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PHYTOCOENOTIC PORTRAIT OF THE EUROPEAN BADGER

O. I. Evstigneev¹, O. V. Solonina^{1,2}

¹ State Nature Reserve "Bryanskii Les", Nerussa Station, Bryansk Oblast, 242180, Russia
E-mail: quercus_eo@mail.ru

² Center for Forest Ecology and Productivity of the Russian Academy of Sciences,
84/32 Profsojuznaya street, Moscow, 117485, Russia
E-mail: caniformia@mail.ru

Abstract. The European badger takes part in creating intracoenotic and intercoenotic flows of plant diaspores. This is evidenced by the fact that its diet includes plant species belonging to different communities, i.e. forest, meadow, marsh and water communities. Badgers move plant diaspores in three different ways: endozoochory, epizoochory, and synzoochory. Therefore seeds of the maximum number of plant species with various adaptations for zoochory are involved in diaspore flows. It has been proved that badgers can move large amount of diaspores over a distance of one kilometer, and in smaller amounts – up to two or three kilometers. Because of the badgers' foraging and construction activities, the species diversity of vascular plants in their settlements has increased by one and half times. Thanks to badgers, the plant species composition of the community becomes mixed. Plant species of the meadow, black alder, boreal and piny ecological-coenotic groups co-dominate in the ground cover of nemoral forests. Badgers searching for food disturb the soil cover and create a mosaic of the ground vegetation cover throughout the family's habitat which amounts to several hundred hectares. This heterogeneity includes three types of microcommunities: 1) with a predominance of vegetatively immobile annual and biennial plants of the ruderal group (*Alliaria petiolata*, *Geranium robertianum*, *Lactuca serriola*, *Moehringia trinervia*, *Polygonum convolvulus*, etc.); 2) with a predominance of vegetatively mobile perennials of the ruderal group (*Galium odoratum*, *Glechoma hederacea* and *Stellaria holostea*), and with a significant participation of phytoceenotically tolerant plants (*Asarum europaeum*, *Polygonatum multiflorum*, *Pulmonaria obscura*, *Viola mirabilis*, etc.); 3) with a predominance of the vegetatively mobile perennials of the competition group (*Aegopodium podagraria*, *Carex pilosa*, and *Convallaria majalis*). This sequence of microcommunities is a microsuccession. Competitive species are the driving force of group development as they gradually crowd out ruderal and tolerant plant species. Competitive species can become a dominant in the ground vegetation cover for a long time. However, the badgers' use of the community territory according to the "shift" system occasionally interrupts these unidirectional microsuccessions. The disturbances created by badgers and cyclical microsuccessions maintain the multispecies composition in the herbaceous cover of forest communities. These facts indicate that earlier the badger was an edificator (key species) in the ground vegetation of undisturbed biocenotic cover. Recently, however, due to overhunting and relentless poachers' attacks, the badger has become a rare endangered species. This animal is not an active environment-transforming part of the community anymore and it as good as stopped active moving of plant diaspores, which is needed for coenotic restoration.

Keywords: European badger, *Meles meles*, zoochory, species diversity of communities, environmental transformation, mosaic of ground vegetation cover, microcommunities, microsuccession, coniferous-deciduous forest.

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ФИТОЦЕНОТИЧЕСКИЙ ПОРТРЕТ БАРСУКА ЕВРОПЕЙСКОГО

О. И. Евстигнеев¹, О. В. Солонина^{1,2}

¹ Государственный природный биосферный заповедник «Брянский лес»,
Россия, 242180, Брянская область, станция Нерусса
E-mail: quercus_eo@mail.ru

² Центр по проблемам экологии и продуктивности лесов РАН,
117485, Россия, г. Москва, ул. Профсоюзная, 84/32
E-mail: caniformia@mail.ru

Аннотация. Барсук участвует в создании внутриценотических и межценотических потоков диаспор растений. Об этом свидетельствует присутствие в его рационе видов, принадлежащих к разным сообществам: лесным, луговым, болотным и водным. Барсук перемещает диаспоры растений тремя способами: эндозоохорным, эпизоохорным и синзоохорным. Благодаря этому в потоки диаспор вовлекаются семена максимального числа видов растений с разнообразными приспособлениями к зоохории. Показано, что барсук может перемещать диаспоры в массовом количестве на расстояние до одного километра, а в умеренном – до двух-трех. Трофическая и строительная деятельность барсука увеличивает видовое разнообразие сосудистых растений на поселениях в полтора раза. Благодаря этому животному флора в сообществе становится смешанной. В травяном покрове неморальных лесов начинают содоминировать луговые, черноольховые, бореальные и боровые виды. Занимаясь поисками пищи, барсук нарушает почвенный слой и создает мозаику травяного покрова на всем пространстве обитания семьи, которое составляет несколько сотен гектар. Эта гетерогенность состоит из трех вариантов микрогруппировок: 1) с преобладанием вегетативно неподвижных однолетников и малолетников реактивной группы (*Alliaria petiolata*, *Geranium robertianum*, *Lactuca serriola*, *Moehringia trinervia*, *Polygonum convolvulus* и др.); 2) с доминированием вегетативно подвижных многолетников реактивной группы (*Galium odoratum*, *Glechoma hederacea* и *Stellaria holostea*), а также со значительным участием фитоценотически толерантных растений (*Asarum europaeum*, *Polygonatum multiflorum*, *Pulmonaria obscura*, *Viola mirabilis* и др.); 3) с господством вегетативно подвижных многолетников конкурентной группы (*Aegopodium podagraria*, *Carex pilosa* и *Convallaria majalis*). Эта последовательность микрогруппировок представляет собой микросукцессию. Движущей силой развития группировок выступают конкурентные виды. Они постепенно вытесняют реактивные и толерантные растения. Конкурентные виды могут надолго стать доминантами травяного покрова. Однако использование барсуками территории сообщества по «переложной» системе периодически прерывает эти однонаправленные микросукцессии. Благодаря нарушениям, которые создают барсуки, и циклическим микросукцессиям поддерживается многовидовой состав в травяном покрове лесных сообществ. Приведенные факты свидетельствуют о том, что барсук в нарушенном биоценотическом покрове был эдификатором (ключевым видом) в ярусе трав. Однако в последнее время из-за перепромысла и упорного преследования браконьерами барсук превратился в редкое исчезающее животное. Этот зверь перестал быть активным средообразователем в сообществе и практически полностью прекратил перемещать диаспоры растений, которые необходимы для восстановления ценозов.

Ключевые слова: барсук европейский, *Meles meles*, зоохория, видовое разнообразие сообществ, средообразование, мозаичность травяного покрова, микрогруппировка, микросукцессия, хвойно-широколиственный лес.

Introduction

Understanding the mechanisms of biological diversity maintenance in nature is the basis for developing methods of rational nature management. Climax (undisturbed) biogeocoenoses of pre-agricultural times differing in their maximum species diversity are highly suited for revealing these mechanisms. However, centuries of human activity have eliminated undisturbed coenoses within the territory of Europe [1, 2]. This makes the reconstruction of the climax structure of individual communities and the entire biogeocenotic cover an important ecological task. Revealing the mechanisms of biological diversity maintenance associated with the vital activity of populations of the remaining edificators [3, 4] is one of the possible ways of such reconstruction. One of the edificators in the forest zone of Central Russia is the European badger (*Meles meles* Linnaeus, 1758), which has recently become extremely rare due to overhunting and poaching [5].

The purpose of this paper is to analyse the role of the badger in the formation and maintenance of structural and species diversity of the vegetation cover.

