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Regeneration of Pinus sibirica Du Tour as a result of trophic relationships with the thin-billed nutcracker (Nucifraga caryocatactes macrorhynchos Brehm C L)

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Abstract. Identifying the patterns of dynamics of natural populations of woody plants at the stage of their renewal is one of the main problems of forest ecology. The reforestation process is determined by both the dynamics of seed production and the specificity of seed dispersal of forest tree species. The five-needled pine renewal the Cembrae subsection with wingless seeds depends on birds of the genus Nucifraga sp., which store and spread their seeds. The aim of this study is to determine the relationship between seed production and regeneration of Pinus sibirica Du Tour using the thin-billed nutcracker (Nucifraga caryocatactes macrorhynchos Brehm C. L.) as a mediator. Long-term studies of these relationships have been carried out in the Siberian pine forests of the North Ural Mountains. As a result, a paradoxical conclusion is made that the number of Nucifraga birds during the period of storing and spreading of seeds in the previous year is a key factor in the abundance of Pinus sibirica seedlings. In turn, the number of seeds, both from the previous year and the current year, affects the number of Nucifraga birds.

1 Introduction

The world's forests are currently facing unprecedented challenges due to global climate change and intensive forest management [1-3]. On the one hand, ongoing studies show an improvement in the state of vegetation in various countries and regions [4-6]. On the other hand, forest cover is decreasing due to logging and fires. A search for the keyword "deforestation" in Mendeley returned 12,468 results in the last 5 years. This is undoubtedly an indicator of a significant amount of research into the problem of deforestation. Certainly, the biophysical effects of this process have global implications [7]. At the same time, the greatest scientific challenges, according to experts, lie in the stages of design, planning and evaluation of reforestation, which require an evidence base to optimize this process on a realistic scale [3]. Similarly, seed production and seed dispersal of forest tree species should be considered as a key step in the whole regeneration process.

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It is generally accepted that the processes of natural regeneration and population stability of the wingless seeded five-needle pines of the *Cembrae* subsection in the boreal dark coniferous forests of the northern hemisphere are due to the close mutualism with birds of the genus *Nucifraga* sp. Nutcrackers contribute to the regeneration and dispersal of these plants by creating seed banks in the soil and spreading seeds over long distances. Unfortunately, only individual links in the complex "seed-nutcracker-seedling" chain are addressed in the majority of studies on this topic. For example, there are studies focusing on the dynamics of yield and seed productivity of forest stands [8-11] or seed dispersal and storage by nutcrackers [12-13]. In some cases, only a general prediction is made as to how these factors affect the subsequent regeneration. The lack of comprehensive information on the relationships at all stages of the "seed-nutcracker-seedling" chain is quite acute. This information is needed to understand the mechanisms of regeneration and the ability of these pines to expand their range.

While anemochore forest tree species are characterised by a direct relationship between seedling production and the abundance of the previous year's crop, information on such relationships for five-needle pines with wingless seeds is rather inconsistent [14-15]. *Nucifraga* birds purposefully establish seed stores in specific micro-ecotopes with specific environmental conditions [16]. This is the difference to anemochore forest forming species and even many zoochore plants. Their seeds are accidentally deposited on a suitable substrate for germination. Therefore, a synecological and interdisciplinary approach, taking into account ornithological and zoopsychological considerations, is required to study the natural regeneration processes of five-needle pines of the *Cembrae* subsection, and not only the traditional silvicultural approach.

The aim of this study is to determine the relationship between seed production and regeneration of *Pinus sibirica* Du Tour using the thin-billed nutcracker (*Nucifraga caryocatactes macrorhynchos* Brehm C. L.) as a mediator.

2 Objects and methods of research

The long-term studies were carried out in the low-mountain province of the northern part of the middle taiga subzone of the eastern macroslope of the Urals (Novolyalinskoye forestry, Sverdlovsk reg. 59°18´N 59°20´E). The sample areas we laid under the canopy of green-moss dark-coniferous forests at an altitude of 450-600 m above sea level. The participation of *P. sibirica* in the selected 200-250-year-old forest stands is 30-60%. We selected forest areas that had not been exposed to any catastrophic effects (fires, mass windfalls, cuttings, etc.) during the last 30-40 years, which could affect the dynamics of *P. sibirica* regeneration.

