



## ZOOCHORY AND PECULIARITIES OF FOREST COMMUNITY FORMATION: A REVIEW

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## ЗООХОРИЯ И ОСОБЕННОСТИ ФОРМИРОВАНИЯ ЛЕСНЫХ СООБЩЕСТВ: ОБЗОР

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**Abstract.** Based on the analysis of the literature on the home range of animals, information on the distances of diaspore dispersals by animals is provided for plants of coniferous-broadleaved forests. Mass and moderate dispersals of diaspores are important for formation of plant communities. Diaspores are moved in mass quantities within the diurnal areas of animals and in moderate quantities within the borders of seasonal areas. A continuous series is built on the range of mass dissemination of plant diaspores by animals, from tens of metres (small rodents) to one kilometre (large mammals). In coniferous-broadleaved forests three groups of plant species have been distinguished on adaptation to diaspore dispersals by animals. The first group includes plants with juicy fruits (e.g., *Malus sylvestris*, *Sorbus aucuparia*, *Vaccinium myrtillus*). A wide range of animals disperse diaspores of these plants at a distance of 20 m to 1,000 m, mainly in the endozoochoric way. The second group includes plants with large and dry seeds (e.g., *Corylus avellana*, *Fraxinus excelsior*, *Quercus robur*). The seeds of these plants are dispersed by animals that stock seeds at a distance of up to 500 m in the synzoochoric way. The third group includes plants with small and dry diaspores (e.g., *Aegopodium podagraria*, *Melica nutans*, *Stellaria holostea* et. all.). Their seeds can be moved by large birds, bears, ungulates in the endozoochoric way in large quantities at a distance of up to 1,000 m. Due to the extremely low number of those animals, plants with small and dry seeds have lost inter-



cenotic diaspore flows that are needed for changes of plant communities and for restoration succession. As a result, subclimax communities with a diminished species composition of plants are formed.

**Key words:** seed dispersal, diaspores, coniferous-broadleaved forest, zoothory, home range, succession

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**Annotation.** На основе анализа литературы по индивидуальным участкам животных приводятся данные о дальности перемещения семян животными для растений хвойно-широколиственного леса. Для формирования сообществ важны массовое и умеренное перемещение диаспор. Массово диаспоры перемещаются в пределах суточных участков животных, а умеренно – в границах сезонных. Выстраивается непрерывный ряд по дальности массового перемещения диаспор растений животными: от одного десятка метров (мелкие мышевидные грызуны) до одного километра (крупные млекопитающие). В хвойно-широколиственном лесу выделено три группы растений по адаптации диаспор к расселению животными. Первая группа – растения с сочными плодами (например, *Malus sylvestris*, *Sorbus aucuparia*, *Vaccinium myrtillus*). Они характеризуются широким набором животных, которые распространяют их семена эндозоохорным способом на расстояние от 20 до 1000 м. Вторая группа – растения с крупными и сухими плодами (*Corylus avellana*, *Fraxinus excelsior*, *Quercus robur* и др.). Распространители их семян ограничены животными, которые растаскивают семена синзоохорным способом. Дальность массового перемещения диаспор этих видов растений – до 500 м. Третья группа – растения с мелкими и сухими диаспорами (*Aegopodium podagraria*, *Melica nutans*, *Stellaria holostea* и др.). Их семена могут перемещаться крупными птицами, медведем и копытными эндозоохорным способом в массовом количестве на расстояние до 1000 м. Однако из-за чрезвычайно низкой численности этих животных растения с мелкими и сухими семенами лишились межценотических потоков диаспор, которые необходимы для смены растительных сообществ и восстановительных сукцессий. В результате формируются субклиматические ценозы с обедненным видовым составом растений.

**Ключевые слова:** распространение семян, диаспоры, хвойно-широколиственные леса, зоохория, индивидуальный участок животных, сукцессия.

## Introduction

The movement of diaspores is the basis of the population life of species and an essential condition for the formation of plant communities during successions [1–3]. Information on the distance of plant diaspore dispersals by different agents (above all, animals) is necessary for the study of successions and forecasts of forest communities development [4–6]. Animals play an active part in ecosystems and determine the species composition of communities by moving diaspores (seeds, fruits, vegetative germs, etc.) [7]. However, scientific publications about direct observation on distances of diaspore dispersals by animals are fragmentary. Information on the dissemination distance for different plant species is necessary to study successions [8, 9]. A possible solution to this problem is the determination of dissemination distance of zoothoric plant diaspores through the size of the individual areas of animal habitats (dissemination agents). So far, this approach has been only partially implemented in a small number of studies for a few plants [10, 11]. The tasks of the present study are 1) to assess distances of diaspore dispersals for the complex of forest plant species in connection with the territorial behaviour of animals and 2) to analyse some mechanisms of forest communities formation in connection with zoothory.

