made for the early stage and peak of the outbreak. The same regularities for the stage of outbreak collapse are unknown.

Forecasting the spatial distribution of the Siberian silk moth outbreaks is a challenge since forest stands differ significantly in their compliance with the pest habitat requirements. Defoliation initially occurs in stands that are favorable for the insect pest reproduction, but as an outbreak develops, the characteristics of damaged forests change significantly. The spatial distribution of the Siberian silk moth during an outbreak depends on larval growth rates in different habitats and migration processes [20]. Here, we describe the characteristics of forest stands where the outbreak stops, meaning stands where outbreak spots are formed at the end of the outbreak peak (highest density of the insects population) and at the stage of population decline (reducing the population density due to starvation, parasitoids, and pathogens) [23].

2. Materials and Methods

2.1. Study Area

The study was conducted in the Yenisei forest district (administratively allocated part of forests) (Figure 1), where at least six outbreaks of the Siberian silk moth had been previously recorded (ca. 1914, 1933, 1942, 1954, 1966, 1993) [7,8,20,24,25]. The last outbreak occurred in 2014–2017.

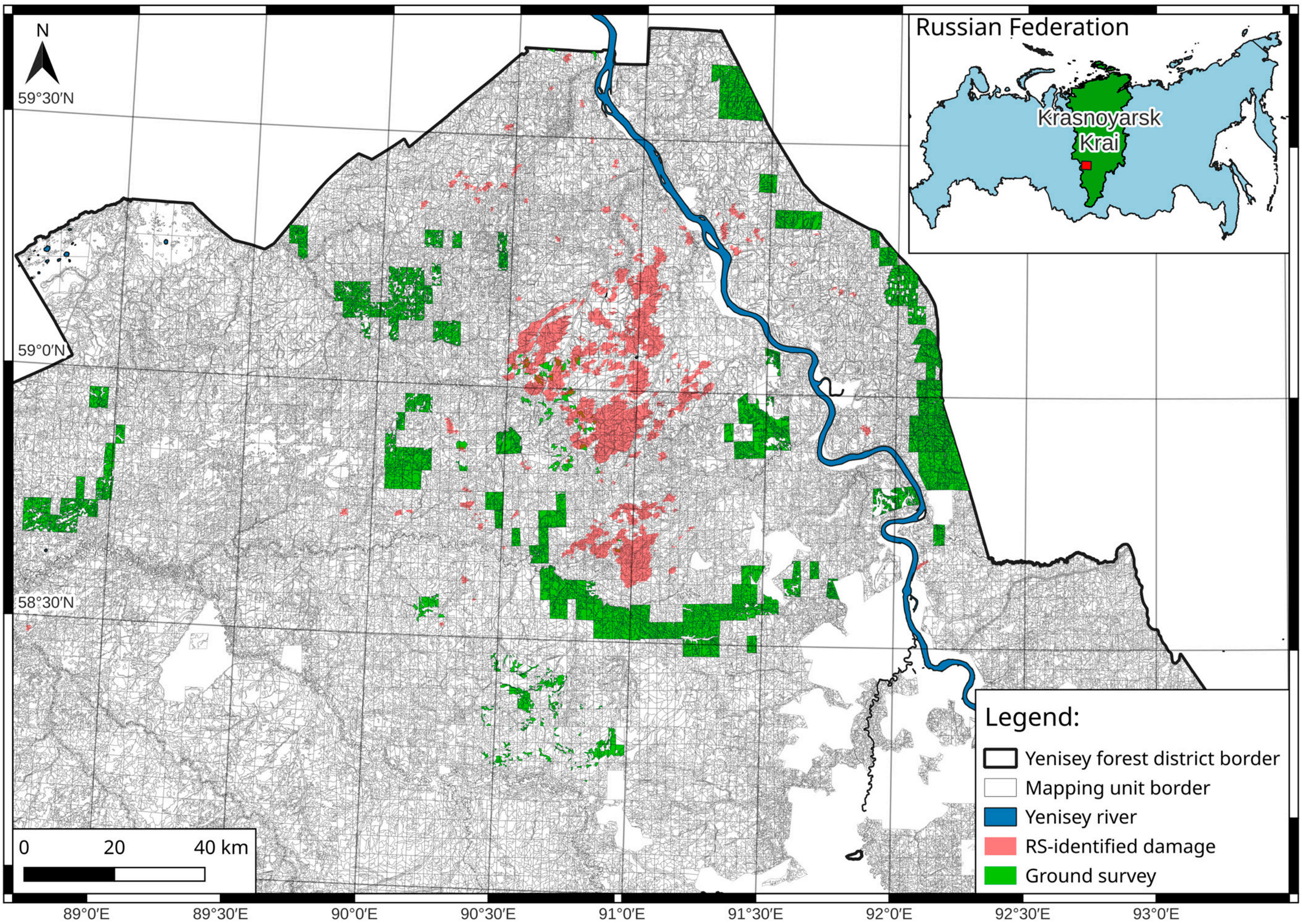

Figure 1. Defoliated stands and field study area. Inset: study area on the map of Russian Federation and Krasnoyarsk Krai. Damaged stands, identified by remote sensing (RS-identified damage), are shown as of September 2016.

