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Animal occurrence in fragmented forest habitats – important factors at the patch and landscape scale

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Abstract. To date, in research, the main determinants influencing animal assemblages in fragmented forests have been considered to be forest island area and degree of isolation. Such a simplistic approach may have detrimental effects on the obtained results and conclusions, since there are a large number of other factors determining animal persistence in forest islands. In order to identify these factors and evaluate their importance, we reviewed the scientific literature on the topic. In addition to the island area, also patch shape, edge effects and local plant community structure are crucial factors affecting animal assemblages at the forest island scale. At the landscape scale, the total number of forest islands and their combined area, matrix permeability, occurrence of wide ecological corridors as well as isolated trees and woodlands appear to be the most significant factors.

Our review further indicates that many of these elements also tend to interact. For instance, edge effects may reduce the area of suitable habitat in a forest patch. Furthermore, some fragmentation effects may be masked by species traits e.g. mobility, food preferences or habitat specialisation. The landscape context also plays a crucial role in animal persistence in fragmented forests. We thus conclude that there is a strong need to investigate the above-mentioned components of habitat fragmentation at the local and landscape scale using appropriate bio-indicators.

Keywords: habitat fragmentation, biodiversity, animals

1. Introduction

Agriculture, deforestation, urbanization and road construction are some aspects of human activity that often contribute to negative changes in the natural environment (Broadbent et al. 2008; Fuentes-Montemayor et al. 2013; Kosewska et al. 2014). Above all, natural and semi-natural forest communities are irreversibly lost to arable fields (Brockerhoff et al. 2008). Agricultural land in Europe constitutes about 50% of its area (Stoate et al. 2009), while forested areas range from several to up to 20%, depending on the country (FOREST EUROPE, UNECE, FAO 2011). The unfavorable impact of agriculture is mainly due to its intensification, resulting in the emergence of large-scale monoculture crops, as well as the use of herbicides, pesticides and chemical fertilizers, often in excessive quantities (Opatovsky et al. 2010). In order to mitigate the negative impact of this, knowledge is needed to explain its essence and consequences. Forests are a mainstay of biodiversity; more than half of the species of plants and terrestrial animals live in forests. Forest ecosystems should therefore be given special attention (Brockerhoff et al. 2008). It is estimated that over the last centuries, the area of forests on Earth has been reduced by almost half. On a global scale, their area has decreased by about 70 million hectares within the last 15 years (1990–2005) (FAO 2012a). Deforestation is particularly noticeable in the case of the tropic zone, where the forest assemblages have been affected by a significant expansion of agriculture (Harvey et al. 2006). During the last century in Africa, at least 10 million ha of forests have been irretrievably lost, and 80% of the originally continuous forest assemblages have been fragmented (Norris et al. 2010). The steady decline of forest areas as a result of deforestation is still visible on most continents (with the exception of Eu-

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rope), resulting in a mosaic of forest and anthropogenic land (Broadbent et al. 2008; Fuentes-Montemayor et al. 2012; Fuentes-Montemayor et al. 2013).

Forest areas in a fragmented environment are characterized by a diversified surface area and differing degrees of isolation of patches/islands (Fahrig 2003). In addition, a number of other changes occur in newly established island environments. Among them, the following are often mentioned: the unfavorable ratio between the length of the island perimeter and its surface area (Fuentes-Montemayor et al. 2012), edge effects (Broadbent et al. 2008), transformed microclimatic conditions (Cabrera-Guzmán, Reynoso 2012), disrupted ecological links between species of flora and fauna (Bruna et al. 2005; Rodriguez-Cabal et al. 2007) or changes in their species structure (Broadbent et al. 2008; Gaublomme et al. 2008; Filgueiras et 2011). As a consequence, this pro-cess leads to the loss of biodiversity, both in individual is-lands and throughout the landscape (Brosi 2009).