The objects of consideration are selected plant species from different layers of coniferous-broadleaved forests of Eastern Europe. The following indigenous vertebrate animals with different sizes of habitat areas were considered as disseminators of seeds: wisent or the European wood bison (*Bison bonasus* L.), brown bear (*Ursus arctos* L.), elk (*Alces alces* L.), roe deer (*Capreolus capreolus* L.), red squirrel (*Sciurus vulgaris* L.), yellow-necked mouse (*Apodemus flavicollis* Melchior), common field mouse (*A. sylvaticus* L.), bank vole (*Clethrionomys glareolus* Schreb.), wood grouse (*Tetrao urogallus* L.), European jay (*Garrulus glandarius* L.), spotted nutcracker (*Nucifraga caryocatactes* L.), greater spotted woodpecker (*Dendrocopos major* L.), fieldfare (*Turdus pilaris* L.), Eurasian nuthatch (*Sitta europaea* L.), willow tit (*Parus montanus* Baldenstein), marsh tit (*P. palustris* L.), and coal tit (*P. ater* L.). The choice of these animals was not accidental. The most complete information on the size of individual areas and species composition of food plants was found in the literature for these species. The main attention was paid to the summer-autumn home ranges of the animals because most of the diaspores ripen at that time. However, diaspores of some plants continued to disperse throughout the winter and spring, such as *Fraxinus excelsior* L., *Sorbus aucuparia* L. and *Picea abies* (L.) Karst. In this

case, areas of animal habitats in the autumn–winter and spring periods were analysed. The animal feed plant species were divided into three groups (forest, marsh, and meadow) to determine the characteristics of the food behaviour of animals.

### Results and discussion

**The scale of zochory.** It is possible to judge the actual participation of animals of coniferous–broadleaved forests in the propagula dissemination of zochoric plant species in the following numbers. The number of excrement allocated by one wisent per year is 5,000 kg, by elk 2,200 kg, and by roe deer 400 kg [12, 13]. From 500 to 2,500 viable seeds were found in one kg of excrement of grazing animals [14]. According to these data, excrements of bison of up to 13 million viable propagula per year, excrements of elk of up to 6 million viable propagula per year, and excrements of roe deer of up to 1 million viable propagula per year may be moved. In addition, 4.2 million raspberry seeds come with excrement of thrush (*Turdus* sp.) annually per hectare of forest areas [15]. Squirrels complete 300 pine and 30 spruce cones per day [16]. *Apodemus flavicollis* and *A. sylvaticus* stock up 2,200 acorns during the autumn months [17]. *Garrulus glandarius* moves up 20,000 acorns for storage during an autumn [18], and *Nucifraga caryocatactes* uses up to 430,000 seeds of *Pinus sibirica* Du Tour [19]. During the winter and early spring, *Dendrocopos major* collects 11,000 to 16,000 pine cones, which together contain 300,000 to 450,000 seeds [20]. *Parus mon-*

*tanus* stores 30,000 seeds during one month of autumn [21], *P. palustris* 17,000 seeds, and *P. ater* 6,000 seeds [22]. These numbers are specific to one individual animal to increase by orders of magnitude if they are converted to the number of the total population that lives in the coniferous–broadleaved forest.

**Significant for zochory features of trophic activity of animals.** The following issues of animal activities are important for diaspor dispersals of zochoric plant species: 1) eating of diaspores and their defecation; 2) storage of diaspores, in which part of the reserve is lost or not used; and 3) treatment of the skin of the trailer and adherent diaspores. Three variants of zochory are distinguished: endozoochory, synzoochory, and epizoochory. Endozoochory is the dispersal of diaspores that passed through the digestive tract of animals and were then ejected with excrements (Fig. 1–3). Synzoochory is the dispersal of diaspores associated with the movement by animals for the purpose of storage in the pantry or eating in the nests and on forges (e.g., of woodpecker) (Fig. 4–7). Epizoochory is the dispersal of diaspores that hitch or stick to animal bodies (Fig. 8) [7]. The included animal species are divided into two groups. The first group includes wisent, brown bear, elk, roe deer, wood grouse, and fieldfare. They spread diaspores mainly by the endozoochoric and epizoochoric ways. The second group includes red squirrel, mice, bank vole, jay, nutcracker, woodpecker, nuthatch, and tits. They spread diaspores mainly by the synzoochoric way.

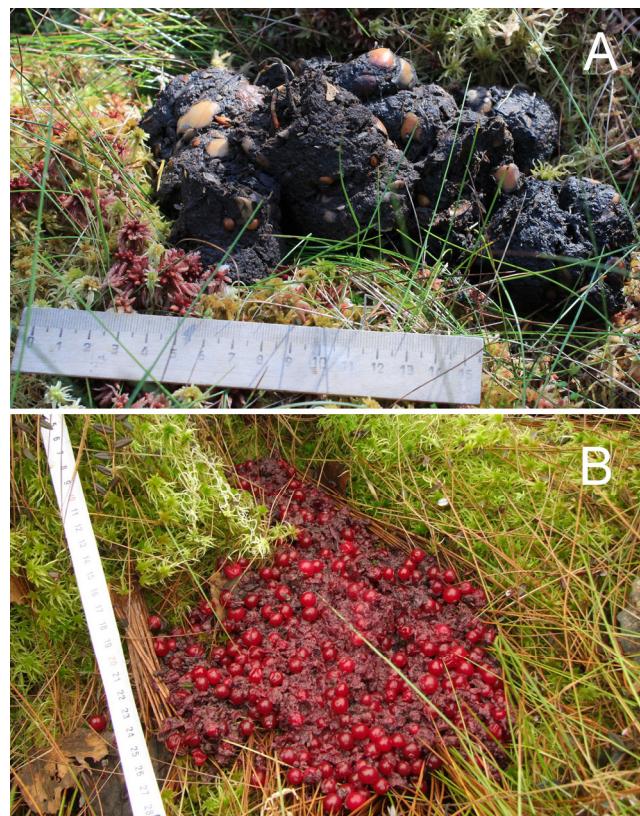


Fig. 1. Examples of endozoochoric dispersals of seeds and fruits by brown bear (*Ursus arctos*) in the Bryansk Forest Nature Reserve:  
A – Bear excrement with remains of apple fruit (*Malus sylvestris* Mill) and seeds of Solomon's seal (*Polygonatum multiflorum* (L.) All.);  
B – Bear excrement with cranberry berries (*Oxycoccus palustris* Pers.).  
Photos by Elena F. Sitnikova