According to official data, the forests of the Yenisei forest district cover about 42.400 km^2. The forest district is 236 km from north to south and 308 km from east to west [26]. Stands dominated by the Siberian silk moth host species (Siberian stone pine and Siberian fir) occupy about 30% of total growing stock. There are no stands dominated by larch in the Yenisei forest district [27]. The forest district is mostly (the west bank of the Yenisei river; 86% of the total area) located on the West Siberian Plain [25], where the last outbreak of the Siberian silk moth has occurred (Figure 1). The landform is plain with gentle sloping ridges; absolute altitudes are up to 100–150 m in the west and 150–200 in the east; swamps occur on a vast area in the forest district [28]. A smaller part (the east bank of the Yenisei river) is located in the lower part of the Yenisei Range [26] and is characterized by low-mountain dissected relief [28].

We used climate data available from the nearest weather station Yeniseysk (58.45° N, 92.20° E) [29]. Mean annual temperature was −1.8 °C. The coldest month of the year was January (mean temperature was −22.1 °C) and the warmest month was July (mean temperature was 18.3 °C). The July mean temperature value corresponds to the northern limit of the occurrence of *D. sibiricus* outbreak spots, which has been drawn along the July isotherm of 18.0 °C [30]. Multi-year mean sum of the average daily temperatures above 0 °C was 2016 °C and the effective temperature sum at the base temperature of 5 °C was 1185 °C. These sums meet the minimum requirements for the occurrence of the Siberian silk moth outbreak [25,30]. Precipitation was distributed fairly evenly throughout the year (from 18 mm (March) to 66 mm (August)). Average annual precipitation was 484 mm, which was within the limits at which outbreaks of *D. sibiricus* are possible [30]. Summer was rather dry: the Selyaninov's hydrothermal coefficient [31] indicates a lack of moisture in May–July for more than half of the years, which can act as a trigger for the increase in the Siberian silk moth population [8]. Similar conclusions on the role of droughts were made for the closely related species *Dendrolimus pini* L. [32,33].

2.2. The Siberian Silk Moth Outbreak in 2014–2017

The outbreak moved farther north than any previously known in the West Siberian Plain [34,35]. Its beginning could not be recorded. Apparently, the increase in the Siberian silk moth population began in 2011–2012 [35]. The first defoliated forest sites appeared in 2014 [34]. In 2016, damaged forests occupied about 200 thousands ha, and the area increased to 800 thousands ha in 2017 [34]. The defoliated forest stands were mostly located on the West Siberian Plain; the forests of the Yenisei Range were slightly damaged (Figure 1).

Defoliation began at altitude of 150–180 m above sea level, on flattened areas or gentle ($\leq 5^\circ$) east-, south-east- and south-facing slopes. Later, the outbreak spread to lower areas, steeper (up to 10°) and less heated slopes [34]. Population density in outbreak spots ranged from 42 to 448 larvae per tree in spring 2016 and up to 1159 larvae per tree in August 2016 [35]. Depending on forest stand characteristics, such a population density corresponds to 30%–100% needle loss [8,36]. In 2017, parts of the outbreak spots (about 550 thousands ha) were treated with a mixture of Lepidocide (bacterial, *Bacillus thuringiensis* var. *kurstaki* Bulla et al.) and Dimilin (chitin production inhibitor, diflubenzuron) or Clonrin (neurotoxin, a mixture of clothianidin and cypermethrin). However, in the studied forest stands, almost no control measures were taken.

2.3. Forest Stand Characteristics

We analyzed the data obtained during a forest inventory conducted in 2016 in order to determine forest stand characteristics. During the field study, the proportion of each tree species in the studied stands was measured from 0 to 10, where 1 ≈ 10% from the stand growing stock. The following stand characteristics were determined: the joint proportion of Siberian stone pine and Siberian fir; age (by the number of tree rings accounted on cores from breast height), height, and diameter of the dominant species; relative stand density (where 1 was the sum of basal area for reference (accepted in the forest inventory practice as a standard for such measurements [37]) stand), stem volume, forest type. Forest types were determined by the ground cover. Moisture conditions and feather mosses cover (rank variables) were described for each forest type according to [38]. Preliminary studies have shown that in order to obtain interpretable results, forest types should be combined into several groups, including forest types with similar ground cover and soil characteristics. Hereafter, these groups of forest types are named by dominate species in ground cover, or, if there was not a single dominate species, by plant association—feather moss (high *Hypnales* abundance), lichen (*Cladonia* spp. and *Cetraria islandica* (L.)), macroura (*Carex macroura* Meinsh), mesophilic herb (mesophyllic species, such as *Maianthemum bifolium* (L.) F.W. Schmidt, *Oxalis acetosella* L., and *Pyrola rotundifolia* L.), sphagnum (*Shpagnum* spp.), swamp (wet soils with dominance of hydrophilic species, such as *Carex globularis* L., *Equisetum sylvaticum* L., and *Filipendula ulmaria* (L.)), tall herb (moist and rich soils with dominance of mesohydrophilic species, for example, *Aconitum septentrionale* Koelle, *Heracleum sibiricum* L. and *Urtica* spp.), and vaccinium (high abundance of *Vaccinium* ssp.). What is more, forest types were grouped according to the soil moisture (six gradations, from extremely dry to extremely wet) and feather mosses cover (three gradations: 0%–30%, 31%–70%, over 70%).

We obtained the data on the damage to forest stands and the Siberian silk moth population density from surveys conducted mainly in August 2016. The surveys covered about 10% of mapping units (the homogeneous parts of forest) in March 2016 and 3% of mapping units in June 2016. In total, data were processed for 6306 mapping units of 178,427 ha. During the field study, we assessed the degree of defoliation in 5-point scale (from 0—no defoliation to 5—complete defoliation) and the Siberian silk moth population density (the number of larvae per tree, determined by shacking off the larvae from trees). We considered stands with a defoliation score of 1 or more and/or a population density of $\geq$25 larvae per tree as an outbreak spot [8]. The forest stand characteristics described above were used as predictors of an outbreak spot occurrence in a mapping unit.

