Nikita M. Debkov[1], Aleksey A. Aleinikov[2], Alexander Gradel[3], Anatoly Yu. Bocharov[1], Nina V. Klimova[1] and Gennady I. Pudzha[4]
[1] Institute of Monitoring of Climatic and Ecological Systems, Siberian Branch of the Russian Academy of Sciences, Tomsk, Russia
[2] Center of Forest Ecology and Productivity, Russian Academy of Sciences, Moscow, Russia
[3] Georg-August-Universität Göttingen, Göttingen, Germany
[4] National Research Tomsk State University, Tomsk, Russia
*** Corresponding author:** nikitadebkov@yandex.ru

IMPACTS OF THE INVASIVE FOUR-EYED FIR BARK BEETLE (*POLYGRAPHUS PROXIMUS* BLANDF.) ON SIBERIAN FIR (*ABIES SIBIRICA* LEDEB.) FORESTS IN SOUTHERN SIBERIA

ABSTRACT. The emergence and spread of non-native invasive forest insects represent a major potential threat to global biodiversity. The present study examines the current invasion of the far eastern four-eyed fir bark beetle *Polygraphus proximus* Blandf. in southern Siberian fir (*Abies sibirica* Ledeb.) forests. We collected data on 38 large sized (2500 m^2) sample plots, situated in fir forests of the Tomsk region. As a direct result of the four-eyed fir bark beetle infestation, stand density decreased by 34-37%, and stand volume by 30%. The mean height, individual age and diameter at the stand level consequently increased. Our results indicated that stands with complete left-sided or normal ontogenetic structure (composed primarily of late virginal firs or firs in young reproductive stage) are more resistant to invasion by the four-eyed fir bark beetle. By contrast, fir forests characterized by more right-sided ontogenetic structure (composed primarily of mature and old reproductive firs), exhibited the least resistance and, with rare exception, degraded rapidly in response to the invasion. Our results also pointed to a mechanism that initiates invasions of the four-eyed fir bark beetle in fir stands of all types of ontogenetic structure, which is the attack of virginal trees and trees in early reproductive stages. Trees up to average diameter are the most susceptible to invasions of the bark beetle. We identified thicker bark, larger DBH and low occurrence of heart rot as the most important parameters for indicating resistance at the single tree level. DBH and bark thickness ($p<0.05$) correlated significantly with tree health status in infested stands. Our overall assessment of the potential natural regeneration of damaged stands is that the Siberian fir forests are resilient to invasive species and that the fir ecosystems can potentially recover from this disturbance.

KEY WORDS: invasion, stability, resilience, stand structure, taiga ecosystems, natural regeneration

CITATION: Nikita M. Debkov, Aleksey A. Aleinikov, Alexander Gradel, Anatoly Yu. Bocharov, Nina V. Klimova and Gennady I. Pudzha (2019) Impacts Of The Invasive Four-Eyed Fir Bark Beetle (Polygraphus Proximus Blandf.) On Siberian Fir (Abies Sibirica Ledeb.) Forests In Southern Siberia. Geography, Environment, Sustainability,
Vol.12, No 3, p. 79-97
DOI-10.24057/2071-9388-2019-35

INTRODUCTION

The impact of herbivorous insects on forest ecosystems has interested researchers around the world (Lyamtsev, Isaev 2005; Palnikova et al. 2006; McCullough 2006; Bidart-Bouzat, Imeh-Nathaniel 2008; Rozendaal, Kobe 2016). Particular attention has been given to studying how invasive insects impact different tree species (Binimelis et al. 2007; Hulme et al. 2009; Bacon et al. 2012). The occurrence of invasive insects is particularly pervasive as these organisms are known for their fast growth, rapid reproduction and high dispersal ability (Roques et al. 2010). Ongoing global changes, including warmer temperatures associated with climate change, significantly affect the structural and functional organization of different habitat types that are further intensified when combined with the damaging effects of invasive organisms (Holdenrieder et al. 2004; Brockerhoff et al. 2006; Boyd et al. 2013) and can significantly reduce overall forest biodiversity (Born et al. 2005; Kenis et al. 2009; Straw et al. 2013). Of particular concern is the future of boreal forests, which are characterized by low species biodiversity and susceptibility to external disturbances (Sanderson et al. 2012). It is well known that since the beginning of this millennium, the processes of degradation of coniferous forests in the circumpolar boreal zone has intensified (Aitken et al. 2008; Allen et al. 2009; Worrall et al. 2010; Yousefpour et al. 2010; Martinez-Vilalta et al. 2012; Anderegg 2013). Long-term models of the situation in North America, for example, predict that the frequency of invasions will increase up to the end of the 21st century (Aukema et al. 2010; Dukes et al. 2009; Koch et al. 2011). There is strong evidence that globalization has facilitated widespread outbreaks of invasive alien pests. Given the strong evidence that invasions at the global level are likely to continue, studies focused specifically on the resilience of native habitats against invasive alien pests have become highly important.

Against this backdrop of ongoing global processes, a unique phenomenon in the southern Siberian taiga has been observed, which is large-scale disturbance manifested in dying of large areas of Siberian fir (*Abies sibirica* Ledeb.) forests as a result of the invasion of the four-eyed fir bark beetle (*Polygraphus proximus* Blandf.), a new aggressive far eastern invader (Krivets et al. 2015a). This beetle was first identified in Siberia in 2008, in the vicinity of Tomsk (Baranchikov et al. 2011). The initial emergence of this invasive organism in southern Siberia has largely been attributed with wood importing by way of the Trans-Siberian Railway (Krivets et al. 2015b). In neighboring Mongolia, however, Abies sibirica distribution is scattered and limited to few of the northern Mongolian mountain ranges.