Research on the impact of fragmentation on living organisms can be placed within one of the two current directions of ecological research: the theory of island biogeography or the theory of metapopulation dynamics. In the first theory, researchers are focused on the characteristics of the island and the degree of its isolation, while in the second, the focus is on the connections between fragmented habitats and the ability of isolated animal subpopulations to disperse (Collinge 1996). The impact of fragmentation on animals can therefore be considered on a different scale. Some of the factors (e.g., the shape of the island) determine the structure of the animal assemblages at the level of a single patch, while others have an impact at the landscape scale (e.g., number of islands). Most studies focus mainly on the surface area of forest islands (Table 1). Bypassing the remaining factors characterizing fragmentation may result in erroneous conclusions about its impact on the state of biodiversity. In addition, the literature on fragmentation provides varying data about the negative, positive or lack of effect of the individual features of habitat fragmentation on the structure of the entire assemblage of animals inhabiting the forest islands. Therefore, there is a need to systematize information on the processes of forest habitat fragmentation and their impact on fauna assemblages.

This article, in particular, presents the reactions of animals to changes in the habitats in which they live. In addition, it indicates the elements that modify these reactions, among others, relating to the spatial scale or the characteristics of the animal species being studied (e.g., food preferences, use of the environment). The conclusions drawn on this basis can be used to manage the forest environment in a landscape transformed by humans and reduce the negative effects of forest habitat fragmentation on biodiversity.

The objective of this paper is to gather and systematize information found in the literature on the basic factors shaping the structure of fauna both at the level of a single island, as well as in the entire landscape. The publicly accessible Google Scholar database of scientific articles was searched. The search criteria used were: habitat, fragmentation, forest and animals. The literature on the subject of habitat fragmentation is extensive. In order to systematize the available information, research papers about the impact of forest fragmentation on the occurrence of animals were selected, including those analyzing the impact of patch area, shape, edge effects and the surroundings (the entire landscape).

2. Factors affecting animal assemblages at the scale of a single forest patch

2.1. Edge effects

Only in the Amazon itself, annual deforestation has resulted in an up to 40,000 km long boundary between forests and anthropogenic areas (Broadbent et al. 2008). This boundary can have essentially two types of transition zones from one ecological system to another: sharp and abrupt or gentle and gradual (Collinge, Palmer 2002). At the interface between the two ecological systems, the structure and conditions of the functioning of fauna are different than in their interior. This phenomenon is referred to as the edge effect (Babak, He 2009), that is, changes occurring in the biocenosis and biotope in a forest habitat bordering open space (Mesquita et al. 1999). The range of these changes is determined by the aforementioned transition between the ecological systems (Didham, Lawton 1999). For example, boundaries with a gradual and gentle nature generate a milder negative impact of the open space on the forest habitat than a sharp boundary (Sławski, Sławska 2000).

Edge effects are identified by three types of changes occurring at the edge of the forest habitat. Abiotic effects (pertaining to changes in physical environmental conditions) cause, among others, differences in humidity and air temperature between the interior and the edge of the patch. These changes often lead to another type of edge effect having a biotic character. This pertains to differences in the number and dispersion of living organisms between the said zones. The last type is the indirect edge effect, which is not related to the direct influence of abiotic factors on animals, for example, through increased insolation, a change in the abundance of the food base, both plant and animal. Indirect edge effects therefore include modifications of broadly understood ecological interactions between living organisms, for example, predation, competition or pollination (Murcia 1995). When there is a large proportion of edge habitat to patch area, edge effects may contribute to changes in the fauna assemblages even deep in-

Table 1. An overview of selected papers analyzing the impact of habitat fragmentation on animals assemblages