2.4. Statistical Processing and Modeling

The statistical processing was performed in R 4.0.2 software environment [39]. We used the Wilcoxon test to perform a pairwise comparison of quantitative features. A multiple comparison of qualitative features was performed using the chi-square test, and z-test was used to perform pairwise comparison of qualitative features. Significance levels were corrected for paired comparisons using the Benjamini–Hochberg procedure [39].

As a dependent variable, we considered the presence of the outbreak spot in a given mapping unit at the time of the field study, as determined by the degree of defoliation and/or Siberian silk moth population density. We used a decision tree (package tree 1.0-40) [40] and a random forest algorithm (packages randomForest 4.6-14 [41] and iml 0.11.1 [42]) to select predictors that most accurately predict the appearance of an outbreak spot in a mapping unit. Training was carried out on a training set, and the model was tested on a validation set (the ratio was 3:1). The model was tested using a 5-fold cross-validation.

To select the best parameters (the depth of the decision tree for both types of models, the number of voting trees for the random forest), we minimized the value of the F1 metric. This approach is well applicable for non-balanced classes (significant excess of the number of objects of one class over another) and allows minimizing the number of both false positive and false negative estimates. We also calculated precision and recall metrics of the classification (caret 6.0-86 package [43]).

3. Results

3.1. Characteristics of Forest Stands Where There Are Some or No Outbreak Spots

During the field survey, the Siberian silk moth outbreak spots were recorded (following the above-described criteria) in 322 mapping units of 13,751 ha (5.12% of the total number of mapping units and 7.71% of the total area). Stands dominated (composed of 50% or more in a stand composition) by *A. sibirica* or *P. sibirica* were recorded in 2036 mapping units (32.3% of the total number of mapping units) of 55,841 ha (31.3% of the total area). Larch (another *D. sibiricus* host) accounted for no more than in 106 mapping units of 1860 ha. Larch takes no more than 20% in any stand composition in the study area.

In stands marked as the Siberian silk moth outbreak spots, the proportion of dark coniferous species was higher compared to stands beside the spots (Figure 2B–D), including the total share of Siberian fir and Siberian stone pine (Figure 3B; $p < 0.0001$), while the proportion of Scots pine was lower (Figure 2E). The differences for deciduous species were not statistically significant (Figure 2F,G). On average, stands in the outbreak spots were younger than non-damaged stands (Figure 3A; $p < 0.0001$). Therefore, the stands in the outbreak spots were of lower values of age-related characteristics (diameter, height, growing stock) compared to stands without defoliation (Figure 2H–J). Mapping units classified as outbreak spots had, on average, a larger area (Figure 2A) and somewhat higher density (0.61 in outbreak spots, 0.56 outside them; Figure 2K).