The four-eyed fir bark beetle *Polygraphus proximus* Blandford, 1894 is a beetle from the subfamily of bark beetles (Scolytinae) of the weevil family (Curculionidae). P. proximus develops under the bark of the tree in four stages: egg, larva, pupa, imago (Krivets at al. 2015b). The primary distribution of this beetle covers the southern part of the Russian Far East (Fig. 1), Northeast China, Korea and Japan. It usually only occurs in forests with trees of the genus Abies (Stark 1952). In the primary distribution within the Russian Far East, the local species of harvested fir are susceptible to the four-eyed fir bark beetle – A. nephrolepis, A. sachalinensis, to a lesser extent A. holophylla and A.

mayriana (Krivolutskaya 1958). However, especially in its secondary distribution range the impact have only recently become evident and the effects of the invader on the autochthon Siberian fir ecosystems are hardly known.

Our objective therefore was to assess and evaluate (1) the impact of *Polygraphus proximus* on the forest structure in Siberian fir stands in its secondary distribution range, (2) the stability of Siberian fir against the four-eyed fir bark beetle, (3) the renewable potential of fir ecosystems and prediction of their succession dynamics.

MATERIALS AND METHODS

Study area

We conducted our research between 2012 and 2018 in the Tomsk region, one of the recipient regions of the four-eyed fir bark beetle invasion. Field studies were conducted in 8 of the 16 administrative districts of the region (Tomsky, Asinovsky, Pervomaysky, Teguldetsky, Shegarsky, Krivosheinsky, Bakcharsky and Chainsky). The course of our field work included inspecting fir stands located in both harvested forests and in natural forests under different protection categories, including specially protected natural territories (Larinsky, Poskoyevsky, Tomsky and Kaltaysky reserves) (Fig. 1).

The present study builds on previous studies that investigated impacts of the bark beetle on selected sample plots in Siberian fir forests through a more basic analytical approach (Debkov 2018a; 2018b). Our study is aimed at a more comprehensive picture by examining the dynamics of these invasions on Siberian fir using more thorough data and broader analyses. Our database for this study includes 38 sample plots (SP).

Specific characteristics of the selected stands

In the vast majority of the surveyed stands, Siberian fir is the dominant species. But we also included stands dominated by Siberian spruce (*Picea obovata* Ledeb.; SP 3 and 33), Siberian pine (*Pinus sibirica* Du Tour; SP 2), Aspen (*Populus tremula* L.; SP 31) and Silver birch (*Betula pubescens* Roth.;

Fig. 1. Distribution areas map of *Polygraphus proximus* and species of the genus *Abies*

SP 38). The composition of the fir stands in terms of relative distribution varies fairly significantly – from approximately 30 to 100 percent. Most of the stands are even aged (76%). About 24% are uneven aged. Most of the studied stands are of average density (67%), but the proportion of high-density communities is significant (33%). The majority of the studied stands are characterized by high productivity (67%), with the remaining at average productivity (33%). The main forest floor type (hereinafter referred to as forest type) according to the dominating species belong all to so-called "grass-types": low grass: *Oxalis acetosella* L., *Carex macroura* Meinsh., *Stellaria bungeana* Fenzl., medium grass: *Aegopodium podagraria* L., *Dryopteris Adans*., *Athyrium filix-femina* (L.) Roth., high grass: *Aconitum septentrionale* Koelle, *Thalictrum minus* L., *Matteuccia struthiopteris* (L.) Tod. All selected stands were observed to be affected by the four-eyed fir bark beetle.

Data assessment and classification of stand health via AWTS-index in the sample plots

We established SPs with a size of 0.25 hectares in each of the selected stands. The minimum number of trees of the main canopy in each plot is 100. We assessed the traditional stand parameters (DBH, tree height, and average tree age) and used different methods for measuring additional parameters on the plots. To measure the degree to which individual fir trees were affected by Polygraphus proximus outbreaks, we assessed health status of individual trees (TS) using to the scale of categories developed by Krivets et al. (2015b): I – healthy, with no signs of weakening, not attacked by the bark beetle; II – weakened, attacked by the bark beetle, but not settled (unsuccessful attempts at colonization); III – heavily weakened, attacked by the bark beetle, but not colonized; IV – drying (dying), colonized by the bark beetle, while upper crown maintains green needles; V – dead standing tree, from the current year, with discolored needles; and VI – dead standing tree, from past years, with visible signs of bark beetle infestation on the stems, the entire crown without needles. Based on this evaluation, we derived the *average weight tree health status* (AWTS-index) for all firs in each SP (formula 1).

The surveyed stands belonged to mature age groups and were characterized at the time of the study by varying degrees of health status – from weakened (AWTS is 1.6–2.5 points) to severely weakened (AWTS varies within 2.6–3.5 points) and degraded (AWTS is 3.6 points and above). The calculation of the AWTS-index was performed by the following formula (Krivets et al. 2015b):

$$AWTS = \frac{\Sigma g_1 + 2\Sigma g_2 + 3\Sigma g_3 + 4\Sigma g_4 + 5\Sigma g_5 + 6\Sigma g_6}{\Sigma G} \quad (1)$$

where AWTS is the average weighted category of tree status in the respective stand; Σg_1, Σg_2, Σg_3, Σg_4, Σg_5, Σg_6 is the sum of the basal areas in the SP of the above mentioned respective categories (1-6; ΣG is the sum of basal areas of all fir trees in the SP. See Appendix A.

Overview of the current distribution of the invasive bark beetle in Russia

Based on the literature, our data and additional data provided by branches of the Russian Forest Protection Center, we will provide an overview describing recent distribution patterns of the bark beetle and the current extent of outbreaks that, in some cases, have reached widespread epidemic levels.

Evaluation of the impact of the invasive bark beetle on the stand structure of fir ecosystems

The experimental material is based on data obtained from 2 permanent SPs (no. 61 and 62), which were established in 2010 on the territory of the Kaltaisky Zoological Reserve and in the harvested forests of the Timiryazevsky forest unit in the Tomsk region. The uniqueness of this material is that the SPs were established before the beginning of the mass investation of the four-eyed fir bark beetle in this territory, which began in 2011 (Kerchev, Krivets

2012). During the establishment phase of the SPs, we observed abundant resin pitches on the fir trunks, which signals that an invasion has occurred (Krivets et al. 2015b), but there were no signs of excessive dryness.