Fig. 2. Examples of endozoochoric dispersals of seeds and fruits by wolf (*Canis lupulus L.*) in the Bryansk Forest Nature Reserve:  
A – Wolf excrement with cowberry (*Vaccinium vitis-idaea L.*) and seeds of lily-of-the-valley (*Convallaria majalis L.*);  
B – Wolf excrement with seeds and remains of apple fruit (*Malus sylvestris*) and pears (*Pyrus communis L.*). Photos by Elena F. Sitnikova



Fig. 3. Example of endozoochoric dispersals of seeds by birds. Jay (*Garrulus glandarius*) ingests the fruit of a guelder-rose (*Viburnum opulus L.*). Picture by Alina S. Teslyuk, a schoolgirl (17 years)

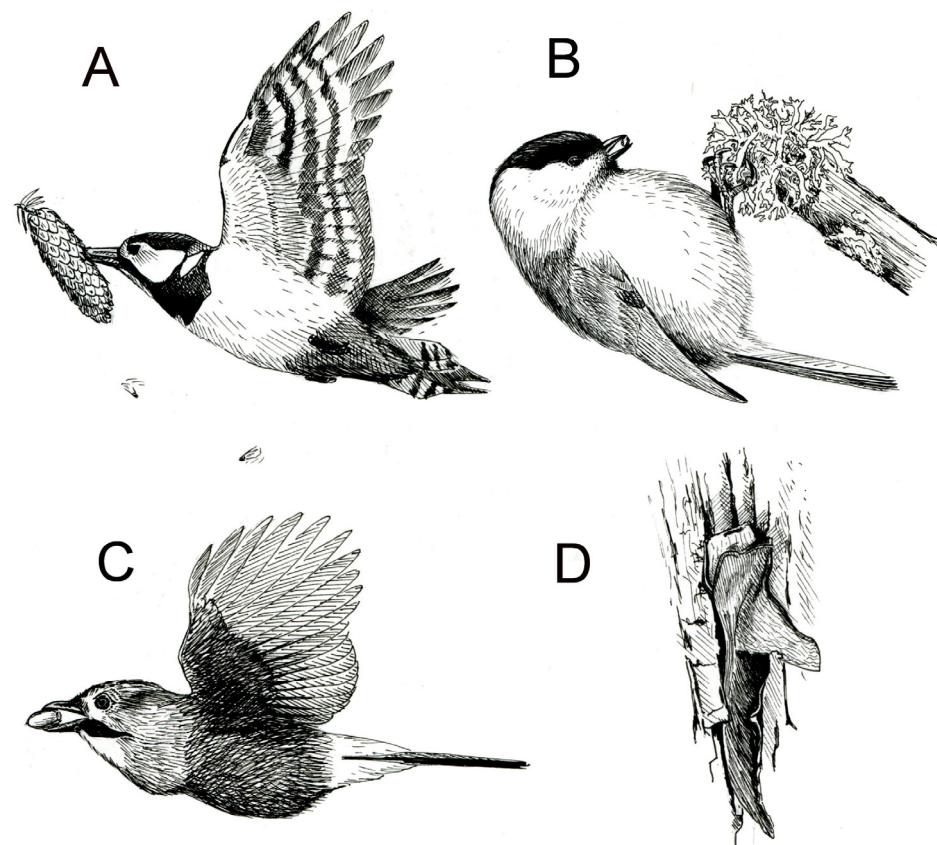


Fig. 4. Examples of synzoochoric dispersals of seeds:  
A – Greater spotted woodpecker (*Dendrocopos major*) carries a spruce cone (*Picea abies*);  
B – Willow tit (*Parus montanus*) hides a spruce seed (*Picea abies*) in lichen;  
C – Jay (*Garrulus glandarius*) moves an acorn of oak (*Quercus robur L.*) in front of expanded part of esophagus and in its beak;  
D – Samara of Norway maple (*Acer platanoides L.*) with eaten embryo;  
Eurasian nuthatch (*Sitta europaea*) puts samara in the tree bark.  
Pictures by Ilya A. Murashev



Fig. 5. Examples of synzoochoric dispersals of seeds in the Bryansk Forest Nature Reserve:  
A – Hazel nuts (*Corylus avellana L.*) stored and pecked by nuthatch (*Sitta europaea*) in the bark of oak (*Quercus robur*).  
Photo by Olga V. Solonina;  
B – Jay (*Garrulus glandarius*) ingests oak acorn found on gulli of wild boar (*Sus scrofa L.*).  
Photo by Alexey V. Gornov