Study objects, area and methods

Object of research. The article focuses on the European badger (Fig. 1) and its effect on vegetation. The research was carried out in the *Bryanskii Les* reserve and the surrounding area. There are 13 known used and abandoned settlements¹ of this animal [6]. The badger is on the list of endangered species of Bryansk oblast [5]. Although it is a forest predator, it can also be found in non-forest areas. It is omnivorous and feeds on both animals and plants [7].

¹ Following in the footsteps of Yu. S. Lobachev [8], we understand settlement as a sett or a group of setts that are occupied by a lone badger or a badger family. Synonyms of this concept are "town" [9], "badger sett" [10], "colony" [11] or "den" [12]. Large settlements are sometimes called "fortresses" [13].

Fig. 1. Object of study, the European Badger (*Meles meles* Linnaeus, 1758). Image by Aleksey Subbotin [14]. The drawing was made with a lead pencil

Study area. The research was mainly carried out in the south-east of Bryansk oblast in the Nerusso-Desnyanskoye Polesie. According to the phytogeographical division, this physiographical region is a northern broad-leaved forest with a small participation of spruce trees, belonging to the Polesie sub-province of the Eastern European province of the European broad-leaved forest region [15]. Additionally, edificatory properties of the badger were studied on the territory of the *Markovskiy Gory* and *Pechnoye* natural monuments. The first monument is located within the Pogarskoye high plains and the second one in the Komarichsko-Sevsky physiographical region. A phytogeographical description of these monuments has been provided earlier [16]. All research sites are part of the Central Russian region of the province of mixed forests of the boreal-forest sub-district of the Palearctic region [17] in terms of zoogeography.

Methods of research. Two groups of geobotanical descriptions were made at badger settlements. In the first group, rectangular plots of 100 m² each were established at each settlement. At the same time, a control plot was established outside the settlement, where the impact of the badger was minimal. In both cases, three layers of the forest were characterised, i.e. the forest stand, undergrowth and underbrush, as well as herbaceous cover. Nine descriptions were made for settlements and control sites. Establishment of the plots for the second group of descriptions was preceded by a preliminary typing of the mosaic pattern of the herbaceous cover surrounding the settlements, according to the degree of disturbance by badgers. Three mosaic pattern types were identified. The first type included sites with 90 to 100 % disturbance of the herbaceous cover, the second had sites with 40 to 90 % disturbance, and the third site had 1 to 40 %. We generated a disturbance gradation-based map

of the herbaceous cover around badger settlements via GPS and MapInfo. Each type of the herbaceous cover mosaic involved establishing rectangular areas of 1 m². In total, 56 descriptions were completed: 14 in the first site type and 21 both in the second and third types. The Braun-Blanquet scale was used to evaluate the participation of species in all groups of geobotanical descriptions [18]. The occurrence of species in the community was expressed in points with equal classes: class I corresponds to occurrence from 1 to 20 %, class II to occurrence from 21 to 40 %, class III to 41 to 60 %, class IV to 61 to 80 %, and class V to 81 to 100 %. Species names are given according to Maevsky [19].

Geobotanical descriptions were used to assess the diversity of communities, i.e. species richness of vascular plants, species density, distribution of species by ecological-coenotic groups and types of plant strategies. Species richness is the number of species in a single community type and defined as the total number of species on all sites belonging to one type of coenosis. Species density is the arithmetic mean of species on fixed-size plots obtained from all descriptions of a single community type [20]. Following in the footsteps of Nitsenko [21], we understand ecological-coenotic groups (ECGs) as large groups of ecologically related species, which in their genesis are associated with different types of communities. We used the classification of species by ECGs, which was developed for the European part of Russia [22] and is available on the website of the Institute of Mathematical Problems of Biology of the Russian Academy of Sciences (<http://www.impb.ru/index.php?id=div/lce/ecg>). We understand the type of plant strategies as the potential ability of a species to dominate or occupy a subordinate position in the community which had developed as a result of long-term evolution in pre-agricultural climax cenoses [23]. To assign species to a particular type of plant strategies, we used the classification developed by Smirnova [24]. In this paper, the ratio of the number of species by ECGs and plant strategies types was determined based on the list of all species found in one variant of the community.

Results and discussion

Omnivory is a feature of badgers and significant for vegetation cover in two aspects. First, eating plant diaspores², badgers spread the parts that

² Diaspore (disseminule) is a part of the plant that provides propagation, reproduction and dispersal of the species [25, 26]. Diaspores can be represented by seeds, fruits, infructescences, vegetative disseminules and other parts of the plant [27, 28].

are necessary for the successional development of communities. Second, foraging for small animals and underground parts of plants, the badger digs the upper soil layer and creates a mosaic structure of the herbaceous cover, which has to be formed constantly to maintain species diversity of cenoses.

Badgers and the composition of plant feed

Data on the species composition of plants that the badger feeds on are important for studying successions in the vegetation cover. This is because, together with the plants, the badger swallows their diaspores and transfers them to a certain distance. At the same time, finding out the composition of plant food allows us to identify badger habitats with the optimal combination of communities.

Literature analysis has shown that the badger's diet contains more than 70 species of vascular plants of natural flora (Table 1). The majority – 60 % – belongs to forest species. It is for a reason that zoologist Jurgenson emphasises the forest features of a badger: smell, hearing and touch are its best developed senses; like many forest predators, it is short-sighted but sees perfectly at a short distance [29]. Detailed analysis of the feed has revealed that forest plants included both nemoral and boreal species. Examples of nemoral plants are *Cerasus avium*, *Convallaria majalis*, *Cornus sanguinea*, *Euonymus europaea*, *Malus sylvestris*, *Viburnum opulus*, *Padus avium*, *Pyrus communis*, *Sambucus nigra*, among others. Examples of boreal plants are *Frangula alnus*, *Rubus idaeus*, *R. nesciensis*, *R. saxatilis*, *Sorbus aucuparia*, *Vaccinium myrtillus*, *V. vitis-idaea*, among others. This indicates that a badger originally inhabits mixed coniferous-broad-leaved forests. According to modern geobotanical concepts, pure coniferous and broad-leaved forests have evolved from mixed coniferous-broad-leaved communities as a result of human activity [1, 30]. It should be emphasised that there is a significant proportion of meadow species in the feed, i.e. 26 %. There are also black alder, sphagnum and water-accompanying plants, with a total participation of 14 % (see Table 1). This means that important badger habitats, apart from coniferous-broad-leaved forests, include dry and wet meadows and clearings, lowland and upland swamps, as well as water communities. No wonder zoologists outline that the optimal badger biotope is a mosaic vegetation cover where forests of different types alternate with meadows, clearings, forest edges, swamps and floodplains of streams [7, 31]. Meadows and clearings in forests are currently created and maintained by humans, whereas in pre-agricultural times, they were formed under the influence of foraging and migration of large gregarious ungulates that largely inhabited coniferous-broad-leaved forests [1].