We made sure that each SP included not less than 200 trees. Tree diameters were measured with an accuracy of 1 mm with a caliper (Haglöf). Model trees outside of the SP perimeter were then selected using the method of proportional representation. The initial number of model trees was 30 pieces within the SP. Felling and bucking trees were carried out using the chainsaw brand STIHL MS 180.

The volume of tree trunks was determined by the complex Huber formula (Anuchin 1982):

$$V = (g_1 + g_2 + ... + g_n) * L + (g_t + l_t) / 3 \quad (2)$$

where g_1, g_2, …, g_n – basal areas in the middle of the 2-meter sections, L – section length, g_t – basal area of the base of the top, l_t – top length.

Evaluation of the impact of the invasive bark beetle on the ontogenetic structure of fir ecosystems

Determining the ontogenetic states of Siberian fir trees and regeneration in the foci of the four-eyed fir bark beetle invasion was carried out taking the developed periodization of Abies sibirica ontogenesis into account, which represent stages of biological age (Mahatkov 1998; Methodological approach 2010; Evstigneev, Korotkov 2016; Smirnova et al. 2017). In our study, we attributed the ontogenetic features to two levels: regeneration and canopy structure. Early and late immature (im1, im2), early virginal plants (v1) were attributed to regeneration, whereas late virginal (v2) and reproductive trees (young reproductive trees: g1; mature reproductive trees: g2; old reproductive trees: g3) were attributed to the canopy.

The ontogenetic structure was measured on 14 SPs. Overall, 1035 fir trees and 1042 saplings were measured. We hypothesized that attack by the bark beetle can change the proportions of the ontogenetic stages of the stands, and by doing so, can lead to disruption of the regeneration process at tree level.

Evaluation of the stability of Siberian fir trees to the impact of the invasive bark beetle

In the context of this study the term "stability" is understood on single tree level as the ability of a fir tree to survive a beetle attack, and on the collective level (stand) as the ability of the forest ecosystem to maintain its structure and nature of functioning in space and time under changing environmental conditions, including biotic factors in the form of xylophagous insects. To gauge the stability of fir trees against the bark beetle we collected data pertaining to key variables of fir trees, that we hypothesized to be decisive indicators of the stability against the beetle attacks. These variables are: tree age, DBH, bark thickness, occurrence of heart rot, and radial growth dynamics. We collected the respective data on 22 plots (Appendix A). We used incremental borers (length of 400 mm; diameter of 5.15 mm, Haglöf) to determine the presence of heart rot and determine tree age. DBH and the bark thickness were measured using calipers. All measurements and core sampling were performed at a height of 1.3 m. In that way on each SP, 10 samples were taken from both living trees (AWTS category I-III), and dead trees killed by the bark beetle (AWTS category V-VI). We hypothesized that the selected variables represent key indicators for conducting a rapid assessment of the stability of fir forests against the four-eyed fir bark beetle.

Evaluation of natural regeneration potential of damaged fir forests

Regeneration was assessed in a modified form according to Pobedinsky (1966) on each of the regeneration plots (RP). Depending on the characteristics of the communities (occupied area and quantitative parameters of regeneration), the assessment was carried out on continuous transects with square-sized RPs of 4 m^2 each, which resulted in 25

RPs or as a discontinuous transects with 30 circular RPs with a size of 10 m^2 each. We assessed species, height, basal diameter, age, density, length and projection of the crown, linear growth of the axial shoot and side shoot of the first order. We additionally selected saplings models composed of 3 individuals per height group to determine the morphological characteristics and age. The distribution pattern of the natural regeneration was estimated by occurrence (the ratio of the number of RPs with at least 1 sapling to the total number of RPs). For studying the spatial distribution of the regeneration, the scattering index, proposed by R.A. Fisher (Svalov 1985) was applied:

$$f = \frac{(\Sigma x^2 * n_2 - N^2 / n) * n}{(n-1) * N} \quad (3)$$

where x = 0, 1, 2, …, regeneration number on RP, n_z – RP number with 0, 1, 2, …, regeneration number; n – sum RPs on the respective SP; N – overall regeneration number on SP.

Statistical analysis of our data was carried out using the STATISTICA 10 program (Statsoft 2010). In addition to the standard descriptive statistics (mean±standart error), the non-parametric Mann-Whitney test and Kruskal-Wallis test were used to test the significance of the respective parameter with a level of $p < 0.05$. The Kruskal-Wallis one-way analysis of variance by ranks test was used to compare the parameters of stability (occurrence of heart rot, age, DBH, thickness of bark, radial growth) against P. *proximus*. Several independent groups were compared by using the AWTS as dependent variable. The Kruskal-Wallis test is used to detect the differences between several independent groups. In the case of two independent groups the result is equivalent to that of the Mann Whitney U test (Sheskin, 2004).

RESULTS

Current distribution of the four-eyed fir bark beetle in Russia

In 2015, the scale of the secondary range of the four-eyed fir bark beetle on the territory of southern Siberia was assessed (Krivets et al. 2015b). At that time, this beetle was observed to be present in 7 regions of the Siberian Federal District of the Russian Federation: Tomsk, Novosibirsk, Kemerovo, Altai and Krasnoyarsk, the Republics of Altai and Khakassia. The approximate area of the invasive four-eyed fir bark beetle range was 560 thousand km^2, which is slightly more than the area of a European country such as France. To date, the presence of the four-eyed fir bark beetle has been confirmed on the territory of another constituent entity of the Russian Federation – the Irkutsk Region. On the territory of the Republics of Altai and Khakassia, the invasive beetle is so far absent. The invasion range in Kemerovo (2 administrative districts, 9.1 thousand km^2), Novosibirsk (1 administrative district, 13.9 thousand km2) and Altai (1 administrative district, 2.5 thousand km2) increased slightly. The increase in the secondary range on territory of Tomsk (9 administrative districts, 172.7 thousand km^2) and the Krasnoyarsk (14 administrative districts, 125.5 thousand km^2) was most pronounced. Thus, for the period from 2015 to 2018 the overall range of invasion appeared to increase by approximately 323.7 thousand km2 (or 58%).