No.	References	Animals used in surveys	Patch/landscape feature investigated					
			area	isolation	patch shape	edge effects	vegetation	matrix
1	Halme, Niemelä (1993)	carabid beetles	+	+				
2	Delin, Andre (1999)	red squirrel	+	+			+	
3	Haddad (1999)	butterflies		+				
4	Gibb, Hochuli (2002)	arthropods	+				+	
5	Watson et al. (2004)	birds	+	+	+		+	+
6	Antongiovanni, Metzger (2005)	birds	+					+
7	Bruna et al. (2005)	ants	+	+			+	
8	Feer, Hingrat (2005)	beetles	+	+				
9	Pardini et al. (2005)	mammals	+	+			+	
10	Uezu et al. (2005)	birds	+	+				
11	Brosi et al. (2008)	bees				+	+	
12	Gaublomme et al. (2008)	carabid beetles	+			+		+
13	Martensen et al.(2008)	birds	+	+			+	
14	Brosi (2009)	orchid bees	+	+	+			+
15	Cherkaoui et al. (2009)	birds	+	+	+		+	
16	Banks-Leite et al. (2010)	birds	+			+	+	
17	Opatovsky et al. (2010)	spiders						+
18	Filgueiras et al. (2011)	scarab beetles	+	+			+	
19	Cabrera-Guzmán, Reynoso (2012)	amphibians reptiles	+		+		+	
20	Fuentes-Montemayor et al. (2012)	moths	+	+	+		+	+
21	Arroyo-Rodríguez et al. (2013)	black howler	+	+	+			+
22	Fuentes-Montemayor et al.(2013)	bats, insects	+		+		+	+
23	Carrara et al. (2015)	birds					+	+
24	González et al. (2015)	arthropods	+	+		+	+	

side the forest patches (Ewers, Didham 2008; Banks-Leite et al. 2010). These changes are mainly manifested in a reduced number and total withdrawal of species associated with the forest habitat (Ewers, Didham 2008). As a consequence, edge effects are one of the factors (next to, for example, area and isolation) determining the state of the biological diversity of fragmented forests (González et al. 2015).

Due to the complex nature and variability in place and time of emerging impacts, the measure of intensity of edge effects on animals within the forest areas becomes an important element. The intensity of impact (strength and range) of the patches' surroundings on their interior is a function of a number of elements. In addition to the character of the boundary itself, important factors include: the contrast between the boundary and the interior of a given ecological system, the location of the forest border with respect to geographical direction, its area, season, animal habitat preferences and the vegetation surrounding the island (Matlack 1993; Didham, Lewton 1999; Niemelä et al. 2007; Banks-Leite et al. 2010; Lenz et al. 2014). In comparison to the inner zone, the edge of forest patches is usually characterized by higher insolation and lower humidity of the air (Shaw et al. 2007; Sławski 2008) and soil (Gehlhausen et al. 2000), often leading to differences in the vegetation structure between these zones (Hofmeister et al. 2013). Compared to the interior of a forest island, the structure at its edge is usually qualitatively, quantitatively and spatially more diverse. Among others, tree seedlings and shrub vegetation occurs in higher densities there (de Casenave et al. 1995; Gehlhausen et al. 2000). This impacts the animal assemblages by modifying the availability of food or sites for shelter and reproduction (Batáry et al. 2014). As a result, some animals (e.g., herbivorous insects) on the border of the forest environment may react with an increase in the number of species and their population. As a result, this zone also exhibits an increased density of insectivorous animal species (Grow et al. 2013; González et al. 2015). However, some animals (e.g., forest amphibian species requiring a shady and humid environment) may also avoid this zone because the microclimate conditions and vegetation structure are too diverse, or there is an increased risk of predators attacking from open spaces (Schneider-Maunoury et al. 2016; Sosa, de Casenave 2016).

Due to the above, omitting the intensity of the impact of edge effects when assessing the consequences of fragmentation can generate numerous errors (Ewers, Didham 2008). Some researchers (Ewers, Didham 2008; Schneider-Maunoury et al. 2016) believe that edge effects determine the changes in animal assemblages occurring in the patch habitats, especially those of a small size. In such a case, the extent of impact of the edge is relatively higher, often causing the lack of a stable zone in the patch's interior (Banks-Leite et al. 2010).