Ecological conditions, abundance of undergrowth and seedlings of *P. sibirica* we counted on 50-80 accounting spots 5x5 m in size, systematically placed relatively evenly over the sample areas. Accounting spots we laid every 20 m within the same type of forest, at the same height in two or three parallel rows. We carried the quantitative records of *P. sibirica* regeneration for the period 1997-2018 out according to two parameters: the number of undergrowth "nests" (characteristic dense groups sprouted from a seed cache) and the number of individuals in them. The age of the undergrowth of *P. sibirica* we determined by the number of vertical annual growths of the terminal shoot with an accuracy of one year. The dynamics of the initial number of annual seedlings generations we reconstructed from the age structure of the undergrowth and the empirical coefficients of its survival curve [16].

The annual dynamics of relative yields of cones (containing an average of 50–80 seeds) was reconstructed on the basis of traces of fallen mature cones (“overgrowth scars”) at the base of annual shoots (cones per shoot (c/s)) of the corresponding calendar years [17]. For this purpose, we used 5-10 branches taken from the upper part of the crowns of 80-100 trees in the corresponding Siberian stone pine stands for the period 1996-2017.

Visual accounting of the relative occurrence of nutcracker for the period 1997–2018 were carried out annually for a 30-40-day period in August-September on permanent routes 7 km long in a strip 50 m wide, located on both sides of the running line [14]. The number of nutcrackers detected during one hour of counting we taken into account.

3 Results and discussion

For Siberian stone pine forests of the Northern Urals during the period under consideration (1996-2017), an indicator of high relative yield may be considered an average of 2.3-2.7 traces of fallen cones on an annual shoot (c/s). Cone yields of this level recorded in 1999, 2004, and 2012 (Fig. 1). These traces on the shoots are clearly visible after 15-17, sometimes up to 20 years. In different years, the number of cones on the shoot varies from 0 to 5. The average value of the relative yield of *P. sibirica* cones for this time period is 1.5 ± 0.14 traces of fallen cones on an annual shoot (c/s). Yield dynamics is characterized by high chronological variability (Cv = 46.5%). Under the canopy of the corresponding maternal stands, the total number of *P. sibirica* undergrowth that appeared on the moss cover (mainly *Pleurozium Schreberi* Brid with a projective cover of 75%) for the period 1997–2018 reaches an average of 3.0 thousand ind./ha in 2.0 thousand "nests"/ha. With an uneven "wave-like" dynamics of renewal (Cv = 50.0%), the average number of seedling generations for this period is 0.4±0.06 thousand ind./ha.

According to the literature data in the Urals, a certain cyclicity traced in the dynamics of *P. sibirica* yields was previously – abundant cone yields repeated after 5-6 years, alternating with average and reduced yields [9, 14, 17]. Such dynamics observed until about 2006 (Fig. 1). At the same time, according to previous studies for the period 1987-2007 [5] the number of generations of *P. sibirica* seedlings is positively correlated (R^2 = 0.59) with the value of the relative yield of cones the year before last (Fig. 2a). The so-called relative outbreaks of *P. sibirica* renewal occurred two years after the high harvest (Fig. 1).

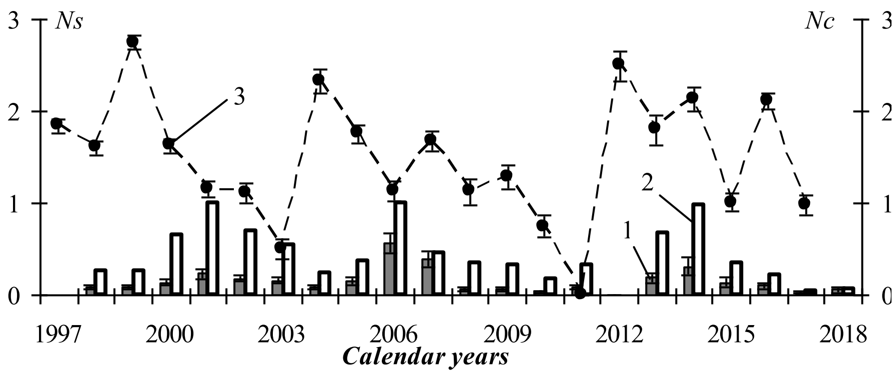

Fig. 1. Annual dynamics of relative cone crops (*Ns*) and regeneration (*Ns*) of *Pinus sibirica* in Siberian stone pine forests in the Northern Urals. 1 – number of undergrowth, thousand per ha; 2 – initial number of seedlings, thousand per ha; 3 – relative crops of cones (cones per shoot) with an average error (± m).