General characteristics of damaged forests

The surveyed fir stands are typical for southern Siberia and belong to the common group of the forest floor types – grass. One of the characteristic features of fir forests in the flat plains of the Siberian taiga is that due to their rather narrow ecological amplitude, they are confined to trophic habitats with sufficient moisture regimes. This is confirmed by a slight variation of the yield classes (II–III).

The health status of fir stands varies greatly. AWTS ranged from 1.4 (no degradation, SP 60) to 5.2 (heavy degradation, SP 53). We observed that 29% of the surveyed stands appeared to be weakened, with 25% as severely weakened, and 46% of the stands showed signs of degradation. See appendix A.

Evaluation of the impact of the invasive beetle on the structure of the fir stands

During the observation period (SP 61 and 62) from 2010 to 2017, stand density increased by 9 and 26%, respectively (Debkov 2018a). This increase was largely due to ingrowth of young firs into the tree canopy. However, despite the increase of firs in stand composition by 2017, due to damage by the four-eyed fir bark beetle, the number of viable trees decreased by 37 and 34%, respectively. This led to an increase in the share of other species, and the relative share of fir in composition decreased by 11.5% and 14.7%, respectively.

The dynamics of diameter distribution (Fig. 2) showed that throughout the 7 years of the observation period the stands became thicker (increase on the right part of distribution), by about one DBH class. On other hand, it was replenished with new trees (the left part of distribution). The presence of the four-eyed fir bark beetle clearly did not affect the right side of the diameter distribution, but it significantly affected the left side by shifting it from asymmetric and peaked (asymmetry coefficient was 1.83 ± 0.15, the excess was 1.73 ± 0.30) towards a normal distribution (asymmetry coefficient of 0.08 ± 0.18, the excess – 0.58 ± 0.36). The average diameter increased from 18.6 ± 0.5 cm in 2010 to 21.5 ± 0.6 cm in 2017. While the standard deviation remained the same, the variation coefficient decreased from 40 to 35%.

An important indicator of the stand is the standing volume. In 2010, at SP 61, the standing volume of fir trees was 131 m^3/ha. When recalculated in 2017, taking the replenishment with new trees and the increased volume of those existing into account, it should have been 186 m^3/ha. However, as a result of being attacked by the invasive beetle, the standing volume remained at the same level (131 m^3/ha), i.e. the loss of standing volume was 55 m^3/ha or 30%. The ratio of loss of density and productivity also indirectly indicates the nature of the damage itself: fir density decreased by 49%, and standing volume by 30%.

The average age of the studied fir trees in 2010 was 84.7 ± 1.6 years, the average height was 20.3 ± 0.4 m and the average diameter was 21.2 ± 0.7 cm. With normal replenishment of the tree canopy by young fir, by 2017 age should have decreased to 79.6 ± 1.5 years, height to 19.1 ± 0.3 m and diameter to 18.8 ± 0.7 cm. This would be expected since ingrowth of young trees should have taken place. But as a result of the four-eyed fir bark beetle invasion, the average age increased significantly to 97.5 ± 2.5 years, the average height to 23.3 ± 0.5 m and the average diameter to 27.6 ± 1.2 cm. The variation coefficients of the mentioned parameter decreased due to the impact of the bark beetle. The stand structure became more uniform and less diverse.

Evaluation of the impact of the invasive bark beetle on the ontogenetic structure of fir ecosystems

The percentage of beetle-infested dead trees in the studied stands with a left-sided ontogenetic structure varied significantly (Debkov 2018b), and generally ranged from 23% to 92% We did, however, observe a connection in terms of the nature of the invasion itself. This is that the initial stage of

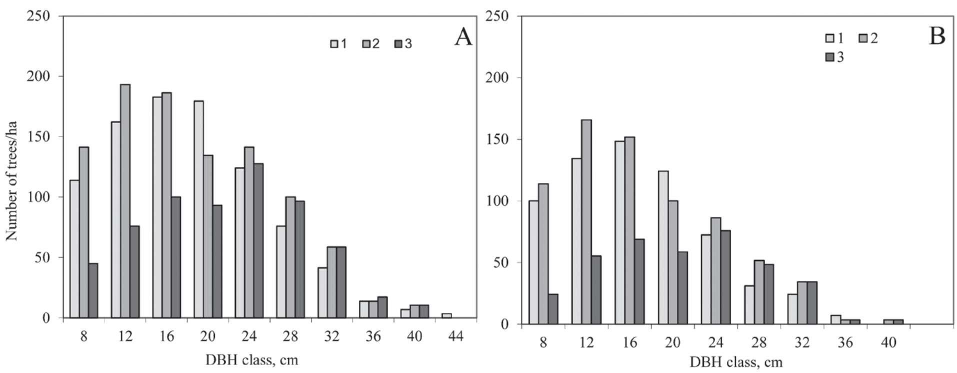

Fig. 2. Dynamics of the diameter distribution of the whole stand (A) and firs in the stand (B). Numbers refer to assessments in respective years: 1 = 2010; 2 = 2017; 3 = 2017 without dead A. *sibirica*

the bark beetle infestation resulted in damage exclusively limited to late virginal trees (v2) and young reproductive trees (g1). Further, the percentage of dead trees within these ontogenetic stages increased, which then included mature (g2) and old reproductive trees (g3). In our study stands, significant mortality of mature and old reproductive trees exceeding the natural background level was not fixed (2.0 ± 0.7% and 1.2 ± 0.7%, respectively). Mortality of younger trees ranged from 10.0 ± 2.9% among young reproductive trees to 38.0 ± 10.4% in late virginal trees (v2). At the same time, it should be noted that significant decay among mature trees, particularly old reproductive trees (g3), was observed in those fir stands where the percentage of trees within these ontogenetic stages were insignificant (less than 5–10%). See Fig. 3 for an overview of fir forests with different ontogenetic structure of living trees.