Table 1

Plant species composition in the European Badger's diet in the forests of Eastern Europe

Ecologico-cenotic groups		Plant species or genus
Forest (43)	Nemoral (31)	<i>Acer platanoides</i> L., <i>Acer pseudoplatanus</i> L., <i>Allium ursinum</i> L., <i>Betula pendula</i> Roth, <i>Carex pilosa</i> Scop., <i>Carpinus betulus</i> L., <i>Cerasus avium</i> (L.) Moench, <i>Convallaria majalis</i> L., <i>Cornus sanguinea</i> L., <i>Corydalis solida</i> (L.) Clairv., <i>Corylus avellana</i> L., <i>Dentaria quinquefolia</i> Bieb., <i>Euonymus europaea</i> L., <i>E. verrucosa</i> L., <i>Fagus sylvatica</i> L., <i>Festuca</i> sp., <i>Fraxinus excelsior</i> L., <i>Gagea lutea</i> (L.) Ker-Grawl., <i>Galathus nivalis</i> L., <i>Lilium martagon</i> L., <i>Luzula sylvatica</i> (Huds.) Gaudin, <i>Malus sylvestris</i> L., <i>Mercurialis perennis</i> L., <i>Padus avium</i> Mill., <i>Populus tremula</i> L., <i>Pyrus communis</i> L., <i>Quercus robur</i> L., <i>Sambucus nigra</i> L., <i>Taxus baccata</i> L., <i>Tilia</i> sp., and <i>Viburnum opulus</i> L.
	Boreal, piny (12)	<i>Cornus alba</i> L., <i>Frangula alnus</i> Mill., <i>Juniperus communis</i> L., <i>Picea abies</i> (L.) Karst., <i>Pinus sibirica</i> Du Tour, <i>P. sylvestris</i> L., <i>Rubus idaeus</i> L., <i>R. nessensis</i> W. Hall, <i>R. saxatilis</i> L., <i>Sorbus aucuparia</i> L., <i>Vaccinium myrtillus</i> L., and <i>V. vitis-idaea</i> L.
Black alder, sphagnum, water (10)		<i>Alnus glutinosa</i> (L.) Gaertn., <i>Lemna minor</i> L. s.l., <i>L. trisulca</i> L., <i>Oxycoccus palustris</i> Pers., <i>Phragmites australis</i> (Cav.) Trin. ex Steud., <i>Potamogeton</i> sp., <i>Ribes</i> sp., <i>Salix</i> sp., <i>Typha</i> sp., and <i>Urtica dioica</i> L.
Meadow, forest-edge (19)		<i>Allium</i> sp., <i>Capsella bursa-pastoris</i> (L.) Medik., <i>Cerasus fruticosa</i> Pall., <i>Cirsium</i> sp., <i>Crataegus</i> sp., <i>Crocus heuffelianum</i> Herb., <i>Equisetum</i> sp., <i>Fragaria vesca</i> L., <i>F. viridis</i> (Duch.) Weston, <i>Hedysarum</i> sp., <i>Lamium album</i> L., <i>Potentilla anserina</i> L., <i>Prunus spinosa</i> L., <i>Ranunculus</i> sp., <i>Rhamnus cathartica</i> L., <i>Rubus caesius</i> L., <i>Rosa canina</i> L., <i>Trifolium</i> sp., and <i>Tulipa</i> sp.
Cultural, adventitious (28)		<i>Amelanchier</i> sp., <i>Armeniaca vulgaris</i> Willd., <i>Avena sativa</i> L. s. l., <i>Beta vulgaris</i> L., <i>Castanea sativa</i> Mill., <i>Cerasus vulgaris</i> Mill., <i>Citrullus lanatus</i> (Thunb.) Matsum. et Nakai, <i>Cucumis sativus</i> L., <i>C. melo</i> L., <i>Cucurbita pepo</i> L., <i>Daucus sativus</i> (Hoffm.) Roehl., <i>Fagopyrum esculentum</i> Moench, <i>Helianthus annuus</i> L., <i>Hordeum</i> sp., <i>Juglas regia</i> L., <i>Malus domestica</i> Borkh., <i>Medicago sativa</i> L., <i>Onobrychis viciifolia</i> Scop., <i>Panicum miliaceum</i> L., <i>Prunus cerasifera</i> Ehrh., <i>P. domestica</i> L., <i>Secale cereal</i> L., <i>Solanum lycopersicum</i> L., <i>S. tuberosum</i> L., <i>Spirea</i> sp., <i>Triticum</i> sp., <i>Vitis vinifera</i> L., and <i>Zea mays</i> L.
Source of information: [7, 8, 32–52]		

Note. The number of plant species is shown in parentheses

Plant feed composition analysis shows that the badger is involved in creating both intracoenotic and intercoenotic flows of diaspores. This is evidenced by its diet, which includes plants of communities of different types, i.e. forest, meadow, swamp and water (see Table 1). Intracoenotic flows of diaspores mean their migration within a single community, e.g. within the coniferous-deciduous forest. These flows are needed to preserve plant populations within the community, maintain species diversity of the coenosis and to provide intracoenotic seed successions. Intercoenotic flows of the diaspores mean the migration of disseminules between communities. These flows are necessary for changing coenoses belonging to different types. Examples of such changes are: 1) overgrowing of meadows with forest; 2) replacement of a pine forest with a coniferous-broad-leaved forest; 3) conversion of shadow deciduous forests with nemoral composition of the herbaceous cover under the influence of mowing, grazing and activities of large wild animals (including badgers) in a bright parkland with a large participation of meadow species and other ecological-coenotic groups of plants.

Badgers and zoochory

Understanding the development of forest communities involves information about the nature of the movement of plant diaspores by different animal species. Literature analysis has shown that badgers involve plant seeds in diaspore flows in different ways: through endozoochory, epizoochory and synzoochory.

Endozoochory means the dispersal of diaspores that had passed through the digestive tract of animals and were then ejected with regurgitates or droppings [27, 28, 53]. Succulent fruits of *Cerasus avium*, *C. fruticosa*, *Fragaria vesca*, *F. viridis*, *Malus sylvestris*, *Prunus spinosa*, *Pyrus communis*, *Rubus caesius*, *R. idaeus*, *R. saxatilis*, *Vaccinium myrtillus* and other species serve as fattening feed for badgers [34, 45]. The pattern of endozoochory movement of seeds depends on the season. For example, in early summer, there are numerous cherry seeds [34, 37], while in the middle summer, seeds of raspberries, stone brambles, bilberries and strawberries are abundant [42, 47, 54]. In late summer, seeds of European blackberries, apples

and pears are numerous [34, 44], while in autumn, cowberry and cranberry seeds are often found in the badgers' latrine pits [44, 50]. The actual participation of badgers in the distribution of plant diaspores can be evaluated by the following figures. In one pile of badger faeces, zoologists found 2.3 thousand bilberry seeds [51], while in another one, they counted 5.0 thousand strawberry nuts [55]. When feeding on green plant parts, at the same time, badgers eat a lot of dry fruits and seeds. Plant diaspores can participate in community formation only if they remain alive after passing through the animal's digestive tract. Obraztsov [56] showed that the viability of pear seeds that passed through the badger's digestive system was 60 %, while that of apple seeds was 83 % and that of blackthorn seeds 100 %. These numbers are comparable to the viability of seeds that have passed through the digestive tract of other predators such as bears, wolves or foxes. Besides, zoologists note that badgers often leave droppings in holes specifically dug or in pits made earlier when foraging for invertebrates. These latrine pits are usually buried by the animals after they are filled [8, 49]. This defecation behaviour undoubtedly contributes to better seed germination since the soil is fertilised and the diaspores are protected from drying out.

Epizoochory means the dispersal of diaspores that cling or stick to an animal's body [27, 28, 53]. In this case, animals only passively transfer the seeds on their bodies, not benefiting from it. Plants with specific adaptations of diaspores to epizoochory, found at the settlements, include, for example, *Arctium lappa* [44], *Geum urbanum*, *Leonurus quinquelobatus*, *Cirsium* sp. (see Table 1), *Carduus* sp., *Galeopsis ladanum* and *G. tetrahit* [57]. Wood avens use modified clingy stilodia of nuts, whereas motherwort and hemp nettle species use the awl-shaped teeth of the flower cup; burdock, thistle and bristlethistle use a prickly and clingy web-like involucre. Part of the seeds, especially small ones, is transferred with the damp soil stuck to fur and paws. An important feature in the badger's behaviour in terms of epizoochory is the cleaning of fur and the removal of adhered seeds and dirt. The animal grooms its fur every day, usually on a site at the sett. Observations have shown that one grooming session can last up to 40 minutes. Sometimes, another badger joins in, helping to groom the areas which are difficult to reach [50].