Approximately, since 2006-2007 there has been a change in yield dynamics (Fig. 1). Instead of the expected abundant yield in 4-6 years after the high-yielding year of 2004, there was a decline in 2009-2010, and absolute crop failure (0 cones per shoot (c/s)) in 2011. It should be noted, that in 2007 the number of complete germinating seeds with developed endosperm in cones was not more than 57%. In other normal years, their content is 93%. Therefore, the apparent average relative yield (1.7 c/s) in 2007 should be considered lower (approximately 1.1 c/s) than in 2006 and 2008. Thus, after the period 2006–2010 of relatively stable reduced yields (0.8–1.1 c/s) and an absolutely crop failure year 2011 are followed by three consecutive years (2012–2014) of increased yields and after a reduced yield (1.0±0.1 c/s) in 2015 – again the year of increased yield (2.1±0.08 c/s). Thus, the dynamics becomes relatively periodic. The frequency of harvest years is increasing (almost to annual), although sharp drops are observed.

After a high yield in 2012 (2.5 c/s), the number of seedlings in 2013 (0.7 thousand ind./ha) is less than two years later in 2014 (0.9 thousand ind./ha) – the next year after a less plentiful yield (1.8 c/s) (Fig. 1). There is also a decline and an extremely weak renewal of *P. sibirica* the next year after increased yields in 2014 and 2016 (2.1 c/s). However, in general, in this period, starting from 2007, there is a positive correlation (R^2 = 0.49) between the density of seedling generations and the relative yield of cones of the previous year (Fig. 2).

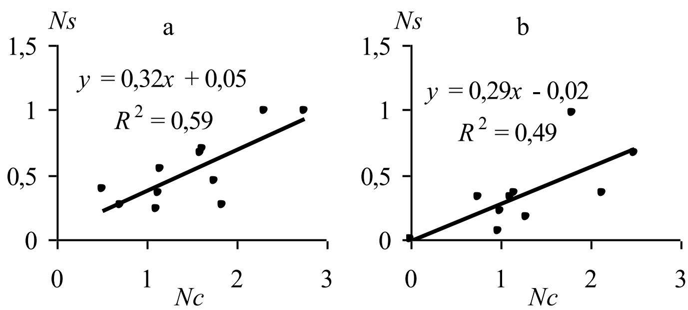

Fig. 2. Relationship between the number of seedlings (*Ns*) and the yield of cones (*Nc*) the year before last (**a**) for the period 1997-2006 and the yield of the previous year (**b**) for the period 2007-2018.

The reason for the revealed connection between the abundance of seedlings and the yield of the year before last, first of all, is seen in the presence soil bank of the *P. sibirica* seeds with their long dormant period and their germination after two winters. But this assumption is refuted by the positive dependence of the number of *P. sibirica* seedlings on the abundance of cones in the last year, which was established later. At first glance, it is quite natural and understandable and is characteristic of all anemochora forest-forming species. A good example is the lack of seedlings in 2012 after a completely lean year.

A correlation relationship differs from a functional relationship in that it fixes only parallelism in the variability of features. The source of such a connection may be the action of some third factors. In relation to our object, one of them is the activity of the nutcracker, as an intermediate link between seed production and renewal of *P. sibirica*. The conducted accounting of the relative abundance (occurrence) of the nutcracker during the period of harvest and distribution of seeds in August-September showed the following. Until about 2006, the fluctuations in the dynamics of its abundance to some extent repeat the sharp fluctuations in the jump-like impulse dynamics of the cone yields of the previous year (Fig. 3). This is confirmed by a significant (R^2 = 0.61) positive relationship (Fig. 4a). Such a delay is characteristic of the relationship of other plants with the main consumers of their seeds with similar impulsive dynamics of seed production [18]. It corresponds to well-known trophic relationships in the “predator-prey” or “producer-consumer” system. According to it after the sharp increasing of the main food base, the number of the predator in the next year naturally increases due to the young.