The percentage of dead trees in the fir stands characterized by right-sided ontogenetic structure also varied fairly significantly (from 18% to 89%), however this was linked with the percentage of old reproductive trees. While tree mortality was observed among firs across all ontogenetic stages, the breakdown was total loss of late virginal and young reproductive trees, 6.0 ± 2.1% of mature reproductive trees, while 10.7 ± 1.2% of old reproductive fir trees survived.

A comparative analysis showed that for stands with a left-sided ontogenetic structure the AWTS was 3.0 ± 0.6 (with a range of 1.6 to 4.6), and for ones with a right-sided ontogenetic structure the AWTS value was 3.6 ± 0.8 (with a range of 1.4 to 5.2). However, these differences are not statistically significant.

Evaluation of the stability of Siberian fir trees to the impact of the invasive bark beetle

In our analysis on the overall forest stands health during the primary and secondary distribution of the bark beetle invasions in the Tomsk region, no significant differences were found (Mann-Whitney test, $p = 0.6333$). This suggested to us that infestations of the bark beetle affect the entirety of the stand, attacking all available trees at one time, which weakens the forage base for future generations. Overall stand health is largely determined by its growth and vitality. As such, more viable stands merely weakened in response to infestation by the beetle, while less viable stands showed rapid degradation. We found that the residence time of the four-eyed fir bark beetle in specific stands played a secondary role and did not change between the areas of primary and secondary distribution.

The average occurrence of heart rot in living fir trees was 13.6 ± 3.6% (Appendix B). The prevalence of rot in dead trees was significantly higher with 22.6 ± 4.9%. However, despite these differences, the Mann-Whitney

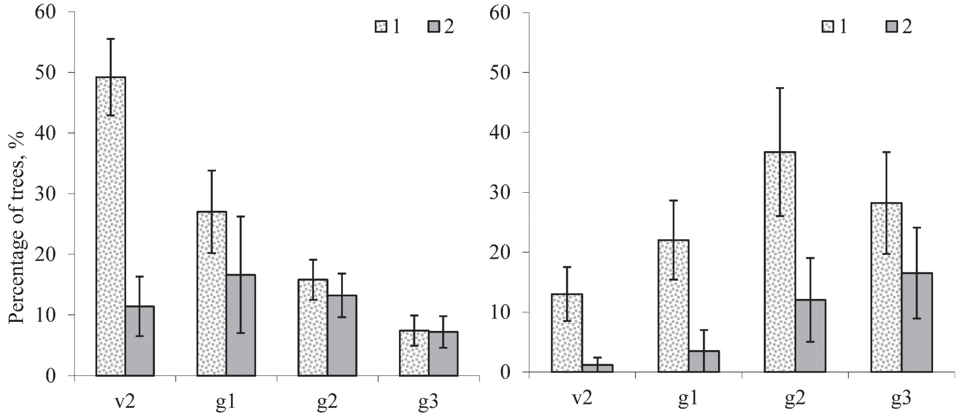

Fig. 3. Fir forests with left-sided and right-sided ontogenetic structure.

v_2 – late virginal plants; g_1, g_2, g_3 – young, mature, and old reproductive plants.
1 – before impact, 2 – after impact.

test did not confirm the hypothesis in terms of the effect of rot on tree health (p = 0.1995). A significant occurrence of heart rot in living trees in severely damaged stands was not confirmed (Kruskal-Wallis test, p = 0.3241). We did, however, note a significant difference in the prevalence of heart rot in dead trees depending on the degree the fir stands had weakened (Kruskal-Wallis test, p = 0.0285).

The average age of living trees (75 ± 5 years) did not differ from that of dead firs (73 ± 3 years). The range of age variation was greater in living trees (40–132 years) than it was for dead fir trees (42–106 years). The Mann-Whitney test rejected the hypothesis tree age has an influential effect on tree health (p = 0.9799). We found no significant relation between age and tree health, in terms of living and dead trees in the series of damaged stands. (Kruskal-Wallis test, p = 0.8124, p = 0.7728, respectively).

We found that the average DBH of living trees was 28.1 ± 1.4 cm. Comparatively, the DBH of dead trees was substantially less, measuring 23.2 ± 1.1 cm. The DBH of living trees varied from between 13.5 and 41.9 cm, whereas DBH for dead firs between ranged from 16.1 to 34.0 cm. The Mann-Whitney test confirmed the significant influence of DBH on the tree health (p = 0.0068). The relation between DBH and tree health, in terms of living and dead trees in the series of damaged stands, was not confirmed (Kruskal-Wallis test, p = 0.4329, p = 0.7112, respectively).

The average thickness of bark from living trees was 8.0 ± 0.3 mm, which represented an absolute range from 5.0 to 11.8 mm. By comparison, the average bark thickness of dead trees was substantially less and measured at 6.2 ± 0.2 mm, within an absolute range of 4.6 to 8.4 mm. The Mann-Whitney test confirmed our hypothesis that bark thickness significantly influences the health status of trees (p = 0.0002). The relation between bark thickness and tree health, in terms of living and dead trees in the series of damaged stands, was not confirmed (Kruskal-Wallis test, p = 0.1941, p = 0.2500). See Appendix B.

The average radial growth in stands in early stages of succession dynamics (SP 32) was 1.56 ± 0.06 mm/year (Fig. 4). The growth gain in dead trees was significantly lower 1.25 ± 0.08 mm/year compared to living firs with 1.71 ± 0.07 mm/year. The Mann-Whitney test confirmed that radial growth is an important indicator of overall tree health (p = 0.0001). The average radial growth in late stages of succession (SP 34) was 2.29 ± 0.06 mm/year. The growth gain in dead trees was significantly lower 1.97 ± 0.12 mm/year than in living firs – 2.38 ± 0.07 mm/year. The Mann-Whitney test confirmed the hypothesis that radial growth is an indicator of tree health status (p = 0.0025). The value of radial growth on SP 32 was higher than on SP 34, which also affected the degree of damage.