Synzoochory means the dispersal of diaspores associated with their transfer by animals for further storing them away in "larders" or eating in nests or on feeding sites [27, 28, 53]. Badgers do not store food in the classical sense. However, they harvest

grass to line the nest chamber and make grass plugs to block the sett during hibernation. When collecting grass, the badger rolls it in balls 20–35 cm in diameter, which are then moved to the sett and left to dry in the sun for several days near the entrance [49, 58]. Some seeds and other diaspores fall out of the dry bundle and, falling on the soil thrown out of the setts, sprout. Zoologists found *Pteridium aquilinum*, *Mercurialis perennis*, *Scilla* sp. in the bundle, as well as species of the *Poaceae* family [57]. The same authors suggest that this could be the way *Carduus* sp., *Rumex* sp., *Lamium purpureum*, *Galeopsis ladanum*, and *Melandrium dioicum* appeared in the settlements. In this case, plants do not have to be particularly adapted for zoochory. Badgers often collect material for a bundle at a distance of 10–30 m from the den, sometimes in a radius of 50 m. There was a case when animals made bundles at a distance of 230 m from the sett and even picked the straw that was lying in a field, 300 m away from the settlement, to use it for bedding [47, 49]. The nest bedding can weigh up to 5 kg [7, 9, 58].

By moving seeds around in different ways, the badger can involve the maximum number of plant species with all possible adaptations for zoochory and even without them (for example, by making bundles of grass with seeds) into the flows of diaspores. This is evidence of the fact that the badger is an active participant in successions in the vegetation cover.

Badgers and the distance of plant diaspore distribution

The study of successions and forecasts regarding forest community development requires information about the distance that different agents, including badgers, move plant diaspores to [1, 59, 60]. The range of movement of plant diaspores can be estimated through the size (radius) of animal habitats [61, 62]. Within a family area of a badger habitat, zoologists distinguish two areas [11, 33, 63].

The first one is the area with the largest number of traces of the animal's vital activity. This zone seems to be similar in size to the daily home range of one animal [64]. It is quite possible that within this zone, badgers move the largest number of plant diaspores because the majority of food, including the seeds, passes through the digestive tract of predators, including badgers, in the first day [56, 65, 66]. It can be assumed that the distance of mass dispersal of plant diaspores by this animal will correspond to the radius of the daily home range, which is 1.0–1.5 km (Table 2).

Table 2

Radius of the European badger family area

Radius of the family area where the greatest number of traces of badger's vital activity was found, m	Range of the radius of the family area where a relatively small number of traces of badger's vital activity was found, m	Source of information
500–1,500	1,500–3,000	[37]
900–1,100	1,100–3,000	[49]
750–960	960–2,300	[64]
520–710	710–1,020	[67]
500–700	700–2,000	[63]
300–700	700–1,500	[68]
250–500	500–3,000	[33]

The second area is the entire family plot, which is used by the animals from the moment they leave the sett after hibernation until the next hibernation. It can be expected that within the family area, only a moderate number of plant diaspores is moved, mainly because a relatively small part of seeds can happen to be outside the daily plot if the seeds stay in an animal's digestive tract for several days. Food, including plant disseminules, especially small ones, can remain in a badger's digestive system for up to 5 days [65]. In this case, the distance of diaspore movement gets close to the radius of the entire badger family plot, which is 2–3 km (see Table 2). Direct observations confirm these assumptions: badger excrements containing oats were found in a settlement that was located 3.5 km from the nearest oat field [47]; the remains of myrobalan plum (*Prunus cerasifera*), which the animal had gathered in a garden located at a distance of over 1 kilometre, were found in a sett [39].

The distance of plant diaspore movement by badgers is comparable to that of large mammals such as bear, roe deer, elk and bison [61]. While animals with relatively small areas of habitat (for example, common squirrel, yellow-necked mouse or jay) create mainly intracoenotic flows of diaspores, mammals with large plots, including badgers, create mainly intercoenotic flows of diaspores, which are necessary for the formation of the mixed flora of communities and for successional transformations of coenoses [62, 69].

Badgers and species diversity of communities

When looking at the locations of badger setts in the *Bryanskii Les* reserve and its surroundings, we revealed that settlements are currently located in communities with the predominance of nemoral species³. These cenoses are represented by broad-leaved and coniferous-broad-leaved forests as well as aspen forests. *Quercus robur*, *Fraxinus excelsi-*

or, *Acer platanoides*, *Tilia cordata* and *Populus tremula* form the main tree stand in badger habitats. Apart from the tree layer species, the undergrowth also includes *Ulmus glabra*, *Malus sylvestris* and *Cornus sanguinea*, *Corylus avellana*, *Euonymus europaea* and *E. verrucosa* shrubs. The herbaceous cover is dominated by *Aegopodium podagraria*, *Carex pilosa*, *Convallaria majalis*, *Mercurialis perennis*, *Glechoma hederacea*, *Lamium maculatum* and *Stellaria holostea*. There is also an admixture of *Asarum europaeum*, *Galeobdolon luteum*, *Lathyrus niger*, *Pulmonaria obscura*, *Viola mirabilis*, among others. Nemoral forests are usually found in sandy areas that include loamy material. Within these areas, badgers choose wooded ridges with slopes suitable for digging setts. Zoologists have proven that in inhabited setts, the sleeping chamber (den, nest), for sleeping and cub delivery, is mainly built in the sand under loam arches. Loam reinforces the sett and forms a waterproof ceiling above the living chamber, whereas sand, which is easy to dig in, has poor thermal conductivity and provides favourable temperature and good drainage if water enters the sett [9].

It is well known that the badger prefers lived-in setts. Formozov [71] emphasises that "this animal always sticks to the places it once chose". Likhachev [9] explains that such site fidelity is caused by the rarity of the places where permanently inhabited setts can be dug. If a badger has found suitable housing conditions, it leaves its home only after persistent persecution by poachers and always seeks to return to its old shelter. Permanent setts that are used for hibernation and for cub delivery and rearing have been existing for hundreds or even thousands of years [72]. As a result, badger setts gradually turn into large sett complexes and then into even larger settlements with a significant area reach. For example, in the Oka reserve, a sett occupying 2,500 m² was found [73], while in Bryansk oblast, a sett of 3,800 m² was found [74]. In England, a settlement of 17,500 m² was found [75]. The researchers found 31 entrance holes in the first case, 17 in the second and 178 in the third.

³ It is believed that the nemoral floristic complex unites the species whose range and history are related to European broad-leaved forests [70].

With such a long-term use of the territory, the vegetation cover of settlements (accumulative effect) gradually changes: the structure of the stand, undergrowth and underbrush is changing, and the species composition of the herbaceous cover is transformed. On old badger settlements, the closure of the forest stand is reduced to 20 % or less. This is because adult trees gradually fall and are not replaced by young ones. Singular undergrowth plants preserved in the settlements show low vitality since the bark is stripped off the stems or damaged by badgers, which eat the sweet sap and the nutritious phloem [57]. For this reason, the bark of

woody plants is frequently found in badger excrements [44, 52]. The trunks of shrubs and undergrowth of trees often have numerous deep scratches left by the badger sharpening its claws (Fig. 2). At the same time, this animal prevents trees and shrubs from taking root by eating their fallen fruits and sprouted seedlings [33, 34, 52, 58]. Therefore, no sprouts of common hazel, wartybark euonymus or witch elm were found in badger settlements, although there were fruit-bearing plants of these species nearby; the number of seedlings of Norway maple and common ash was a quarter lower than it was outside the settlement.