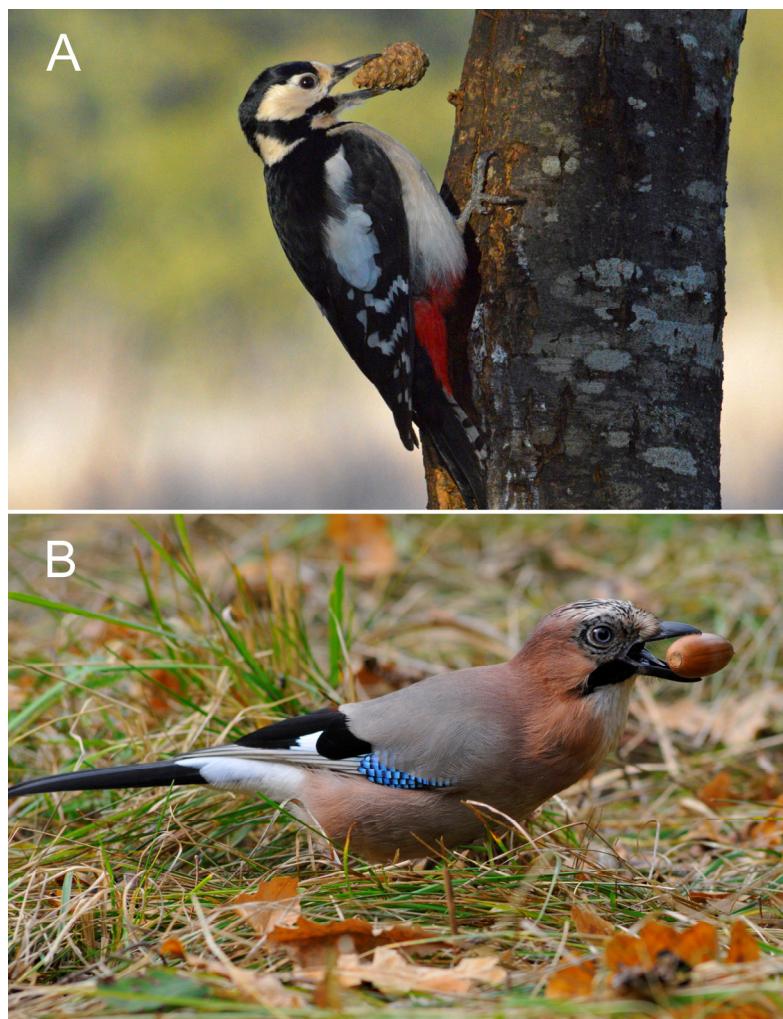


Fig. 6. Examples of synzoochoric dispersals of seeds:  
A – Female of greater spotted woodpecker (*Dendrocopos major*) with pine cone (*Pinus sylvestris L.*) finds suitable forge;  
B – Jay (*Garrulus glandarius*) wants to hide an acorn in the suitable pantry. Photos by Nikolay P. Shpilenok

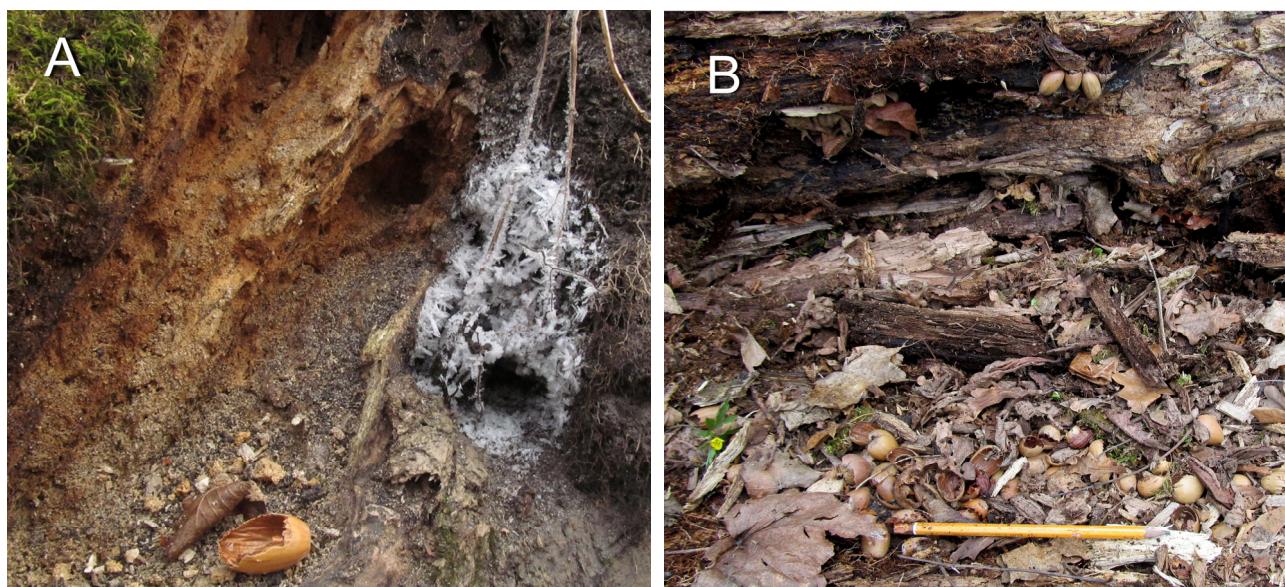


Fig. 7. Examples of synzoochoric dispersals of acorn (*Quercus robur*) by yellow-necked mouse (*Apodemus flavicollis*) in Nerussa-Sevniy zakaznik (Bryansk oblast):  
A – Shell of an acorn eaten near burrow; exit of inhabited holes covered in frost (end of November 2014);  
B – Eaten acorns in pantry under the deadwood; deadwood is raised (April 2015). Photos by Olga V. Solonina