Evaluation of the natural regeneration potential in damaged fir stands

The species composition of natural regeneration in all studied fir stands is completely dominated (81–100%) by *Abies sibirica, Picea obovata* (1–9%),

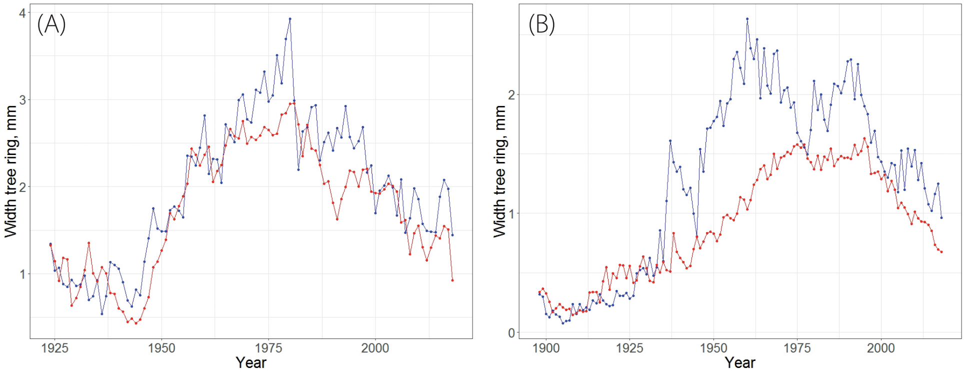

Fig. 4. Dynamics of radial growth at a later (A) and earlier (B) successional stage of development fir forests. Red line – trees killed by *P. proximus*, blue line – live trees

Populus tremula (1–9%) and *Pinus sibirica* (1–4%) which are most often present as accompanying species. The viability of natural regeneration can be determined by considering morphological indicators given in Appendix C, which characterize the assimilation apparatus (crown) of saplings.

The mean of occurrence rate in the RPs of saplings was 73 ± 5% (limits 22–100% on the SPs), and no significant differences were found in the degree of damage of the stand (Fig. 5). The average mean number of saplings was 5091 ± 1039 per ha (range: 260–19200 per ha). We assume a threshold value of 1500 per ha to ensure the natural restoration of fir forests. This value was observed in approximately 76% of the studied stands.

The dynamics of spatial structure of natural regeneration was heterogeneous. The scattering coefficient steadily exceeded 1, while it was higher in mixed stands and dominated by small and medium-sized saplings. This indicates clumped groups of regeneration on one hand (with an occurrence below 65%) and a variable density with regular/uniform occurrence of saplings (above 65%) on the other. For degraded fir forests, the scattering coefficient is 1.9 ± 0.3 (limits 1.1–3.4), for severely weakened with fir trees – 6.0 ± 1.8 (limits 1.4–14.1) and for weakened – 3.0 ± 1.0 (limits 1.0–5.9). We did not find a significant difference in the values of this indicator (Mann-Whitney test, $p = 0.0530$). See appendix C.

DISCUSSION

Before discussing our results in the context of single tree - stand- and landscape level, some specific facts on the biology of the beetle should be mentioned. According to Kerchev (2013) the average fertility of the female in the invasive range is 45,2±15,3 eggs, which corresponds to the data in the primary distribution (Yamaguchi 1963). In laboratory, it takes about 50 days under the bark until the first young beetles fly out. Due to sufficient temperatures during the growing season in Western Siberia, as well as in the primary range (Kurentsov 1941; Krivolutskaya 1958), the four-eyed fir bark beetle develops two generations. Most favorable are summer days with sunny calm weather and air temperature above 15ºC (Krivets et al. 2015b). Overall 24 species of predatory insects of the four-eyed fir bark beetle have been registered in Western Siberia (Kerchev 2013). Among these, most of the local species are facultative predators of the families *Tenebrionidae, Laemophloeidae, Colydiidae, Histeridae* and *Staphylinidae*. The most popular is the obligate predator of the four-eyed fir bark beetle – the bark beetle Medetera penicillata Neg. (Diptera, Dolichopodidae), a species previously unknown to Siberia, described in Japan and Primorsky Krai (Negrobov 1970), and apparently imported together with P. proximus. Currently, this species is considered as being the most prominent regulator of the four-eyed fir bark beetle population.

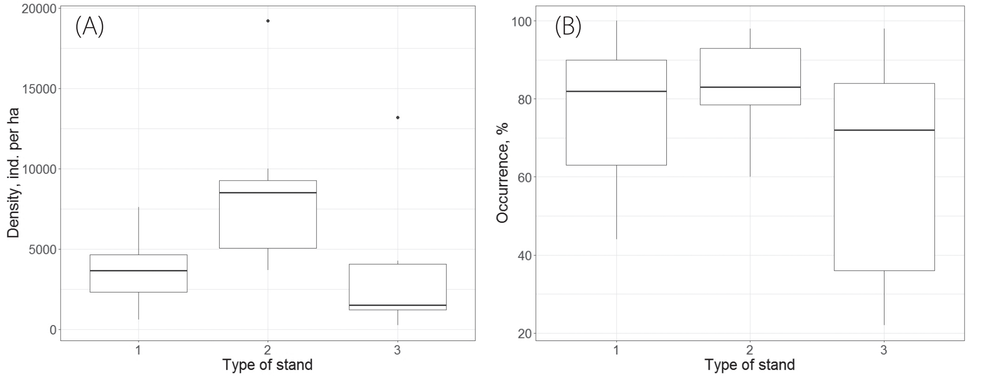

Fig. 5. The density (A) and occurrence (B) of natural regeneration in fir forests damaged by the four-eyed fir bark beetle. Type of stand: 1 – weakened, 2 – severely weakened, 3 – degraded

Tree size matters

The loss of tree species or part of their population changes the local environment, disrupts the main ecosystem processes, including decomposition rates, nutrient movement, carbon uptake and energy flow. In contrast to earlier studies (Baranchikov et al. 2011), we found that the degree of the bark beetle infestation damage in a stand is related to tree diameters. Trees with smaller diameters were clearly more often affected and more seriously damaged than larger trees. Overall, we observed that while invasions by the four-eyed fir bark beetle are systematic and thorough in nature, in that all trees within the stand, including undergrowth, are affected, the most damaging impact is to smaller trees.