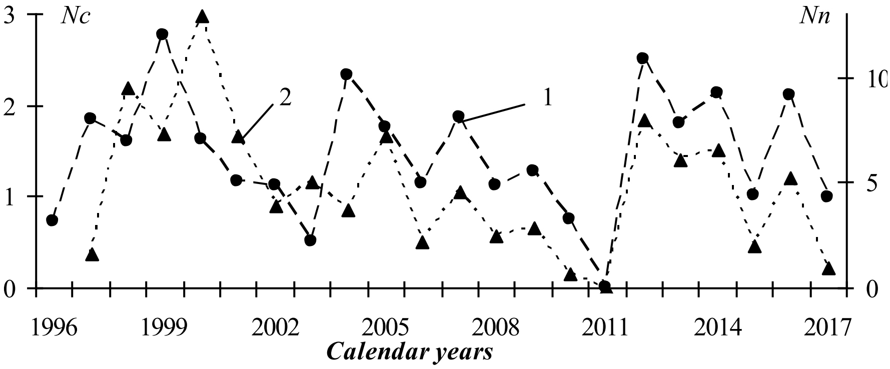

Fig. 3. Annual dynamics of *Pinus sibirica* relative cone crops (*Nc*), traces of fallen cones per annual shoot (1) and the relative nutcrackers number (occurrence) (*Nn*), individuals per hour (2), in the Northern Urals.

Changes in the dynamics of seed production, apparently, led to changes in the dynamics of the annual occurrence of nutcrackers during the period of seed harvesting. Since 2006, annual fluctuations in the dynamics of yields and occurrence of nutcracker become synchronous (Fig. 3). As a result, there is a close (R^2 = 0.91) relationship between their occurrence and the current year's yields (Fig. 4b). Such synchronicity is observed sometimes in fluctuations in the number of other consumers of *P. sibirica* seeds [8] due to their migrations in search of an abundant food supply.

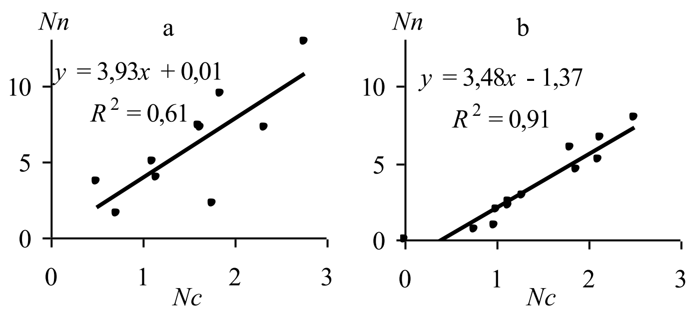

Fig. 4. Relationship between the relative number of nutcracker (*Nn*) and the yield of cones (*Nc*) of the previous year (**a**) for the period 1997–2006 and current year (**b**) for the period 2006–2017.

At the same time, there is a certain almost constant synchronism of fluctuations in the dynamics of *P. sibirica* renewal with fluctuations in the number (occurrence) of nutcrackers of the previous year during the period of seed harvest (Fig. 5). Accordingly, outbreaks in the number of seedlings are observed the next year after an increase in the occurrence of nutcracker, and a decline in renewal follows the next year after its reduction. As a result, there is a close (R^2 = 0.77) positive relationship between the relative abundance of *P. sibirica* seedlings and the relative abundance (occurrence) of nutcrackers (Fig. 6) in August-September of the previous year, during the period of active harvesting and seed dispersal.

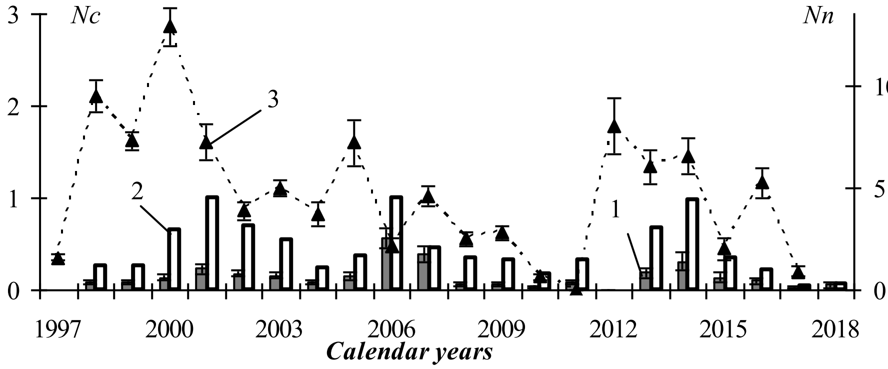

Fig. 5. Annual dynamics of the relative number of nutcracker (*Nn*) and *P. sibirica* renewal (*Nc*) in the Northern Urals. 1 – number of undergrowth with an error of average values (± m), thousand ind./ha, 2 – initial number of seedlings, thousand ind./ha, 3 – relative number of nutcrackers on the route (individuals per hour) with an error of average values (± m).

It may be assumed that the number of nutcrackers plays a more significant role in the regeneration of *P. sibirica* for the next year than the factor of seed productivity of Siberian stone pine forests.