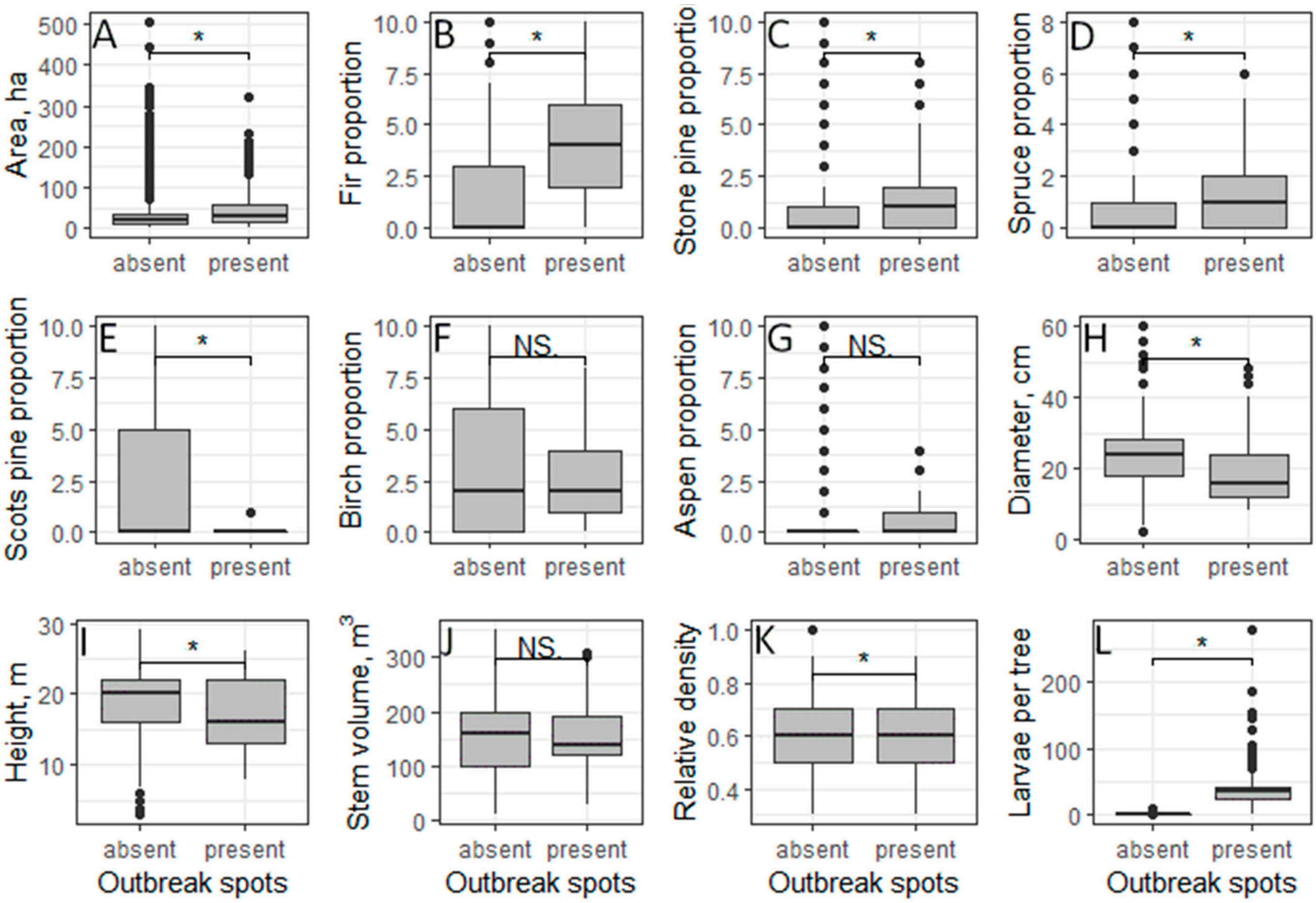

Figure 2. Quantitative characteristics of forest stands in the outbreak spots and outside them. The characteristics are: (**A**)—area of mapping unit, (**B**)—fir proportion in stand volume, (**C**)—the same for Siberian stone pine, (**D**)—the same for spruce, (**E**)—the same for Scots pine, (**F**)—the same for birch, (**G**)—the same for aspen, (**H**)—mean diameter, (**I**)—mean height, (**J**)—stem volume, (**K**)—relative density, (**L**)—number of larvae per tree. The significance according to the Wilcoxon test: *—≤0.05, NS—differences are not significant.

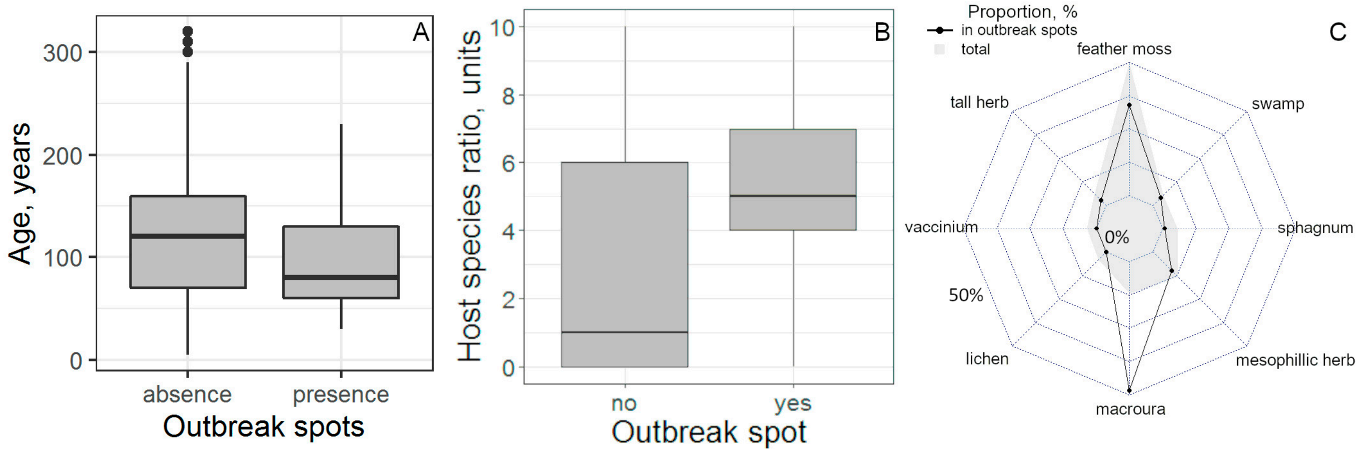

Figure 3. Comparison of forest stands characteristics that are most important in modeling: mean stand age inside and beside outbreak spots (**A**), joint ratio of *P. sibirica* Du Tour and *A. sibirica* Ledeb. inside and beside outbreak spots (**B**) and proportion of groups of forest types in outbreak spots versus Yenisei forest district in toto (**C**).

Forest stands where outbreak spots occurred differed significantly from those where there were no outbreak spots recorded in terms of groups of forest types ($p < 0.0001$). In general, feather moss forests dominate the study area (49.9% of mapping units). There was also a significant (>10%) share of macroura and mesophilic herb forests (Figure 3C). Outbreak spots also occur mostly in feather moss, macroura, and mesophilic herb forests, but the distribution has slightly different proportions (Figure 3C). Outbreak spots occurred mostly in macroura forests (48.4%) and less in feather moss (34.2%), mesophilic herb (9.9%), tall herb, vaccinium, sphagnum, and lichen groups of forest types ($p < 0.05$).

Stands of different moisture conditions ($p < 0.0001$) and feather mosses cover ($p < 0.0001$) are differently represented in the outbreak spots and outside them. These differences are mainly related to the higher proportion of moderately moist forest stands in the outbreak spots compared to the forest stands outside them ($p < 0.0001$) (Table 1). Outbreak spots were more common in forest stands with less area of forest floor covered with feather mosses ($p < 0.0001$). Stands outside the outbreak spots were characterized by higher feather mosses coverage values ($p < 0.0001$) (Table 1).

Table 1. Stands distribution by moisture conditions and feather mosses cover (% of mapping units).