Invasions of non-native organisms on native biota often lead to extremely negative consequences that have obvious, direct and measurable economic repercussions. Forest degradation occurs in cases where the impacts of invasions are severe enough to cause a reduction of the host tree species population and relevant, disruptive changes to forest ecological functions and biodiversity. One example of this is the heavy damage to white pine (Pinus strobus) forests invaded by white pine blister rust *Cronartium ribicola* (Ostry et al. 2010).

One result we observed in some stands was the increase of several stand parameters (height, age, diameter), while productivity, crown density and stand density decreased. The yield class however was unaffected. Importantly, infestation by the bark beetle appeared to have a homogenizing effect on the stand level in terms of height, age and diameter, which represents one of most consequential, long-term impacts on fir forests. The obtained data characterizing the occurrence of heart rot showed that standing dead fir trees are roughly two times more likely to be infected by heart rot compared to living trees. Some authors (Donyakina et al. 2013) believe that infection by fungal diseases, in particular, annosus root rot *Fomitopsis annosa*, which leads to the development of rot, is a major factor contributing to the susceptibility of fir trees to infestation by the four-eyed fir bark beetle.

We found no clear connection linking tree age and natural predisposition to attack by the four-eyed fir bark beetle. But one study on the impacts of pine bark beetle *Ips confusus* in forests growing in the southwestern United States dominated by pinyon pine (*Pinus edulis*) showed that it was primarily larger, older trees that suffered the most negative effects (Floyd et al. 2009).

Our study revealed that after infestation the mean DBH compared to dead fir trees is about one DBH class higher (4 cm). The less disturbed stands are characterized by the presence of stronger trees, which, in our case, were firs with a diameter of 30 cm. Based on our results, we can consider trees with diameters of 30 cm as the upper limit for potential attack by the four-eyed fir bark beetle. We should note that one of the first studies on invasions of the four-eyed fir bark beetle (Baranchikov et al. 2011), reported an absence of any association between the reproduction and spread of the beetle with tree diameter sizes. Our own results could not confirm this. This was also the case for other authors (Bleiker et al. 2003), who showed that as a result of impact of western balsam bark beetle *Dryocoetes confusus* on fir state of subalpine fir *Abies lasiocarpa*, trees of medium and above diameter are often damaged, which the authors explained is due to lower resistance levels of old-aged trees. Our data show that tree mortality in fir stands correlated directly to mean diameter.

The assumption that bark thickness plays a crucial role in tree susceptibility to attack by the four-eyed fir bark beetle has been confirmed. We effectively established that strong individuals exhibit higher resistance when bark thickness measures 8–10 mm and higher. Therefore, when the invasive four-eyed bark beetle attacks stands characterized as more stable, it will necessarily target thin-barked individuals. One aspect of trees growth is the radial growth, which was previously shown to be connected with tree resistance against invasion by the bark beetle (Baranchikov et al. 2014). This was confirmed in our study. We consider radial growth as an indicator of tree health. Healthier trees are more likely to survive an attack.

Attacked Siberian fir stands have the potential to regenerate

The most important element of a forest ecosystem is its capacity for natural regeneration. The impact of invasive organisms can either lead to complete destruction of young generations, or significantly slow down processes of their growth and development to such an extent that there is a change in dominant tree layer (McLaren et al. 2009). Our data indicate that invasion by the four-eyed fir bark beetle represents clear, but not extreme, pressure on regeneration processes. The frequency and quality of fir regeneration in most of stands subjected to invasion of the four-eyed fir bark beetle are generally satisfactory and, in the long-term, will ensure that natural restoration of fir forests continues.

This is particularly important when considering that the effects of an invasive organism can often lead to an increase in regenerative functions of the damaged ecosystems, for example when gaps formed in canopy resulted from the death of eastern hemlock *Tsuga canadensis* trees subjected to invasion of organisms that attacked its undergrowth (Fajvan, Wood 1996; Small, M.J. Small, C.J. Dreyer 2005). At the same time, both in the above-mentioned examples, and according to data (Jenkins 2003) in forests dominated by Fraser fir *Abies frazeri*, a decrease in the frequency of natural regeneration was observed. Accompanying species can strengthen the regeneration process, even if we did not observe this particular dynamic in our own study. However, it was concluded that even these features of regeneration make it possible to continue domination of the main tree species in long term, eastern hemlock *Tsuga canadensis* (Weckel et al. 2006) and Fraser fir *Abies frazeri* (Stehn et al. 2003), respectively.

Interestingly, one significant impact of the beetle was in the second layer of suppressed trees, of those just beginning to grow into canopy, as well as to some parts of tree canopy itself. The severe damage commonly observed in this category of trees represents a clear disruption of fir forests natural growth dynamics. A critical remaining question pertains to the frequency of such infestations. Indeed, at present, the fir forests in areas where the bark beetle invasions have occurred show strong natural regeneration. This suggests that fir will likely continue as the dominant species in the Tomsk region.

The impact of the bark beetle on dark taiga ecosystems in the context of climate change and increased utilization pressure in the region