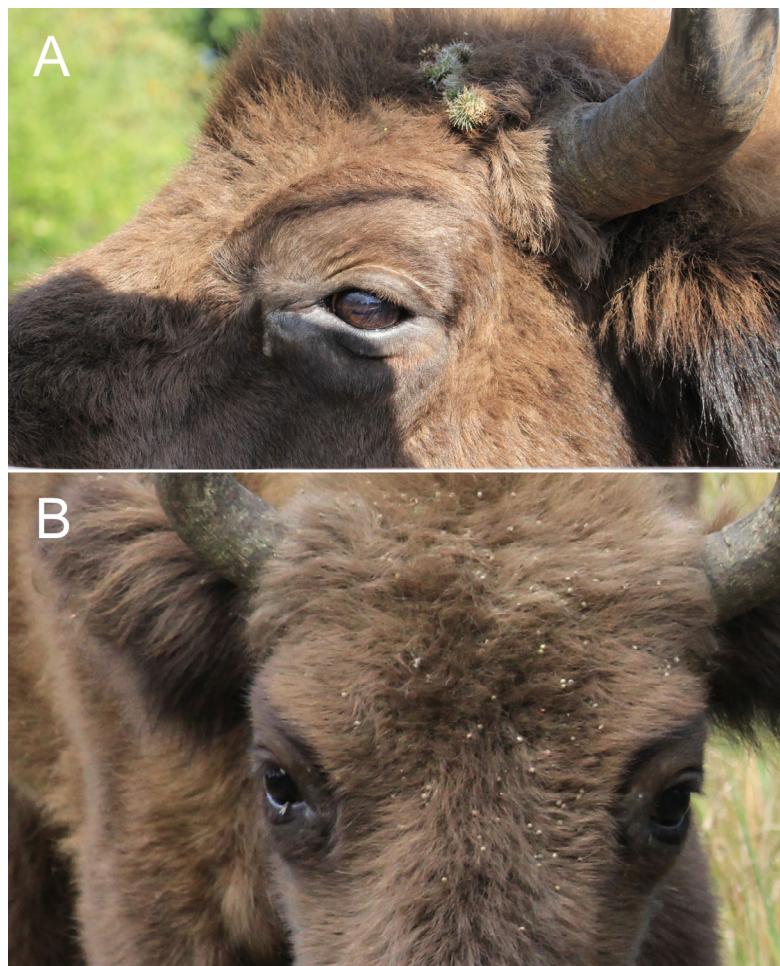


Fig. 8. Examples of epizoochoric dispersals of seeds by European wood bison (*Bison bonasus*) in the Bryansk Forest Nature Reserve:

A – Infructescence of great burdock (*Arctium lappa* L.) in bison wool;

B – Seeds of *Torilis japonica* (Houtt.) DC and other plants in the muzzle of a bison. Photo by Elena F. Sitnikova

Other necessary conditions for zoothochory and the formation of communities include 1) maintaining the viability of diaspores that have passed through the digestive tract of the animal and 2) underutilisation of collected and stocked diaspores. For instance, the viability of the seeds passing through the digestive system of *Turdus pilaris* is maintained at 70–100 %, *Garrulus glandarius* at 60–100 %, *Ursus arctos* at 30–100 % [23], and species of the family *Bovidae*, which include *Bison bonasus*, up to 95 % [7]. *Dendrocopos major* usually consumes no more than three-quarters of seeds [20], and the rest are dispersed or scattered with pine and spruce cones (see Fig. 4,A). Observations showed that *Nucifraga caryocatactes* consumes less than half of stored seeds [19, 24] and *Parus montanus* only one-fifth of stored seeds [21].

**The territorial behaviour of animals and zoothochory.** A few studies have shown that the distance of diaspore dispersals of zoothochoric plant species can be estimated indirectly through the size of home ranges of animals [10, 11]. With all the diversity, there are similarities in the territorial be-

haviour of animals. Two zones are usually distinguished within the home range of one animal or its family: 1) the centre, which is actively used and protected, and 2) the periphery, which is operated and protected only intermittently or not protected at all [25]. Animals tend to actively use and protect the nest sites and daily areas. It can be assumed that plant diaspore dispersals are carried in large quantities within the central zone and in moderate quantities or sporadically within the boundaries of the peripheral zone. The area of the animal's home range has a complex configuration. In this regard, estimates of diaspore dispersal distances in this article are based on two assumptions: 1) the animal's home range is a circle and 2) the maximum distance that the animal carries the diaspores corresponds to the radius of the area of the home range.

**Plant diaspore dispersals by animals in mass quantities.** The distance of mass dispersal of diaspores can be estimated through the dimensions (radius) of the animal's daily home range. This is due to the fact that the bulk of the diaspores usually pass through the digestive tract during the first

day: *Turdus pilaris* within 1–3 hours [23], *Ursus arctos* within 8–24 hours [26], *Alces alces* within 10–20 hours [27], *Capreolus capreolus* within 20–24 hours [28], and species of the family *Bovidae* within two days [29]. An epizoochory study showed that a significant portion of adhering diaspores (60–100 %) falls off from the fur of animals in the first days [30].

Judging by the sizes of the animal's daily areas, a continuous series of mass dispersals of diaspores

by animals is built (Table 1). *Bison bonasus*, *Alces alces*, *Ursus arctos*, and *Tetrao urogallus* move plant diaspores within 1 km; *Capreolus capreolus*, *Turdus pilaris*, and *Garrulus glandarius* 0,5 km; *Nucifraga caryocatactes* 200 m; *Sitta europaea* and *Parus palustris* 100 m; *Parus montanus*, *P. ater*, and *Sciurus vulgaris* 50 m; and small rodents 20–30 m. We can expect that plant regeneration would be the most successful within the diurnal areas of animals where mass dispersal of diaspores exists.