2.2. Size of the island

As mentioned earlier, forest fragmentation is associated primarily with the formation of a series of forest complexes (patches) with smaller areas. As a consequence, qualitative and quantitative changes occur in the local animal assemblages (Schoereder et al. 2004, Magura, Ködöböcz 2007). One of the more important factors modifying the intensity of these changes is the area of the patch. When it decreases, very often, the number of species and their populations also decrease (Filgueiras et al. 2011; Cabrera-Guzmán, Reynoso 2012; Fuentes-Montemayor et al. 2012). This dependence is one of the pillars of MacArthur and Wilson's theory of island biogeography (Magura et al. 2001); however, there are also reports illustrating the reverse trend (Halme, Niemelä 1993; Niemelä 2001; Cabrera-Guzmán, Reynoso 2012). This is usually explained by the fact that on small islands, apart from stenotopic species, strongly adapted to the conditions of one type of environment, eurytopic species also occur, characterized by significant adaptation abilities to changing environmental conditions. This allows them to use many different habitats. In addition, on small islands, species may appear from a neighboring habitat, treating such a small island as part of the whole environment. These animals live in open spaces, but are able to penetrate the forest environment in an opportunistic way. Their occurrence on small islands is related to the unfavorable perimeter-to-surface area ratio characteristic of such environments, increasing the relative share of edge habitat at the expense of the typically forested inner zone (Halme, Niemelä 1993; Magura et al. 2001; Schoereder et al. 2004). For example, when studying carabidae in the forest communities of various sizes, Halme and Niemelä (1993) found that with a decrease in the area of the forest, the share of species typical of open areas increased, and as a result, so did the total species richness. Similar results were obtained by Magura et al. (2001) and Gibb and Hochuli (2002). However, it should be clearly stated that from the point of view of protecting the biodiversity, the presence of typically forest species (withdrawing due to fragmentation processes) is more important than the presence of eurytopic species, or those characteristically found in the areas transformed by humans, especially since these animals are decisive in terms of competition on the small islands, resulting in the disappearance of the forest species (Halme, Niemelä 1993).

There are also other reasons why large-sized islands are not always characterized by a greater biodiversity of animals (Filgueiras et al. 2011). The relationship between the area of the island and the fauna assemblages can, for example, be modified by the availability of food or sites for overwintering or breeding (Halme, Niemelä 1993; Magura et al. 2001; Watson et al. 2004; Feer, Hingrat 2005). Species with similar habitat requirements but different food preferences may react in different ways to changes in the surface area of the island (Uezu et al. 2005; Martensen et al. 2008). Watson et al. (2004), in studying the species richness of avifauna, found the presence of fruit-eating species, primarily in the large forest patches. However, this was mainly related to the positive impact of the surface area on the occurrence of fruit plants. A similar relationship was noted by Magura et al. (2001) with regard to the size of the island, the number of dead trees and the presence of some species of insects, for example, the blue ground beetle *Carabus intricatus* L., which overwinters in dead wood. However, Feer and Hingrat (2005) showed an indirect relationship between the surface area of an island and the occurrence of coprophagous beetle species. In their studies, the number of species and their populations were not so much related to the surface area of the island as to the presence of large mammals, determined by the size of the patch (Feer, Hingrat 2005). The element that modifies the impact of an island's size on animals may also be the location of the species in the food chain. It has been found, for example, that animals from higher trophic levels (e.g., spiders, parasitoids) are the most susceptible when the forest patch surface area declines. These animals are often characterized by a limited number of preferred prey species. In a situation where there is no prey in small patches due to a high density of predators, these animals are unable to change their eating habits and they then die (Gibb, Hochuli 2002).