Outbreak Spots	**Soil Moisture**	**Feather Mosses Cover (%)**			**Total**
		0–30	**31–70**	**70–100**	
Present	Moderately moist	57.1 [1]	16.5	0.9	74.6
	Moist	4.0	11.2	5.6	20.8
	Wet	0.9			0.9
	Extremely wet	3.7			3.7
	Total	65.8	27.7	6.5	
Absent	Extremely dry	0.3			0.3
	Dry	3.2	0.2		3.4
	Moderately moist	26.7	24.6	10.1	61.4
	Moist	5.0	6.4	11.6	23.0
	Wet	4.7	0.2	0.2	5.1
	Extremely wet	6.5			6.5
	Total	46.3	31.2	21.7	

[1] Share in the total number of mapping units where there were some or no outbreak spots.

3.2. Modelling the Occurrence of Outbreak Spots

The decision tree that gives the best prediction is in Figure 4. The depth of the decision tree was four, F1 = 0.43, precision is 0.63, and recall was 0.42 (hereinafter, we use the values of classification metrics calculated during cross-validation on the training set). The best predictors were the proportion of host species (Siberian fir and Siberian stone pine) in a stand species composition, stand age, and group of forest types. The host species take 5.2 units (52% of stem volume) in the species composition of stands in the outbreak spots, while inside stands, where no outbreak spots have been recorded, host species take 2.7 units (27% of stem volume) in the stands composition (Figure 3B). The average stand age in the outbreak spots was 97 years, while stands outside the outbreak spots are older (123 years) (Figure 3A). The decision tree predicted that in the study area outbreaks are more likely to occur in macroura and mesophilic herb groups of forest types (Figure 4).

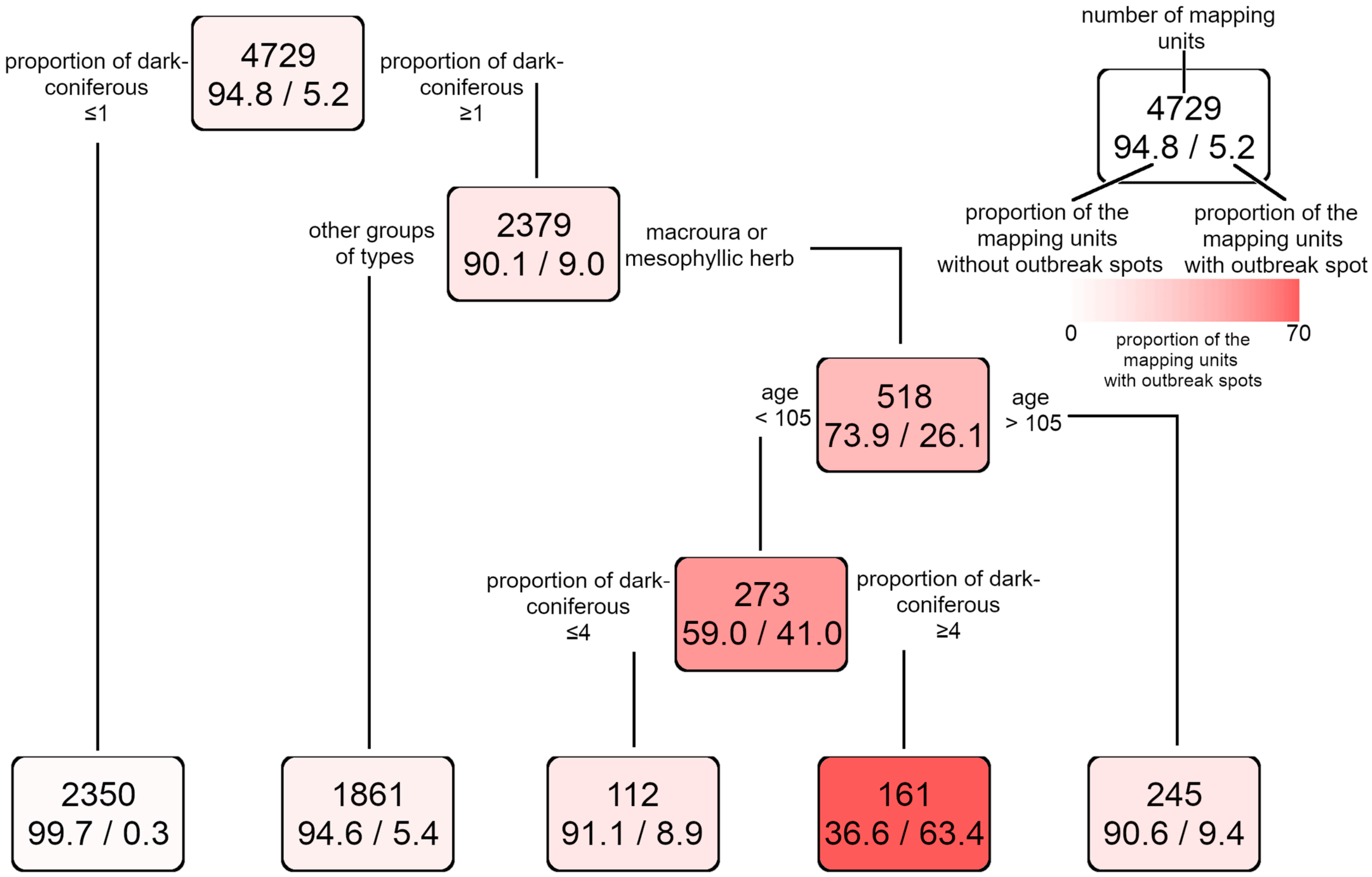

Figure 4. Decision tree predicting the occurrence of the Siberian silk moth outbreak spots depending on forest stands characteristics.