Several studies have recently described a general retreat and degradation of dark coniferous forests throughout Northern Asia, parts of Europe and Russia (Zamolodchikov 2012; Kharuk et al. 2013; Kharuk et al. 2016). These authors describe the decline not limited to fir, but include the other two main dark coniferous species (*Pinus sibirica* and *Picea obovata*). Kharuk et al. (2013; 2016) view the bark beetle infestation as secondary disturbance force and one aspect of the large-scale decline of fir and Siberian pine growing in the southern Siberian Mountains. The same authors consider warmer temperatures associated with climate change, and subsequent drought conditions, as the major forces driving forest degradation in the region. In Mongolia, according to Dulamsuren (2004), *Abies sibirica* occurs westwards of Lake Hovsgul and in the Khentey Mountain range and, due to its limited distribution range, it is included in the national Red List of threatened Species. Species like Abies sibirica that thrive in humid environments are, in this region, naturally limited to growing at higher elevations with higher precipitation and on sites with northern or northeastern exposition. Due to their remote distribution, fir stands in Mongolia have relatively high conservation value due to the fact that they have remained largely undisturbed in that they include stands that have never been used for commercial exploitation. There is no evidence to date that invasions of *Polygraphus proximus* have occurred in Mongolia, but this very mobile bark beetle constitutes a potential threat to the valuable Mongolian and Siberian fir stands, especially in the context of current prevailing drivers of forest change in the region, such as forest fires, illegal logging and climate change (Dulamsuren 2011; Kharuk et al. 2013; Gradel 2017; Juřička et al. 2018). The observed decline of fir in Siberia has primarily occurred in stands subjected to drought stress, which is an underlying factor that weakens the forest stands and make them more susceptible to invasive insects. A relation of increased establishment and spread of bark beetle and climate warming was also found for other regions in the world (Carrol et al. 2003; Dordel 2005; Seidl et al. 2008; Katz 2017). Climate warming is considered to be a main driver for the recent range expansion and accelerated reproduction of the Mountain pine beetle in North America (Carrol et al. 2003; Mitton and Ferrenburg 2012). In Central Europe, artificial spruce plantations have recently facilitated the establishment and spread of *Ips duplicatus*, and more widespread outbreaks are predicted to increase (Petercord and Lemme 2019). Thus, we can also expect further expansion of the four-eyed fir bark beetle to neighboring regions. Due to the specific nature of local climate conditions, such as increasing aridity, Siberian fir forests along the Siberian Mongolian border region are naturally sparse and grow in only few mountain ranges in the region. The occurrence of an invasive bark beetle would add to already existing pressures on these dark coniferous ecosystems. In a study on spruce forests in northern Mongolia, James (2011) found a growth decline of spruce that was significantly connected with higher temperatures. Similarly, Gradel et al. (2018) reported a decline of spruce during a four-year monitoring interval of a dark coniferous forest outpost situated on a mountain top and surrounded by fire damaged Mountain forest steppe. In this stand, the spruces were gradually replaced by light taiga species, such as birch and larch (Gradel et al. 2018). Possible causes may be changes in water balance, short-term infestations of insects or warmer temperatures associated with global warming (Gradel et al. 2018). Spruce stands are known to be highly sensitive to temperature increase (Zang et al. 2011). Along these same lines, Kharuk et al. (2013) reported in their study of southern Siberia that among several species growing within the same stand, Siberian pines suffered from drought, whereas birch and aspen trees were not affected. The same authors pointed out that stand decline of Siberian pines (> 75 % tree mortality) mainly occurred on southern slopes, where the bark beetle appear to thrive. Exposition is therefore also of importance in terms of stands' susceptibility to disturbance, especially in the context of increasing temperatures. In a study on the relation between wild fires and infestation by the Silk moth (*Dendrolimus sibiricus* Tschetv.) in Siberia, Kharuk and Antamoshkina (2017) found that pest outbreak areas are up to seven times more often affected by fires compared to reference sites. Since fires are also expected to become more frequent throughout the region due to global warming (Tchebakova et al. 2011) we can conclude that the four-eyed fir bark beetle may very well represent an additional, potentially dangerous threat to the disturbance-sensitive dark coniferous ecosystem.

Despite considerable research of the problem of *P. proximus* invasion in Siberian fir forests, there are gaps that require further research. In particular, the mechanism of fir stability to the impacts of the four-eyed fir bark beetle at the physiological and biochemical levels has not been studied sufficiently. Specific features of the feed substrate (for example, its moisture content) on invasive bark beetle population are poorly assessed. In future research, the climatic conditionality of the mass reproduction of *P. proximus* needs to be understood better.

CONCLUSIONS

Our results indicate that stands with left-sided ontogenetic structure are less susceptible to invasion by the four-eyed fir bark beetle. Fir forests with right-sided structure are less stable and exhibit rapid degradation as a result of infestation. We established that there is a mechanism that drives invasions by the four-eyed fir bark beetle for stands of all types of ontogenetic structure, which is that these invasive insects primarily attack late virginal and young reproductive trees. Over time, these trees can completely vanish from communities, and mature and old productive trees can suffer extensive damage. During the mass reproduction phase, there is also significant loss of late immature and early virginal fir trees during the invasive insects' expansion phase (up to 50%).

The transformative role of an invasive beetle has its own rules that do not only depend on stand characteristics. Infestation by the four-eyed fir bark beetle largely causes tree death of second layer suppressed trees and thinner trees within the canopy. As a result, the total density of the stand is reduced and exceeds the rate of replenishment with new trees. We also showed that the most significant impact of the invasive bark beetle is on trees with diameters of up to average thickness levels (DBH < 30 cm). Fir trees with heart rot and more radial growth that are relatively small in diameter and have thinner bark are the first individuals targeted by the invasive four-eyed bark beetle and suffer the greatest damage. These factors that make these trees vulnerable (with the exception of age) should be assigned particular importance when considering the stability of fir forests against the four-eyed fir bark beetle.

Siberian fir forests have a good natural ability to regenerate despite stand weakening or full degradation. This fact leads us to conclude that fir stands in the infestation zone of southern Siberia will likely survive potential expansion of the range of the four-eyed bark beetle.

ACKNOWLEDGEMENTS

The reported research was funded by the Russian Foundation for Basic Research and the government of Tomsk region, grant № 16-44-700782 and as part of a State Assignment of the Center for Forest Ecology and Productivity, Russian Academy of Sciences (no. AAA-A-A18-118052400130-7).

The authors wish to thank Svetlana A. Krivets, Elvina M. Bisirova, Ivan A. Kerchev and Natalie A. Chernova (Institute of Monitoring of Climatic and Ecological Systems, Tomsk, Russia) for gathering data, branches of the Russian Forest Protection Center (Tomsk, Altai, Novosibirsk, Krasnoyarsk) for providing data on the distribution of the four-eyed fir bark beetle and Aimee Orsini (Berkeley) for language editing.

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Received on March 4th, 2019 Accepted on August 8th, 2019