Fig. 2. Traces of life activity of the European badger on the stems of woody plants. On the left is the bark of the sycamore maple (*Acer pseudoplatanus*) peeled in early spring for the extraction of sweet juice. On the right is the peeled bark of elderberry (*Sambucus* sp.) with many deep scratches from the badger's claws [52, 76]

This impact has resulted in the gradual thinning of the tree stand, the disappearing of the undergrowth and the increase of herbaceous cover illumination in comparison with the surrounding forest. This contributes to the introduction of light-demanding plants into previously dark nemoral forests. Their diaspores are constantly brought in by badgers, and badger activity significantly increases species density and species richness of vascular plants in the settlements as compared to the settlement surroundings (Table 3). Diversity indicators increase mainly due to meadow species brought here from open sunny places, i.e. forest edges, clearings and meadows. Meadow plants include *Achillea millefolium*, *Anthriscus sylvestris*, *Carex echinata*, *Chelidonium majus*, *Chenopodium album*, *Clinopodium vulgare*, *Erigeron annuus*, *E. canadensis*, *Equisetum pratense*, *Fragaria ves-*

ca, *Galium mollugo*, *G. physocarpum*, *Hypericum perforatum*, *Lactuca serriola*, *Leonurus quinquelobatus*, *Polygonum convolvulus*, *Prunella vulgaris*, *Rorippa sylvestris*, *Solidago virgaurea*, *Taraxacum officinale*, *Veronica chamaedrys*, *Viola canina*, among others. Black-alder-associated species, which are not typical of nemoral forests, i.e. *Athyrium filix-femina*, *Ribes nigrum*, *Solanum dulcamara* and *Urtica dioica*, appear in the herbaceous cover of sett complexes. At the same time, the species composition of the nemoral group is significantly expanded in badger settlements in comparison with the control group. *Actaea spicata*, *Ajuga reptans*, *Cystopteris fragilis*, *Festuca gigantea*, *Geranium robertianum*, *Lamium maculatum*, *Lathyrus niger*, *Moehringia trinervia*, *Scrophularia nodosa* and *Viburnum opulus* can be found here. The participation of light-loving piny plants and

some shade-tolerant boreal species is increasing in the community. Piny species include *Pteridium aquilinum* and *Rubus idaeus*, whereas boreal ones

include *Luzula pilosa*, *Maianthemum bifolium* and *Rubus saxatilis*.

Table 3

Number of vascular plant species in the herbaceous layer in badger settlements and in the control

Settlement number	Nature of the settlement	Number of species	
		Settlement	Control
1	Inhabited	42	31
2	Inhabited	41	23
3	Inhabited	37	20
4	Inhabited	33	17
5	Inhabited	33	14
6	Uninhabited	25	15
7	Uninhabited	25	15
8	Uninhabited	21	20
9	Uninhabited	21	16
Species density, $M \pm m_M$		30.9 ± 2.73	19.0 ± 1.80
Mann-Whitney test, value, U		6.0 ($p = 0.0026$)	
Species richness		79	53

Note. M is the arithmetic mean, m_M is the arithmetic mean error, p is the significance value of differences in species density; significant differences are shown in bold. Species density is the average number of species on nine plots of 100 m^2 . Species richness is the total number of species on all nine plots of 100 m^2 .

Geobotanical surveys of settlements have shown that foraging and construction activities of badgers change the ecological-coenotic composition of communities; the flora becomes mixed (Fig. 3). Due to badgers' activities, pure nemoral forests are being replaced by cenoses where meadow species start to co-dominate. At the same time, the role of black alder, boreal and piny plants, which are not

typical of modern nemoral communities, is increasing. Based on previous studies, light forests with mixed flora were the primary form and were typical of undisturbed (climax) coenoses of pre-agricultural times. Such communities were created and maintained by different groups of animals [1, 3, 77].

Fig. 3. The ratio of plant species of different ecological-coenotic groups in the settlements of badgers and in the control. Species richness is indicated in brackets. The area of the circle corresponds to species richness. Nine vegetation sample plots (100 m^2 each) were established at the settlement and at the control

Badgers and soil cover disturbances

Based on the literature, digging activity of animals comparable in size to badgers creates heterogeneity of the soil cover in the community, which is characterised by a peculiar ecological regime [78, 79, 83]. The area of individual digging sites (disturbances) of these animals is usually small, not more than several square decimetres or metres. The elements of such a mosaic are called microsites or micro-habitats [18, 80]. Unique microgroups (microcoenoses) of plants and animals [81, 82], which are characterised by specific dynamic processes called microsuccessions [3, 83], are formed on microsites. Badgers create two types of soil disturbance, which differ in functional purpose.

The first type of disturbances is the result of the badger's construction activity. These violations are related to soil spoils (the so-called "butans"⁴ or mounds) made at the settlement during cleaning, renovation, expansion and deepening of old setts, as well as the construction of the new ones (Fig. 4). Setts can be 3–6 m deep [7, 10]. The area of individual mounds of earth is 2 to 23 m². Thereat, animals carry 0.7 to 8.1 m³ of soil [49] to the surface. In some cases, the spoil area reaches 55.0 m², with a volume of up to 10.0 m³ [42]. The soil thrown to the surface is enriched with minerals, and the microrelief near the sett changes: butans up to 80 cm high, foot-worn by badgers, are formed. These micro-habitats have a unique species composition of plants and soil invertebrates [78, 84, 85].

Fig. 4. Disturbance of the soil cover by the European badger associated with soil ejection during cleaning, renewal, expansion and deepening of old setts, as well as the construction of new ones. Image courtesy of E. F. Sitnikova

The second type of disturbances is a consequence of the badger's foraging activity. Looking for invertebrates and small vertebrates, as well as juicy underground plant parts, it has to dig through the upper soil layers. These disturbances are usually dispersed throughout the family area. The badger mainly shows four patterns of digging, which

are a result of different foraging ways [47]. The first type is small digs with an area of 30 cm² and up to 10 cm deep (Fig. 5, A, B). They are created by badgers looking for grubs of cockchafer and other invertebrates. For one meal, the animal makes 30 to 2,700 small digs per 100 m² [42, 45, 86, 87], disturbing up to 8 % of the soil cover area. The second type is round-shaped violations with an area of about 500 cm² and up to 35 cm deep (Fig. 5, C). These digs are made by badgers extracting diggers and bumblebees. The third type is

⁴ "Butan" is an individual steppe hill; a mound, a hill on the plain, a hillock dug by marmots, steppe marmots or tarbagans [89]. This term is also used by some zoologists who study badgers [8, 49, 58].

oblong and round-shaped pits with an area up to 1,000 cm² and up to 45 cm deep (Fig. 5, D, E). They appear during digging into dens of mice, voles, moles, shrews and other small vertebrates [42, 47]. In Leningrad oblast, when surveying the area around the settlement, zoologists estimated that badgers dug up 209 mole channels of 284 [87]. At the same time, predators hunt not only moles; they also search for earthworms and other invertebrates that inhabit underground mazes. The fourth type of disturbances is represented by the top layer of soil that badgers dug up and turned over with muzzles and front claws over a considerable distance (Fig. 5, F). The area of such disturbances can

reach 900 m² and even a quarter of a hectare [42, 88]. In appearance and scope of changes, they are similar to traces of boar feedings [40]. In the upper soil layer, badgers look for earthworms and other invertebrates, as well as for tubers and bulbs of spring ephemerals – *Corydalis solida*, *Gagea lutea*, *Galanthus nivalis*, rhizomes of summer broad-leaved grasses – *Mercurialis perennis*, *Dentaria quinquefolia*, etc., fallen fruits of trees and shrubs – *Acer platanoides*, *Carpinus betulus*, *Cerasus avium*, *Corylus avellana*, *Fagus sylvatica*, *Fraxinus excelsior*, *Quercus robur*, *Tilia cordata*, etc. [33, 34, 48, 52].