The selection of species studied is important in research on the impact of patch size on fauna assemblages (Nietupski et al. 2011). Depending on the taxonomic group, animals may react differently to the decline of forest area due to fragmentation (Cabrera-Guzmán, Reynoso 2012). It has been found, for example, that amphibians are more numerous in large-sized fragments of forest, while reptiles show a reverse dependence. Amphibians require a humid environment to live and develop, which is practically absent in small patches due to increased air circulation and insolation. These animals, unlike reptiles, breathe not only with lungs, but also through their skin, which makes them particularly sensitive to a desiccating environment (Cabrera-Guzmán, Reynoso 2012). The above considerations again lead to the conclusion that the species most suitable for research on the impact of fragmentation on biological diversity are those from the forest environment. These animals usually need stable living conditions (including the microclimate and vegetation structure) that are found only inside large forest patches (Magura et al. 2001; Watson et al. 2004). Sometimes, however, some of them do not react negatively (e.g., by reducing the population size of the species) to a decrease in the area of the patches. In most cases, this will apply to species having individual ranges smaller than the area of the smallest forest fragment included in the research. Negative changes in their occurrence will be observable only when the surface area of the patch drops below a certain threshold (Cherkaoui et al. 2009). Thus, despite the aforementioned discrepancies in the relationship between the size of the island and the occurrence of animals, it should be noted that from the point of view of biodiversity conservation, the impact of forest fragmentation and the subsequent decrease in the size of forest assemblages have a clearly negative impact on biodiversity.

2.3. Shape of the island

Another factor influencing the structure of animal assemblages in the interior of a forest fragment is its shape (Orrock et al. 2011; Fuentes-Montemayor et al. 2012). Only a few studies on the impact of forest habitat fragmentation on animal assemblages took this into account (Table 1), but its significance seems important (Ewers, Didham 2006; Cherkaoui et al. 2009; Orrock et al. 2011). Forest patches with the same area and similar vegetation structure can significantly differ in terms of the living conditions of the animals because of their shape. As an example, Coligne (1996) gives the example of two areas with an identical surface area, but with different shapes (elongated or compact). Essentially, compact islands – with shapes close to a square or circle – are characterized by a smaller share of the edge environment, which, as mentioned above, is susceptible to the influence of open space (Coligne 1996; Fuentes-Montemayor et al. 2012). More of this kind of environment is found in forest patches with an elongated shape or with a strongly developed border (a large number of highly irregular shapes). In this situation, the forest island, like its small counterpart, does not contain an environment with stable living conditions, and even its large area cannot eliminate the negative effects of edge (Ewers, Didham 2006; Cherkaoui et al. 2009). As a result, the occurrence of some animal species (e.g., forest butterfly species) may be limited to the interior of the forest fragments (Hamazaki 1996; Fuentes-Montemayor et al. 2012). This may result in the presence of various animal species depending on the shape of the patch – elongated or compact (Cherkaoui et al. 2009). For this reason, verifying a patch's shape is an important tool in assessing the biotic and abiotic conditions for the life of animals in a fragmented environment (Helzer, Jelinski 1999; Cherkaoui et al. 2009).

The direction in which animal assemblages (species number and their population sizes) change depending on the shape of the island may differ from the one described above. For example, in his studies on the greenhouse millipede (*Oxidus gracilis* C.L. Koch), Hamazaki (1996) found an increased number of these invertebrates in an elongated island environment. Brosi et al. (2008) and Brosi (2009) stated that the way animals react to the shape of an island depends on their habitat preferences. In the case of Apidae, an increasing proportion of an island's edge resulted in the disappearance of the representatives of the Meliponini tribe and larger numbers of Apini and Euglosini tribes, mainly due to their preferences in relation to the boundary for forest assemblages (Brosi et al. 2008; Brosi 2009). On the other hand, animals that are not attached to a single type of environment, which can occur at the edge of a forest environment and in open space (eurybionts), do not react with a decrease or increase in the number of species or population with an increasing share of a forest island edge environment (Watson et al. 2004). Such animals include insects from the *Cincidela* spp., which occur both at the edge of forest islands and in open spaces (Orrock et al. 2011). The shape of the island also does not cause any change in the structure of the forest species assemblages having small individual territories, especially those living in large patches, which, despite an unfavorable shape (e.g., elongated islands), have a sufficiently large internal zone to provide this group with stable living conditions for shelter, prey and reproduction. Such animals include the Passeriformes, which are characterized by a small body size and small individual territories (Watson et al. 2004; Cherkaoui et al. 2009).