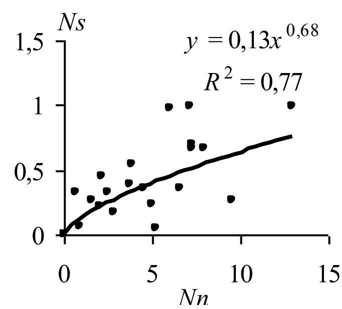

Fig. 6. Relationship between the number of seedlings (*Ns*) and the relative number of nutcrackers (*Nn*) in August-September of the previous year.

It is assumed that the nutcracker uses up to 85% of its reserves for food and feeding of chicks [8]. In this case, the bulk of seedlings appear from pantries not used by the nutcrackers due to their death or migration. A characteristic feature of birds is that, due to an increase in their population, their caution decreases, and they become more accessible to predators as prey [18], therefore, the number of dying birds is increases. In other words, the higher the number of nutcrackers in the region during the period of harvest of *P sibirica* seeds, the more they die during the winter. Consequently, the more seed storages will not be used by them and will germinate (for example, in 2001 and 2006). On the other hand, in lean years, the lack or instability of the food base can lead to a reduction in the number of birds and even to their refusal to nest [20]. In our case, this was observed in an absolutely lean year of 2011, when nutcrackers did not meet in the fall and did not nest in the next 2012. They began to appear only by August 2012. After a lean year, the subsequent high yield may not be fully utilized as stored feed by the few remaining consumers [21]. Consequently, with a plentiful harvest, but a small number of nutcrackers, the number of seed storages will not be high, and the number of seedlings for the next year will be insignificant (for example, in 1998 and 2005). In cases where the yield of the current year is lower than the previous one, its maximum use is observed, in this case, the storage of seeds by an increased number of birds [20]. Apparently, the minimum number of seedlings (no more than 0.1 thousand ind./ha) observed in 1999, 2015 and 2017. (Fig. 1) after average or increased yields is caused by the almost complete use of seed stocks by the nutcracker to feed a larger number of chicks (Fig. 5) and, possibly, by low mortality of birds.

The size of the nutcracker population directly depends on the density of seed trees and the number of cones in the region during the period of seed harvest [8, 13]. Nutcrackers can travel up to 650 km in search of their main food resources [22], and possibly even more. The migration of nutcrackers can also be caused by increased competition between them [23] with an increase in the number of birds after a plentiful yield and lack of food in the current year. Previously, it was found that the overall yield dynamics of *P. sibirica* in the mountainous and plain parts of the Urals and adjacent areas of Western Siberia is practically the same [9]. It is possible that fluctuations in the dynamics of seed production in these regions no longer coincided, which caused a change in the dynamics of the occurrence of nutcracker (Fig. 3) and the manifestation of a relationship with the crops of the current year (Fig. 4b). In all likelihood, sharp jumps in the annual dynamics of the occurrence of nutcracker and a change in its relationship with yields are caused both by quantitative changes in the local population and migrations of representatives of other regions. An example is the sharp increase (more than doubling) in the number of birds in 1998, 2000, 2007, 2012 and 2016, or sharp decline in 2001, 2006, 2010, 2015 and 2017 (Fig. 3). Apparently, the number of nutcrackers in a given region depends simultaneously on both the yield of the previous year and the yield of the current year (including in adjacent regions). In the first case, it affects the number of chicks in broods and a typical trophic relationship appears (Fig. 4a). Perhaps, the number is supplement by migratory birds in some years. In the second case, it causes the migration of birds, and fluctuations in their annual dynamics coincide with yields (Fig. 4b). At the same time, despite such changes and a significant variation over the years in the number of nutcrackers, the relationship of *P. sibirica* renewal with its relative abundance of the previous year during the period of seed storage remains unchanged (Fig. 6).

4 Conclusions

The results of many years of research into the regeneration of Siberian pine in the North Urals have led us to a paradoxical conclusion. The previous year's seed yield is not a key factor in the regeneration of *P. sibirica*. The number of *Nucifraga* in the previous year during seed collection and dispersal is much more important for the natural regeneration of this woody plant. In turn, the number of nutcrackers depends on the seed yield, both the previous and current year, and to some extent on the yields in neighboring regions. The reasons for the change in the population dynamics of the nutcracker and the change in its dependence on the number of seed yields, as well as the nature and intensity of the use of stocks, remain unclear. Therefore, further research is needed. The results of our research are important for restoring Siberian pine forests throughout the *Pinus sibirica* range.

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