However, this decision tree (Figure 4) does not allow predicting outbreaks in feather moss forests. Notably, among the mapping units where outbreak spots have been recorded, the feather moss group of forest types was second only to the macroura one (Figure 3C). We constructed a separate decision tree (not shown) to study the damage to feather moss forest stands. Even at the optimal depth equal to nine, the prediction accuracy was unsatisfactory (F1 = 0.27, precision was 0.56, recall was 0.18). Nevertheless, the study of the underlying decision rules made it possible to reveal the main patterns in the distribution of outbreak spots in feather moss stands. Of the 110 mapping units where the outbreak spots occurred, 50 belonged to two terminal nodes. The first node was characterized by a smaller area, small diameter (<15 cm), and age of 60–65 years. The second node was characterized by a large area (≥61 ha; mean and standard deviation of 105 ± 41 ha) and the share of spruce of at least 30%. The average stand age in such outbreak spots was 163 ± 37 years. The total proportion of Siberian fir and Siberian stone pine in both nodes was no less than 20%.

The best of the random forest models (depth of 12,250 voting trees) with them being of higher classification quality than decision trees (F1 = 0.95, precision was 0.91, recall was 1.00) generally confirm the conclusions made (Figure 5A). The most important for prediction are the total share of Siberian fir and Siberian stone pine, group of forest types, and stand age. The values of features indicating the highest outbreak occurrence probability are close to those indicated by the decision tree shown in Figure 4.

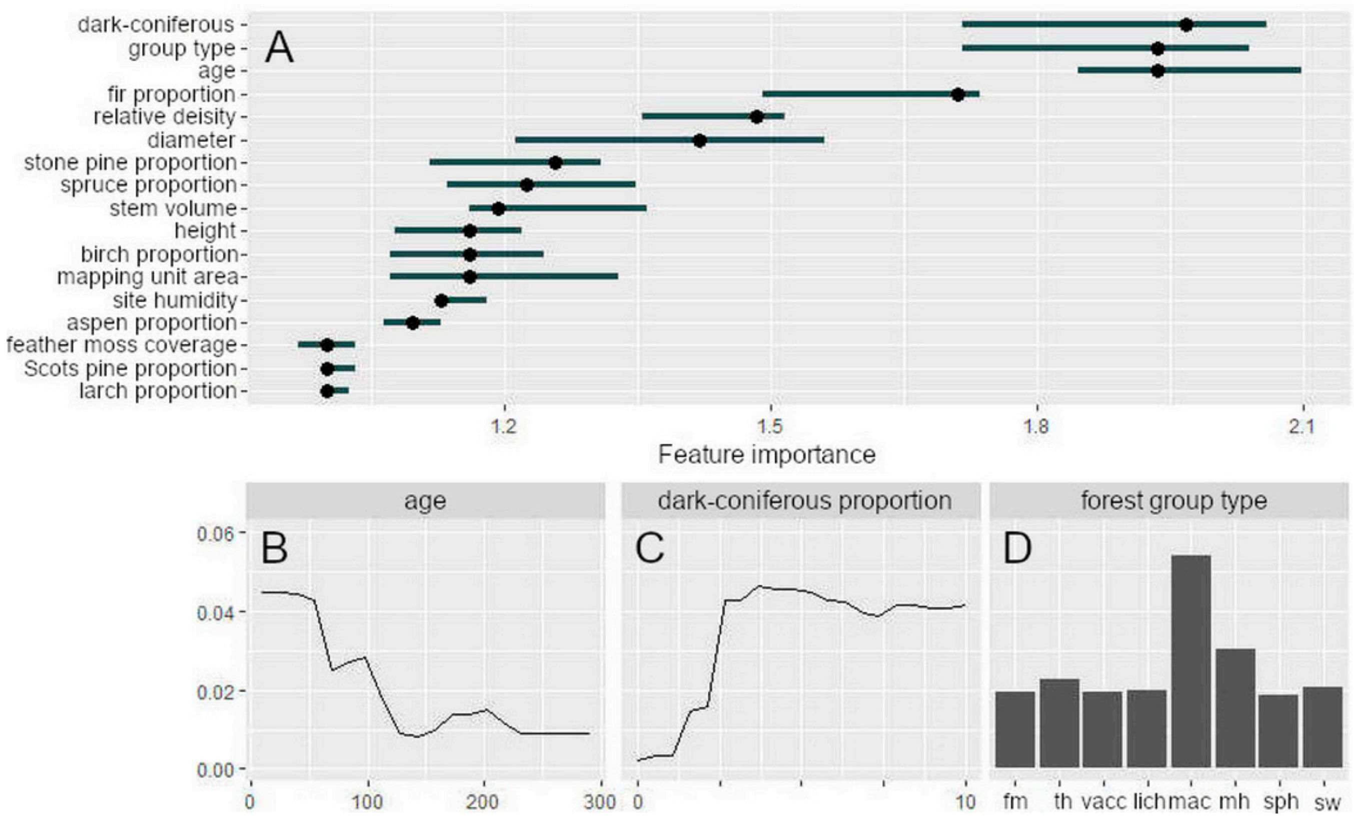

Figure 5. The importance of stand characteristics in prediction with random forest. Up (**A**): influence of characteristics on prediction accuracy (dot—median value, lines—borders from 5% to 95% of quantiles). Down: influence of the most important characteristics ((**B**)—age, (**C**)—dark-coniferous (host) species proportion in stand, (**D**)—group of forest types) on the probability of outbreaks occurrence. Groups of forest types on graph (**D**): fm—feather moss; th—tall herb; vacc—vaccinium; lich—lichen; mac—macroura; mh—mesophilic herb; sph—sphagnum; sw—swamp.