Table 1

## Sizes of animal individual areas and distances of plant diaspore disseminations

Animal species	Sizes of individual animal areas, ha			Distances of plant diaspore dispersals, m	
	Daily	Seasonal	Sources of information	in mass quantity	in moderate quantity
Animals that distribute diaspores mainly in the endozoochoric and epizoochoric ways					
<i>Bison bonasus</i> L.	70–400 <sup>1</sup>	1,100–11,000 <sup>1</sup>	[32, 36]	470–1,100	1,900–5,900
<i>Ursus arctos</i> L.	30–400 <sup>1</sup>	1,500–3,500 <sup>1</sup>	[37]	310–1,100	2,200–3,300
<i>Alces alces</i> L.	30–300 <sup>1</sup>	200–700 <sup>1</sup>	[13]	310–1,000	800–1,500
<i>Tetrao urogallus</i> L.	80–250 <sup>2</sup>	380–1,660 <sup>1</sup>	[38]	500–900	1,100–2,300
<i>Capreolus capreolus</i> L.	4–100 <sup>1</sup>	10–200 <sup>1</sup>	[13, 28]	110–560	220–860
<i>Turdus pilaris</i> L.	13–80 <sup>4</sup>	150–700 <sup>2</sup>	[22, 39]	200–500	700–1,500
Animals that distribute diaspores mainly in the synzoochoric way					
<i>Garrulus glandarius</i> L.	13–71 <sup>2</sup>	250–360 <sup>1</sup>	[22, 40]	200–470	900–1,100
<i>Nucifraga caryocatactes</i> L.	5–15 <sup>2</sup>	310 <sup>1</sup>	[22, 41]	130–220	1,000
<i>Dendrocopos major</i> L.	2–7 <sup>3</sup>	7–13 <sup>4</sup>	[20, 22]	80–150	150–200
<i>Sitta europaea</i> L.	1–3 <sup>2</sup>	18–35 <sup>1</sup>	[22]	60–100	240–340
<i>Parus palustris</i> L.	0,8–2,5 <sup>2</sup>	2,3–6,8 <sup>1</sup>	[22, 42]	50–90	90–150
<i>Sciurus vulgaris</i> L.	0,6–1,0 <sup>1</sup>	3,7–6,1 <sup>1</sup>	[43]	45–60	110–140
<i>Parus montanus</i> Baldenstein	0,5–1,2 <sup>2</sup>	5,0–10,5 <sup>1</sup>	[22]	40–60	130–180
<i>Parus ater</i> L.	0,4–0,6 <sup>2</sup>	2,0–3,1 <sup>1</sup>	[22, 44]	35–45	80–100
<i>Apodemus flavicollis</i> Melchior	0,06–0,12 <sup>1</sup>	0,15–0,29 <sup>1</sup>	[45, 46]	15–20	20–30
<i>Clethrionomys glareolus</i> Schreb.	0,04–0,20 <sup>1</sup>	0,10–0,48 <sup>1</sup>	[45, 47]	10–25	20–40
<i>Apodemus sylvaticus</i> L.	0,04–0,20 <sup>1</sup>	0,10–0,49 <sup>1</sup>	[48]	10–25	20–40

Note. Seasons: <sup>1</sup> summer – autumn, <sup>2</sup> autumn, <sup>3</sup> winter, <sup>4</sup> spring – summer. Distance of mass dissemination of diaspores was calculated as the radius of daily animal individual areas and the distance of moderate dissemination as the radius of seasonal animal areas.

**Plant diaspore dispersals by animals in moderate quantities.** Plant diaspores are moved in a moderate amount in the peripheral boundaries of habitats of the animal or its family (e.g., weekly or seasonal areas). Diaspores fall into the peripheral zone for different reasons. Firstly, the diaspores sometimes delay for some time in the digestive tract of the animal: in *Alces alces* up to two days [27], *Ursus arctos* and species of the family *Bovidae* up to four days [23, 29], and *Capreolus capreolus* up to six days [31]. Secondly, the animal clears its hair cover from adhering diaspores during the first few days or until the next molt. Thirdly, jays and nutcrackers soon collect a crop on their own site and continue to harvest in a neighbouring area [22]. Fourth, some animals rehide (hide in another place) part of the reserves usually [21].

The distance of moderate dispersal of diaspores can be estimated through the dimensions (radius) of the animals' seasonal home range. The range of seasonal areas is different. Accordingly, the distance of moderate dispersal of diaspores by different animal species is distinguished. A continuous series of moderate diaspores dispersal by animals is built. *Bison bonasus* and *Ursus arctos* move plant diaspores within 2–6 km; *Alces alces*, *Tetrao urogallus*, and *Turdus pilaris* within 1.5–2 km; *Capreolus capreolus*, *Garrulus glandarius*, and *Nucifraga caryocatactes* within 1 km; *Sitta europaea* within 300 m; *Dendrocopos major*, *Parus montanus*, *P. palustris*, *P. ater*, and *Sciurus vulgaris* in a radius of 100–200 m; and small rodents within 30–40 m (see Table 1). We can expect that plant regeneration will be satisfactory within sea-

sonal areas of animals where moderate dispersal of diaspores exists.

**Plant diaspore dispersals by animals in single quantities.** Long-distance movement of animals contributes to dispersal of individual plant diaspores over long distances. This distance can be estimated by the length of nomading or migrations of animals. For example, the extent of migration of *Bison bonasus* and *Alces alces* is 100–300 km and of *Capreolus capreolus* 10–70 km [13, 28, 32]. Adapting to changing environmental conditions, the animals change their feeding behaviour; for example, *Garrulus glandarius* and *Nucifraga caryocatactes* in a good oak fruiting year make reserves in a small area, and during a poor harvest of acorns they fly over long distances of 6 km or more [22, 33].