Fig. 5. Disturbance of the soil cover associated with foraging activity of the European badger: A, B – small digs (both plane and elevated) with an area of 30 cm² and up to 10 cm deep, made during the extraction of larvae of cockchafer and other invertebrates; C – round-shaped disturbances with an area of about 500 cm² and up to 35 cm deep, made during the extraction of diggers (remains of honeycombs are visible in the excavation); D, E – oblong and rounded pits with an area of up to 1,000 cm² and up to 45 cm deep, made during excavations of the setts of small mouse-like rodents (an ejected bedding of rodents is visible near the excavation); F – an excavated and inverted topsoil in which badgers searched for invertebrates, rhizomes, tubers and bulbs of plants. Image courtesy of: A – [55]; B, F – O. V. Solonina; C – [90]; D – E. F. Sitnikova; E – [47]

Most of the figures characterising badger's digging activities will increase by manifold if calculated for the entire season and for the entire family living in the settlement. All this is proof that the badger is originally an edificator of the herbaceous cover. Due to vigorous construction and foraging activity, it can actively create a mosaic pattern in the herbaceous layer throughout the family's habitat. Zoologists have shown that a

badger family area can reach several hundred hectares [64, 67].

Badgers and mosaic pattern of the herbaceous cover

Three zones are distinguished in the herbaceous cover in terms of the intensity of the disturbances produced by badgers (Fig. 6).

Fig. 6. Mosaic of herbaceous cover on the badger settlement and its surroundings. Legend:
A – the first zone with a predominance of meadow and nemoral vegetatively immobile plants of the ruderal group (*Alliaria petiolata*, *Geranium robertianum*, *Lactuca serriola*, *Moehringia trinervia*, *Polygonum convolvulus*); B – the second zone with a predominance of nemoral vegetatively mobile plants of the ruderal group (*Galium odoratum*, *Glechoma hederacea*, *Stellaria holostea*); C – the third zone with a predominance of nemoral vegetatively mobile plants of the competitive group (*Aegopodium podagraria*, *Carex pilosa*, *Convallaria majalis*); D – active setts; E – abandoned setts; F – paths

The first and second zones are significantly modified by badgers, as they are most actively used throughout the existence of the settlement. The third zone is used less frequently. However,

even here, traces of the badger's life activity can be observed. All three zones differ significantly in terms of plant species composition, their abundance, dominance and ecological-coenotic struc-

ture and, as a result, in the prevailing microgroups of grasses. In the following section, we will discuss these differences in more detail.

The first zone. This zone is represented by well-foot-worn areas with a system of setts with fresh and old mounds of spoil origin (Fig. 4, 7). The closure of the tree stand is low, as mentioned above, making it an ideal place for badgers to rest,

bask in the sun, waddle from side to side, clean both partner's and own fur, play and raise their offspring [91, 92]. Besides, this area includes game spots and wide paths connecting the sett entrances. The area of the first zone, which is the actual settlement (complex), covers 1,000 m². It accounts for 15 % of the herbaceous cover area significantly disturbed by badgers (Fig. 6, A).

Fig. 7. The first zone of vegetation: A – a foot-worn mound of soil and a path near an active hole. Image courtesy of O. V. Solonina; B – playing field, as well as a place for resting and grooming; C – badger cubs near a hole in search of soil invertebrates. Image courtesy of E. F. Sitnikova

Active use of sites and paths with compacted soil with poor gas exchange and low water capacity affects the herbaceous cover. In these conditions, the grass survival rate is low and grass closure is extremely low, amounting only to 1–2 %. Species density of the groups is small and amounts on average to 3.3 species per 1 m². However, species richness shows the highest values: 19 species of vascular plants were found in this zone (Table 4). Herbs belong to different ecological-coenotic groups, i.e. meadow, nemoral, black-alder and piny groups. Thereat, more meadow species obviously prevail (Table 5). Meadow species include *Achillea millefolium*, *Anthriscus sylvestris*, *Chelidonium majus*, *Clinopodium vulgare*, *Convolvulus arvensis*, *Fragaria vesca*, *Hypericum perforatum*, *Lactuca serriola*, *Leonurus quinquelobatus*, *Polygonum convolvulus*, *Rorippa sylvestris*, *Taraxacum officinale*, and *Viola canina* (Table 6). The presence of these species is associated with the badger. Seeds

could have been partially transported via epizoochory on paws together with loam and on fur and via endozoochory in digestive tracts. The nearest meadow is located 100 m away from the badgers' settlement. Another part of the seeds was apparently transported by animals with the grass bundles (rolls) which were collected in a forest clearing 30 m away from the sett. To recap, badgers first dry the grass and then use it as bedding in their sleeping chambers or to block the sett entrances before hibernation. Some seeds fall off during drying. Only four nemoral plant species were found here: *Alliaria petiolata*, *Geranium robertianum*, *Geum urbanum* and *Moehringia trinervia*. The piny and black-alder groups include only one type each, i.e. *Rubus idaeus* and *Urtica dioica* (see Table 6). It is known that raspberries are a favourite food of badgers [44], whereas nettles attract badgers because of their high contents of proteins and vitamins [93].

Table 4

Characteristics of the herbaceous layer in different zones of vegetation
in the badger settlement and in its surroundings

Characteristics of the herbaceous layer	Herbaceous layer zones		
	First	Second	Third
Number of plots of 1 m ²	14	21	21
Range of the herbaceous layer cover, %	1–2	5–30	65–85
Average cover of the grass layer, %, $M \pm m_M$	1.4 ± 0.13	14.3 ± 1.53	72.1 ± 1.17
Range of the species number on the plots	1–5	2–6	1–8
Species density, $M \pm m_M$	3.3 ± 0.34	4.3 ± 0.27	4.9 ± 0.42
Mann-Whitney test, value, U	85 ($p = 0.0368$)		
Mann-Whitney test, value, U	71 ($p = 0.0110$)		
Mann-Whitney test, value, U	183 ($p = 0.34551$)		
Species richness	19	16	13

Note. M is the arithmetic mean, m_M is the arithmetic mean error. p is the significance value of differences in species density, significant differences are marked in bold

Table 5

Number and proportion (%) of species in different ecological-coenotic groups
in the herbaceous cover of various vegetation zones in the settlement of badgers

Ecologico-cenotic groups	Herbaceous layer zones		
	First	Second	Third
Meadow	13 (68.4)	–	–
Nemoral	4 (21.0)	16 (100.0)	12 (92.3)
Boreal and piny	1 (5.3)	–	1 (7.7)
Black-alder	1 (5.3)	–	–

Table 6

Points of occurrence (Roman numerals) and cover-abundance points (Arabic numerals and +)
in different zones of herbaceous cover on the badger settlement and its surroundings.
Broad-leaved nemoral forest. ECG – ecological-coenotic groups of plants, TP – types of plant strategies