Significant contribution to the prediction accuracy was made by the proportion of fir, the stand density, and average diameter. The highest probability of outbreak spot occurrence is achieved at fir taking from 30% to 70% in the stand composition and at stand diameter of 15 cm or less. Stands with a density of 0.5 and less are almost not damaged. The highest probability was reached at a density of 0.6–0.8; in more high-density stands, the probability of outbreak spots occurrence decreases slightly. Other characteristics, including the area of the mapping unit, have a noticeably smaller contribution.

4. Discussion

The constructed models confirm that the probability of damage increases with an increase in the proportion that host species (Siberian stone pine along with Siberian fir) take in a stand composition [44] (Figures 4 and 5B). It was already shown that the defoliation by *D. sibiricus* increases as suitable host species proportion increases [19,20]. Our results coincide with [19]: the average value of the share that *A. sibirica* and *P. sibirica* take in stands damaged by the Siberian silk moth is 5.22 according to our data and 5.21 according to [19]. It is necessary to point out the presence of few stands (2 mapping units), where outbreak spots were recorded in the absence of dark coniferous species. The outbreak could not have developed from the native (not migrated from nearby outbreak spots) population of the Siberian silk moth in such unfavorable conditions. We believe that larvae of the new generation fed on a single host tree there after parent imago migrating from neighboring defoliated forest stands [45]. The insignificant amount ($\leq$3% of the total stem volume) of host species is not taken into account according to the methods used in our study (for simplicity, the tree species rarely found in the mapping unit are excluded from species composition), but in fact they can present in the forest stand. The studied forest stands were defoliated to a low extent, which is typical for forest stands with a smaller proportion of host species (median value of 30%, maximum value of 60%) [19]. This is not entirely consistent with our data (Figure 5B), which we will discuss below.

The forest type is an integral characteristic reflecting the result of interaction of many environmental factors [46]. The influence of these factors on plant communities is discussed in the cited research [46], but many of them directly or indirectly affect other organisms as well. A key factor for the Siberian silk moth is the moisture regime. It is well known that the pest outbreaks occur in moderately moist stands of macroura, mesophilic herb, and feather moss groups of forest types [10,19–21,24,45]. *Dendrolimus sibiricus* larvae require certain wintering conditions; in particular, they prefer wintering under the mosses *Brachythecium* spp., *Pleurozium* spp., and related species [47]. The presence of such moss cover is more or less typical for all the above-mentioned groups of forest types [38]. The Siberian silk moth avoids extremely wet (sphagnum and swamp) [38] stands due to the mass mortality of wintering larvae at high soil moisture [48,49]. In the West Siberian Plain, the feather moss stands are somewhat wetter than the macroura and mesophilic herb ones [50]. This explains the fact that their proportion among forest stands where outbreaks have been recorded is disproportionately low relative to their distribution in the study area (Figure 3C). At the same time, the landscape characteristics that form the forest type (soil, landform, etc.) [46] influence the pest outbreak spots occurrence. For example, outbreaks of *Orgyia pseudotsugata* (McDunnough) occur mostly on thin soils in watersheds and upper parts of slopes [51,52].

The previously described dependences between the spatial distribution of Siberian silk moth outbreaks and the age of stands are not entirely consistent with our observations. Out study showed that dark coniferous forest stands were damaged, first of all, upon reaching the age of maturity [8], meaning 80 years or more [53]. During the last outbreak in the Yenisei forest district, the average age of damaged stands was 98 years, and the median age value was 80 years (Figures 3A and 5B). During an outbreak that occurred earlier in the adjacent territory (the interfluve of the Taseeva and Yenisei rivers), these values were 129 and 120 years, respectively [19]. *D. sibiricus* damages dark coniferous stands of the same age class (80 years and older) in the Baikal region [22]. Notably, the onset of an outbreak in the study area in the 1990s occurred in stands with an average age of 70 years [20], which is much closer to our results. Stand age values in the Siberian silk moth outbreak spots close to our data were obtained in Altai [21]. Consequently, our results only partly coincide with those of previous studies.

The above listed differences can be explained by the patterns in outbreaks development. Here, we compare the results obtained earlier [19,20] for the outbreak peak [23] with the results of studies carried out at the population decline stage. The Siberian silk moth displays high migratory activity (about 100 km) [45]. The pest moves from damaged stands, which are most favorable for its development, both during an outbreak peak and collapse of the population. This is also typical of another well-flying (normally up to 100 km downwind) defoliator, *Choristoneura fumiferana* (Clemens) [54,55]. As a result, the population density of such species may increase in habitats that are less suitable for the occurrence of outbreak spots [8]. Such an interpretation explains the low population density of the Siberian silk moth in most stands (Figure 2L) and low defoliation level.

The patterns in distribution of the Siberian silk moth outbreak spots in the studied forest stands have a historical background. Siberian silk moth outbreaks, which have repeatedly occurred in the studied area [7,8,20,24,25], lead to progressive successions. Stands that died due to defoliation often burn down [8,56]. During post-fire successions, deciduous forest stands are formed [56], where the understory is composed of dark coniferous species [19,57] that become dominant as deciduous trees die [57]. The average and median age values of forest stands damaged during the last outbreak of *D. sibiricus* correspond to their regeneration in sites where forests have died after defoliation during outbreaks in 1898–1901 or 1914–1916 [20,57]. This assumption is confirmed (indirectly, but convincingly) by the high proportion of *Betula* ssp. and *P. tremula* in the stands (mean of 32%, median of 30%, upper quartile of 50%), since they have not yet died due to senescence after recovery in the burned areas [57].