Long-distance dispersal of diaspores is necessary mainly for the expansion of the population area [34]. These movements are more common for species in which diaspores are attached to the animals (see Fig. 8), as well as for species with small seeds that can delay in the digestive tract for many days. Researchers who study dissemination believe that mass drift of diaspores is essential for the success of long-distance migration and for formation of communities at this distance, and cases of a single drift of seeds for tens of kilometres from the

mother plant do not have a special significance for the formation of plant communities [7, 35]. Based on the analysis of a large volume of scientific publications, Udra [2] attributes this to the fact that single-growing individuals with autogamy have extremely low seed productivity that does not allow them to form a complete population.

**The role of large animals in zoolochory.** Animals with large and small areas of home range play a different role in successional dynamics. Animals with large areas organise mainly inter-coenotic flows of diaspores. These flows are necessary to change the communities. Examples of such changes are 1) the formation of a forest community in a meadow and 2) the conversion of dark broadleaved nemoral communities to a light park forest with a steppeified herb cover. Two factors suggest that large animals move seeds from one community to another. Firstly, the feed of these animals includes plant species from different types of communities; species from forest, meadow, and marsh ecosystems are found in significant number in the food composition of European bison, elk, roe deer, brown bear, and wood grouse (Table 2). Secondly, the study of ungulate nutrition has showed that animals transfer a significant portion of seeds outside of the community, with bison at more than 80 % [49] and red deer at about 90 % [50].

Table 2

Number of plant species in animal feeds and their ecological-coenotic composition

Animal species	Number of plant species in animal feed	Main sources of information	Percent of plant species by ecological-coenotic groups		
			Forest	Water-marsh	Meadow, forest edge
<i>Bison bonasus</i> L.	385	[51–53]	24	16	60
<i>Capreolus capreolus</i> L.	256	[28, 31]	27	27	46
<i>Alces alces</i> L.	163	[54, 55]	29	35	36
<i>Tetrao urogallus</i> L.	156	[7, 18, 22, 38, 56]	35	26	39
<i>Ursus arctos</i> L.	144	[23, 26]	37	22	41
<i>Garrulus glandarius</i> L.	44	[7, 18, 22, 23, 57]	73	9	18
<i>Nucifraga caryocatactes</i> L.	41	[7, 18, 22, 57, 58]	68	20	12
<i>Turdus pilaris</i> L.	39	[7, 22, 23]	64	15	21
<i>Dendrocopos major</i> L.	32	[7, 22, 57]	88	6	6
<i>Sciurus vulgaris</i> L.	32	[7, 16–18]	78	9	13
<i>Sitta europaea</i> L.	17	[18, 22, 57]	82	–	18
<i>Parus palustris</i> L.	42	[18, 22, 57]	62	12	26
<i>Parus montanus</i> Baldenstein	31	[18, 22, 57]	58	6	36
<i>Parus ater</i> L.	21	[18, 22, 57]	76	5	19
<i>Apodemus flavicollis</i> Melchior	38	[7, 17, 23]	81	3	16
<i>Clethrionomys glareolus</i> Schreb.	32	[7, 17, 23]	72	6	22
<i>Apodemus sylvaticus</i> L.	28	[7, 17]	79	–	21

**The role of small animals in zoolochory.** Animals with a relatively small home range create mainly intra-coenotic flows of diaspores. These

flows are necessary to maintain the population within a community, for maintenance of the species diversity of a community, as well as for ensur-

ing propagula for microsuccession within community. Examples of intra-coenotic successions are 1) the regeneration of treefall gaps in a forest community and 2) the forming of plant microgroups in forests. Feed composition demonstrates that animals with a small home range move diaspores preferably within a community. Thus, plant species of forest communities dominated in the nutrition of *Garrulus glandarius*, *Nucifraga caryocatactes*, *Sitta europaea*, *Parus* sp., *Sciurus vulgaris*, *Apodemus* sp., and *Clethrionomys* sp. (Table 2). Additionally, it is known that *Nucifraga caryocatactes* hides no more than half of seeds outside *Pinus sibirica* forests [58, 59]. Observations in the Bryansk Forest nature reserve showed that *Garrulus glandarius* moves only one-third of seeds outside the forest community, *Sitta europaea* only one-fifth, and *Parus ater* and *P. palustris* just a small percentage of seeds [8].

#### Features of zoolochory in coniferous-broadleaved forests.

Three groups of plant spe-

cies were distinguished on adaptation to diaspore dispersal by animals (Table 3). The first group includes plants with juicy fruits (e.g., *Malus sylvestris*, *Sorbus aucuparia*, *Vaccinium myrtillus*). A wide range of animals disperse diaspores of these plants at a distance of 20 m (small rodents) to 1,000 m (large birds and mammals) in the endozoochoric and synzoochoric ways (see Fig. 1–3). The second group includes plants with large and dry seeds (e.g., *Corylus avellana*, *Fraxinus excelsior*, *Quercus robur*). The seeds of these plants are dispersed in the synzoochoric way by animals (small rodents, *Sciurus vulgaris*, *Parus* sp., *Sitta europaea*, *Garrulus glandarius*, *Nucifraga caryocatactes*) that stock seeds at a distance of 20 m to 500 m (see Fig. 4–7). The third group includes plants with small and dry diaspores (e.g., *Aegopodium podagraria*, *Melica nutans*, *Stellaria holostea* и др.). Diaspores of these species are dispersed by ungulates in the endozoochoric way in large quantities at a distance of up to 1,000 m (see Table 3).