Plant name	Vegetation zones			ECG	TP
	First	Second	Third		
1	2	3	4	5	6
<i>Achillea millefolium</i> L.	I (+)	–	–	Mea	T
<i>Adoxa moschatellina</i> L.	–	I (+)	–	Ne-Fo	R
<i>Aegopodium podagraria</i> L.	–	II (+)	III (+-5)	Ne-Fo	C
<i>Alliaria petiolata</i> (Bieb.) Cavara & Grande	II (+)	–	–	Ne-Fo	R
<i>Anthriscus sylvestris</i> (L.) Hoffm.	I (+)	–	–	Mea	R
<i>Asarum europaeum</i> L.	–	III (+-1)	III (+-1)	Ne-Fo	T
<i>Campanula trachelium</i> L.	–	I (+)	–	Ne-Fo	T
<i>Carex digitata</i> L.	–	I (+)	–	Ne-Fo	T
<i>Carex pilosa</i> Scop.	–	III (+)	III (+-5)	Ne-Fo	C
<i>Chelidonium majus</i> L.	III (+)	–	–	Mea	R
<i>Clinopodium vulgare</i> L.	I (+)	–	–	Mea	R
<i>Convallaria majalis</i> L.	–	II (+-1)	III (1–4)	Ne-Fo	C
<i>Convolvulus arvensis</i> L.	I (+)	–	–	Mea	R
<i>Cystopteris fragilis</i> (L.) Bernh.	–	I (+)	–	Ne-Fo	T
<i>Dryopteris filix-mas</i> (L.) Schott	–	I (+)	–	Ne-Fo	T
<i>Fragaria vesca</i> L.	I (+)	–	–	Mea	R
<i>Galium odoratum</i> (L.) Scop.	–	III (+-2)	III (+-2)	Ne-Fo	R
<i>Geranium robertianum</i> L.	I (+)	–	–	Ne-Fo	R
<i>Geum urbanum</i> L.	III (+)	–	–	Ne-Fo	T
<i>Glechoma hederacea</i> L.	–	IV (+-2)	III (+-2)	Ne-Fo	R
<i>Hypericum perforatum</i> L.	I (+)	–	–	Mea	T
<i>Lactuca serriola</i> L.	I (+)	–	–	Mea	R
<i>Leonurus quinquelobatus</i> Gilib.	I (+)	–	–	Mea	R
<i>Maianthemum bifolium</i> (L.) F. W. Schmidt	–	–	I (+)	Bo-Fo	T
<i>Mercurialis perennis</i> L.	–	II (+)	III (+-2)	Ne-Fo	C

End of Table 6

1	2	3	4	5	6
<i>Moehringia trinervia</i> (L.) Clairv.	I (+)	–	–	Ne-Fo	R
<i>Paris quadrifolia</i> L.	–	–	I (+)	Ne-Fo	T
<i>Polygonatum multiflorum</i> (L.) All.	–	II (+-1)	II (+-3)	Ne-Fo	T
<i>Polygonum convolvulus</i> L.	I (+)	–	–	Mea	R
<i>Pulmonaria obscura</i> Dumort.	–	III (+)	III (+-1)	Ne-Fo	T
<i>Rorippa sylvestris</i> (L.) Bess.	I (+)	–	–	Mea	R
<i>Rubus idaeus</i> L.	I (+)	–	–	Bo-FE	R
<i>Stellaria holostea</i> L.	–	II (+-2)	II (+-1)	Ne-Fo	R
<i>Taraxacum officinale</i> Wigg.	I (+)	–	–	Mea	R
<i>Urtica dioica</i> L.	III (+)	–	–	BA-Fo	R
<i>Viola canina</i> L.	I (+)	–	–	Mea	R
<i>Viola mirabilis</i> L.	–	II (+)	I (+)	Ne-Fo	T
Number of species	19	16	13	37	37

Note. ECG (ecological-coenotic groups): Ne-Fo – nemoral-forest, Bo-Fo – boreal forest, Bo-FE – boreal-forest edge (piny), Mea – Meadow, BA-Fo – black-alder-forest. TP (type of plant strategy): C – competitive, R – ruderal, T – phytocenotically tolerant

Well-worn areas and trails are dominated by ruderal species (Fig. 8, I). These are poorly competitive plants, and their existence in the community depends on disturbances of the herbaceous cover [24] caused by setting animals, including badgers. Ruderal species belong to two groups. The first group includes perennial vegetatively mobile plants, i.e. *Convolvulus arvensis*, *Fragaria vesca*, *Rubus idaeus*, *Urtica dioica*, among others. They are represented by singular plants, which, in case of trampling, are able to quickly capture the territory due to their high vegetative mobility (Fig. 10, A). The second group is formed by annual and biennial vegetatively immobile grasses such as *Alliaria pet-*

iolata, *Geranium robertianum*, *Lactuca serriola*, *Moehringia trinervia* and *Polygonum convolvulus*. These plants show no vegetative growth and reproduction at all. However, they have a complex of biological features of the "nomad⁵ type" (as termed by Denslow [94]). It is aimed at rapid reclamation of disturbances and quick transition to the latent state. Nomad plants form a stock of seeds in the soil [95]; they have a high seed productivity, a long germination period and high rates of development. They are unable to pass to the quasi-senile state and secondary dormancy. These species do not retain a territory for longer than 1 year [24].

Fig. 8. Cyclic development of microgroups of herbaceous cover on badger settlements and in the surroundings.

Types of microgroups: I – with a predominance of meadow and nemoral vegetatively immobile plants of the ruderal group (*Alliaria petiolata*, *Geranium robertianum*, *Lactuca serriola*, *Moehringia trinervia*, and *Polygonum convolvulus*); II – with a predominance of nemoral vegetatively mobile plants of the ruderal group (*Galium odoratum*, *Glechoma hederacea*, and *Stellaria holostea*); III – with a predominance of nemoral vegetatively mobile plants of the competitive group (*Aegopodium podagraria*, *Carex pilosa*, and *Convallaria majalis*). Red arrows show the direction of microgroup development determined by competitive plants. Black arrows show the directions of microgroup transformations determined by badgers. Development cycles: A – extended, B – shortened

⁵ Nomad, i.e. associated with relocation [96].

Second zone. The second zone is directly adjacent to the first zone, to the foot-worn areas with setts, and is a site where badgers actively feed (Fig. 6, *B*). For example, it is the zone where a female badger with cubs forages constantly, since the brood mostly stays near the sett all summer and autumn [91, 97]. Other members of the family also feed during the daily rest [42]. Some zoologists argue that badgers try to forage right near the settlement, just 150–200 m away, for 2–3 weeks before hibernation and after hibernation in spring [47]. When extracting soil invertebrates and small mouse-like rodents, as well as when digging up

roots, rhizomes, tubers and bulbs, badgers make a large number of digs, loosen the litter and soil layers lying below. Disturbances created by badgers in this zone amount to 70–95 % in total (Fig. 9). Loosening reduces the bulk density of soil and increases its fertility, and such soil has increased temperature and improved gas exchange as well as an increased intensity of microbiological processes and an increased availability of nutrients for plants [98, 99]. The area of the second zone covers 5,500 m² and accounts for 85 % of the area of the herbaceous cover significantly disturbed by badgers (see Fig. 6, *B*).

Fig. 9. Herbaceous cover around a settlement of the European badger. The top photo is of the second zone. The herbaceous cover is badly damaged by badgers. Phytocoenotically tolerant plants predominate, i.e. vegetatively immobile spring vetch (*Lathyrus vernus*) and wood avens (*Geum urbanum*), vegetatively poorly mobile Solomon's seal (*Polygonatum multiflorum*), etc. The bottom photo is of the third zone. The herbaceous cover is slightly damaged by badgers. Vegetatively mobile plants of the competitive group, mainly pilose sedge (*Carex pilosa*), dominate. Image courtesy of O. V. Solonina

Active setting activity of the animals results in the formation of microgroups, with a relatively low projective cover from 5 to 30 %. Species richness of vascular plants is lower in comparison with the first zone (see Table 4). There are no light-demanding meadow or piny species (see Table 5), mainly due to the shading of the herbaceous cover, which is located under the closed canopy of a stand of *Acer platanoides*, *Tilia cordata* and others. All 16 discovered species were shade-tolerant grasses of the nemoral group. At the same time, the species density of the second-zone microgroup is significantly higher than that of the first one (see Table 4).