The post-fire dynamics change the suitability of habitats for the Siberian silk moth in time. For instance, swamping (which is unfavorable for *D. sibiricus* larvae), usually formed after fire, is suppressed by the forest regeneration (due to increased transpiration rate) [56]. As a result, instead of initial forests (which were most likely of the feather moss type in the study area (Figure 3C)), mesophilic herb forests appear [58]. However, forest litter and mosses gradually accumulate increasing moisture due to their water-retaining capacity [59]. This is consistent with the general trend typical of the forests of the West Siberian Plain, where mesophilic herb forests are replaced by more hydrophilic forest types as they age [60]. The change takes several hundred years [59], and by 2016 it was still at the very beginning.

Thus, in the plain part of the Yenisei forest district, on the periphery of the *D. sibiricus* outbreak in 2014–2017, the outbreak spots were formed mainly in forest stands that died as a result of its outbreaks that occurred 100–120 years ago. During post-fire succession, a significant part of the dead forest stands first regenerated with deciduous species, which then began to be replaced by dark coniferous species. The process of hydromorphization of such habitats has not yet gone far. Therefore, the ground cover there is typical not only for the feather moss group of forest types, but also for macroura and mesophilic herb ones, where the Siberian silk moth find favorable conditions for larval over-wintering.

Less commonly, outbreak spots occurred in mature and overmature feather moss forest stands with a sufficient stocking of hosts. Such outbreak spots occupy mapping units with a relatively big area, which indicates the homogeneity of these sites and, indirectly, the absence of strong external influences throughout the life cycle of the dominant tree generation. Such impacts would lead to the fragmentation of stands and an increase in site conditions diversity, which is not actually observed. Thus, we can assume that the stands were not affected at all by past outbreaks of the Siberian silk moth or were damaged slightly, being on the border of the pest ecological niche. This is also indicated by a significant (more than 30%) share of spruce in the stands composition. When studying outbreaks in the Lower Angara region, it was concluded that conditions become unfavorable for *D. sibiricus* with an increase in the proportion of spruce [19]. Nevertheless, the homogeneity of site conditions in such stands contributes to the formation of migration outbreak spots there. It was proved with dendrochronological reconstructions of outbreaks that forest stands' homogeneity has a positive effect on the population density of *C. fumiferana* [61] and *C. freemani* Razowski (=*occidentalis* Freeman) [62].

The relative density values (another stand characteristic important for the Siberian silk moth outbreak spots formation) turned out to be somewhat higher in the outbreak spots than outside them, although the difference was not big (less than 0.1; Figure 2K). It has been previously indicated that *D. sibiricus* outbreaks are more common in low-density stands [45]. The damage decreased as the density increased [19]. However, it should be noted that the differences between our data and the results of predecessors are insignificant. In dark coniferous stands, the density of 0.4–0.7 is most favorable for outbreak spots occurrence [8,19]. We are tending to explain that the Siberian silk moth prefers stands with a higher average density (as well as other deviations from the previously described patterns) by historical reasons; the density was higher in those stands that had not been damaged earlier or were damaged slightly, and which, on the periphery of the outbreak, according to other characteristics, were the most favorable for *D. sibiricus*.

The influence of global warming on *D. sibiricus* ecological preferences is questionable. There are some data about northward shift [7] and increased frequency [63] of their outbreaks in the global climate change epoch, but not about shift in defoliated sites features. It can be cautiously assumed that outbreak spots in warmer climate will shift in dryer sites. Warming enhances the probability of the thaws, which leads to mass death of overwintering larvae due to wetting [64].

5. Conclusions

Predicting the spatial distribution of Siberian silk moth outbreak spots requires an integrated approach that takes into account the stands characteristics, succession dynamics, and the stage of an outbreak. This is also confirmed by the formation of outbreak spot during the collapse of population in 2014–2017 in the Yenisei forest district (southern taiga in the east of the West Siberian Plain and in the lowland of the Yenisei Range). The most evident and widely observed pattern is an increase in the probability of damage to forest stands with an increase in the proportion of host species there (*A. sibirica* and *P. sibirica* in the study area). However, many characteristics of forest stands in the outbreak spots did not correspond to previously described features. For instance, on the periphery of the damaged area, the Siberian silk moth outbreak spots, which occurred as a result of migration from previously defoliated areas, were concentrated in moderately moist forest stands with an age of 100 years or less. Another combination of characteristics favorable for the formation of an outbreak spot is an old (on average ~160 years) forest stand with a predominance of feather mosses on the ground cover and a significant proportion of spruce, which has retained uniformity over a large (on average ~100 ha) area. The fact that the migration centers of *D. sibiricus* appear in areas whose characteristics (small age or a high proportion of spruce) are considered not quite favorable for the pest can be explained by the history of forest formation in the study area. Migratory outbreak spots are most likely to appear in stands formed after the past outbreaks (at the end of the 19th–beginning of the 20th century). Successions in such forest sites have not yet reached the stage at which forest characteristics become optimal for *D. sibiricus*. Therefore, migration outbreak spots appeared either in Siberian fir-/Siberian stone pine-dominated forests that have recently regenerated on the sites of those that died due to previous defoliation, or in older stands, the damage to which was weak due to unfavorable conditions. Since the outbreaks of Siberian silk moth are periodical, these findings can be useful for early management measures for damage prevention.

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