Table 3

Examples of diaspore mass dispersal distances of coniferous-broadleaved forest plants by vertebrate animals [13, 16–18, 22, 23, 31, 33, 51, 52, 55, 56]

Plant species	Diaspore mass dispersal distance by animals <sup>1</sup> , m																																				
	<i>Apodemus flavicollis</i>	20	<i>Clethrionomys glareolus</i>	25	<i>Apodemus sylvaticus</i>	25	<i>Parus ater</i>	45	<i>Parus montanus</i>	60	<i>Sciurus vulgaris</i>	60	<i>Parus palustris</i>	90	<i>Sitta europaea</i>	100	<i>Dendrocopos major</i>	150	<i>Nucifraga caryocatactes</i>	220	<i>Garrulus glandarius</i>	470	<i>Turdus pilaris</i>	500	<i>Capreolus capreolus</i>	560	<i>Tetrao urogallus</i>	900	<i>Alces alces</i>	1000	<i>Ursus arctos</i>	1100	<i>Bison bonasus</i>	1100			
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18																				
Plants with juicy fruits disseminated in the endozoochoric and synzoochoric ways																																					
<i>Sorbus aucuparia</i> L.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+							
<i>Rubus</i> spp.	+	+	+			+	+	+		+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+							
<i>Malus sylvestris</i> Mill.	+	+	+				+	+	+		+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+							
<i>Vaccinium myrtillus</i> L.	+	+				+	+	+		+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+							
<i>Lonicera xylosteum</i> L.	+	+	+			+				+				+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+							
<i>Sambucus racemosa</i> L.	+	+	+						+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+							
<i>Frangula alnus</i> Mill.		+							+				+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+							
<i>Euonymus</i> spp.	+	+	+	+					+				+		+	+	+	+	+	+	+	+	+														
<i>Pyrus communis</i> L.	+							+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+							
<i>Convallaria majalis</i> L.	+	+												+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+							
<i>Swida sanguinea</i> (L.) Opiz	+			+																																	
Plants with large and dry diaspores disseminated in the synzoochoric way																																					
<i>Picea abies</i> (L.) Karst.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+							
<i>Acer</i> spp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+							
<i>Pinus sylvestris</i> L.	+				+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+							
<i>Tilia cordata</i> Mill.	+	+	+			+	+	+		+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+							
<i>Quercus robur</i> L.	+	+	+					+		+		+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+							

End of table 3

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>Corylus avellana</i> L.	+	+	+			+		+	+	+	+						
<i>Fraxinus excelsior</i> L.	+	+	+		+		+	+	+	+	+						
<i>Carpinus betulus</i> L.	+			+			+	+	+	+	+						
<i>Ulmus</i> spp.	+	+	+					+	+								
Plants with small and dry diaspores disseminated mainly in the endozoochory way																	
<i>Carex pilosa</i> Scop.												+	+	+	+	+	+
<i>Lathyrus vernus</i> (L.) Bernh.	+	+										+	+	+	+	+	+
<i>Geum urbanum</i> L. <sup>2</sup>	+											+	+	+	+	+	+
<i>Milium effusum</i> L.												+		+	+	+	+
<i>Festuca</i> spp.												+	+		+	+	+
<i>Melica nutans</i> L.												+	+				+
<i>Galium</i> spp. <sup>3</sup>												+	+		+	+	+
<i>Stellaria</i> spp.												+	+	+	+	+	+
<i>Aegopodium podagraria</i> L.												+	+	+	+	+	+
<i>Pulmonaria obscura</i> Dumort. <sup>4</sup>						+						+	+	+	+	+	+
<i>Viola</i> spp. <sup>4</sup>					+							+	+		+	+	+

Note. <sup>1</sup> Seed dispersal distance is equal to radius of daily animal individual area (see Table 1). <sup>2</sup> The species also adapted to epizoochory. <sup>3</sup> Some species adapted to epizoochory. <sup>4</sup> Species also adapted to myrmecochory. «+» – Plants that are marked as part of animal feed.

However, current numbers of most large animals are negligible or zero in coniferous-broadleaved forests due to human activity. Consequently, participation of plant species with small and dry diaspores has become unlikely in succession outside native forests. The seeds of these species are dispersed only by animals with small home ranges (ants, small rodents, tits) at a distance not exceeding 60 m. Thus, in the modern vegetation cover, inter-coenotic flows of diaspores are practically absent for plants with small and dry seeds, which are necessary for expansion of the population area, avoidance of unfavourable changing conditions in the plant community, and participation in successions. The extremely low number of populations and incomplete species composition of large animals that disperse plant diaspores are reasons for the formation of subclimax forests with poor plant species composition [4, 5, 53, 60–64].

### Conclusion

Mass and moderate dispersals of plant diaspores by animals are important for the formation of plant communities, but long-distance dispersals of single diaspores are significant for expansion of the habitat area of plant populations. Mass and moderate diaspore dispersals of zoolochoric plant species are carried within the individual home ranges of animals, and a single dispersal in the course of long-distance movements of animals during migrations. The distance of mass and moderate

dispersals of zoolochoric plant diaspores can be assessed by the size of individual home ranges of animals, and a single dispersal by the length of migrations.

The role of zoolochory in population and community life depends on the distance of plant diaspore dispersals by animals. The dispersal distance may be smaller or larger than the size of communities. If diaspores move within the community, zoolochory helps maintain populations within the community and conserve the species diversity of the plant community. If diaspores are transferred outside of community limits, zoolochory introduces populations in other communities and creates conditions for changes of coenoses.

The diversity and high number of animals with their different sizes of home ranges introduce a maximum number of seeds, fruits, and vegetative propagula into diaspore streams. The reduction in species diversity and abundance of animals (dissemination agents) due to human activity limits the participation of zoolochoric plant species in successions, significantly weakens inter-coenotic flows of diaspores, and leads to the formation of subclimax communities with diminished species diversity.

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