In the second zone, ruderal species are still dominant (Fig. 8, II). However, this group has no annuals or biennials, and the greatest coenotic significance is shown by vegetatively mobile plants, i.e. *Galium odoratum*, *Glechoma hederacea* and *Stellaria holostea* (see Table 6). They are characterised by the highest occurrence and cover points and quickly recover from disturbances caused by badgers due to high vegetative mobility. Bedstraw, ground ivy and stitchwort differ from ruderal "nomad" species by a longer (over 2 years) duration of the territory retention [24]. Notably, tolerant plants, with *Asarum europaeum*, *Polygonatum multiflorum*, *Pulmonaria obscura* and *Viola mirabilis*, sometimes *Campanula trachelium*, *Carex digitata*, *Cystopteris fragilis* and *Dryopteris filix-mas* as typical components of the herbaceous cover, demonstrate maximum participation in this zone. At the same time, all competitive broad-leaved grass species are found in the community, i.e. *Aegopodium podagraria*, *Carex pilosa*, *Convallaria majalis* and *Mercurialis perennis*. However, their participation is minimal (see Table 6).

The third zone. It is usually located beyond the second zone, sometimes directly adjacent to the first zone (Fig. 6, C). Here, badgers also dig and loosen the soil for food. However, the intensity of the impact on the herbaceous cover is not as high as in the second zone. Disturbances created by the animals here only account for 15–35 %.

This part of the coenosis enjoys a relatively large herbaceous cover of 65–85 % (see Fig. 9), mainly because as the setting activity of animals decreases, competitive plants of the nemoral group start to dominate, i.e. *Aegopodium podagraria*, *Carex pilosa* and *Convallaria majalis* (see Table 5, 6). They are characterised by high vegetative mobility and productivity, large biomass and a significant duration of the territory retention [24]. This allows the competitive plants to create coenotically isolated thickets that displace weak competitive species

(Fig. 8, III). Therefore, *Adoxa moschatellina*, *Campanula trachelium*, *Carex digitata*, *Cystopteris fragilis* and *Dryopteris filix-mas* are not found in this zone. In addition, it is difficult for new species to enter these groups. Only isolated individuals of extremely tolerant plants appear, i.e. *Maianthemum bifolium* and *Paris quadrifolia*. The participation of small grasses in the community is minimal, and these species show a low level of vitality and are in low numbers (see Table 6). As a result, species richness amounts only to 13 species. Species density of the herbaceous cover is, however, similar to that of the second zone (see Table 4).

The vegetation of the zones and their borders is dynamic and changes over time. This is due to the fact that badgers sometimes abandon part of their setts or the entire settlement for several years [50]. Zoologists believe that the disappearance of animals is caused by the reduction in their numbers as a result of epizootic and other diseases [7]. Gorshkov believes that badgers can be forced out from the territory by wild boars, who compete with badgers for food, destroy their setts and kill their cubs [42]. Sometimes, animals leave the inhabited place because of a strong infection with ectoparasites [37]. Currently, overhunting and poaching are the main reasons for a decline in badger populations. First, the well-foot-worn areas and paths in front of the setts (the first zone) and the adjacent second zone in abandoned settlements become completely overgrown with ruderal mobile grasses within 3 to 4 years (Fig. 10, A–C), followed by an overgrowth with competitive grasses (see Fig. 8; Fig. 10, D). When the badger population increases, the animals return to the abandoned sett, renovate it and disturb this unidirectional microsuccession in the herbaceous cover. Thus, extended and shortened cycles of vegetation development are formed. Extended cycles of microgroups are formed if badgers return to a sett at the stage of overgrowing with competitive grasses (see Fig. 10, D). Shortened cycles occur if they return during the sett's overgrowing with vegetatively mobile species of the ruderal group (see Fig. 10, A–C) or if badgers create small bare spots in between competitive plants that are then quickly replaced by ruderal species (see Fig. 8).

A survey of badger settlements has shown that the foraging activity of this animal continuously creates a mosaic pattern of herbaceous cover and forms a multi-species community of vascular plants. Spatial redistribution of microgroups dominated by different types of plant strategies (ruderal, tolerant or competitive) help to maintain this diversity.

Fig. 10. Abandoned setts of the European badger at different stages of overgrowing with herbaceous cover: A – microgroup of plants with a predominance of ruderal vegetatively mobile common nettle (*Urtica dioica*) and red raspberry (*Rubus idaeus*); B – microgroup of plants with a predominance of ruderal vegetatively mobile common nettle (*Urtica dioica*) and ground-ivy (*Glechoma hederacea*); C – microgroup of plants with a predominance of ruderal vegetatively mobile greater stitchwort (*Stellaria holostea*) and tolerant vegetatively immobile wood avens (*Geum urbanum*); tufted hairgrass (*Deschampsia cespitosa*) grows near the sett; D – microgroup with a predominance of nemoral vegetatively mobile plants of the competitive group – pilose sedge (*Carex pilosa*) and lily of the valley (*Convallaria majalis*). Image courtesy of E. F. Sitnikova

Conclusion

The composition of plant feeds shows that the badger is involved in creating both intracoenotic and intercoenotic flows of plant diaspores. This is evidenced by the presence of plants of different communities in its diet, i.e. forest, meadow, swamp and water plants. The badger can move plant diaspores in three ways: via endozoochory, epizoochory and synzoochory. That is why seeds of the largest possible number of plant species with various adaptations to zoochory are involved in diaspore flows. Literature analysis has shown that badgers can move large amounts of diaspores over

a distance of 1 kilometre and smaller amounts up to 2 or 3 kilometres. Foraging and construction activities of this animal contribute to a significant increase in the species diversity of vascular plants within settlements. Badgers change the ecological-coenotic composition of the community, the flora becomes mixed. Forest, meadow, black-alder, boreal and piny plant species begin to co-dominate in the herbaceous cover of nemoral forests.

While foraging, the badger actively creates a mosaic pattern of the herbaceous cover over the entire area of the family plot, which is several hundred hectares. This mosaic is represented by three variants of microgroups: 1) with a predominance of vegetatively immobile annuals and biennials of

the ruderal group; 2) with a predominance of vegetatively mobile perennials of the ruderal groups and with significant participation of phytocoenotically tolerant plants; 3) with a predominance of vegetatively mobile perennials of the competitive group. This sequence of microgroups alternating over time represents a microsuccession. Competitive species are the driving force behind the development of these groups. They gradually crowd out ruderal and tolerant plants and can become dominant in the herbaceous cover for a long time. However, badgers' use of the community territory on a "shift" basis occasionally interrupts these unidirectional microsuccessions. In this case, extended and shortened cycles of microgroup development are formed. Extended cycles are formed if badgers dig through thickets of competitive plants over a large area to minimise the closure of the herbaceous cover. Shortened cycles can be formed if foraging animals return to their previously dug areas 2 or 3 years later, during the domination of vegetatively

mobile grasses of the ruderal group. In this case, the stage with a predominance of competitive plants is omitted. The multi-species composition of the herbaceous cover is maintained by the disturbances caused by badgers and cyclic microsuccessions. The mechanism for maintaining this diversity is based on the spatial redistribution of microgroups dominated by plant species with different strategies.

These facts indicate that in an undisturbed biocoenosis, badgers were edificators of the herbaceous cover and played an active part in the formation and maintenance of the mixed nature of the community flora. Besides, they contributed to the restoration of the species diversity of the coenoses that were lost as a result of the destructive human impact. However, due to overhunting and persistent persecution by poachers, this species has recently become extremely rare and endangered and has ceased active transformation of the environment.

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