3. Factors affecting animal assemblages at the scale of the whole landscape

As a result of expansive human activity, an increasing proportion of natural ecosystems are being transformed. Depending on the region of the world and the considered scale, anthropogenic space is characterized by the different proportions and composition of human-modified areas and relatively natural environments. As a result, human-modified areas are gaining in importance for global level biodiversity in the world (Carrara et al. 2015).

A large number of authors, in studies conducted to date on the effects of fragmentation, focused mainly on the characteristics of individual patches, without considering the role of their surroundings, which together with these patches forms a landscape. Meanwhile, according to some reports, this role is extremely important (Collinge, Palmer 2002). Analyzing the effects of fragmentation through the prism of a patch's characteristics is a limited approach, because the fragmentation of the environment occurs in the entire landscape (Fahrig 2003). In addition, the structure of fauna assemblages in a specific place is the result of many factors, not only those in micro-areas (e.g., the surface of the island, its shape, vegetation structure), but also those at the macroscale (e.g., number and total area of forest islands, their share of the landscape) (Debinski et al. 2001; Arroyo-Rodríguez et al. 2013; Fuentes-Montemayor et al. 2013).

A key element in protecting biodiversity in the landscape is the preservation of animal species associated with forests. Not only the insular nature of forest ecosystems, but also the loss of their total area as a result of fragmentation can lead to the domination of eurybiotic and invasive species, as well as the absence of representatives of forest fauna (Umetsu, Pardini 2007). It is claimed that there is a threshold value for the share of the forest environment in a landscape, below which the most sensitive species disappear due to the increased effects of fragmentation (Fahrig 2003). For example, it has been proven that the loss of forests in a landscape to less than 10% of its former size results in the disappearance of most forest species of birds. Therefore, maintaining a high level of biological diversity of forest animal species in the landscape is strongly dependent on preserving a large area of the forest ecosystem (Radford et al. 2005; Carrara et al.; 2015). Large forest area in the landscape means less isolation (Fahrig 2003), which promotes species that are unable to travel long distances, for example, forest cricket species that are unable to fly (Ribas et al. 2005). An important element is also the total number of islands that make up the total area of forests. Their high number is associated with a significant share of edge environment in the landscape, and thus, the quantitative and qualitative structure of animal assemblages reveals the dominance of species associated with this type of environment; for example, an increase in the abundance of the honey bee *Apis mellifera* L. (Watson et al. 2004; Brosi et al. 2008). An important factor for maintaining forest fauna in the landscape, in addition to the number of forest assemblages, is their origin. It turned out that artificial forests do not provide such animals with the same conditions as natural forests or those with conditions close to these. The artificial forest, especially in the early stages of development, is characterized by a simplified vegetation structure. The tree stand is essentially of a single age, without a well-developed shrub and herbaceous plant layer, which provide a food base, shelter and breeding sites. For this reason, some species do not find suitable conditions for living in such a forest. One of them is the uniform treecreeper *Hylexetastes uniformis* Hellmayr from the Furnariidae family, which occurs only in the natural Amazonian forests (Moura et al. 2013; Batary et al. 2014).

Connectivity as a landscape feature plays a significant role in facilitating the dispersion of animals. Different types of habitats are used for this purpose, depending on the stage of the animals' developmental cycle, gender, dispersal possibilities, seasons, and their need to move within the landscape (Law, Dickman 1998; Debinski et al. 2001; Joly et al. 2001; Fuentes-Montemayor et al. 2013). The nature of the environment surrounding the forest patches determines the intensity of edge effects and the mobility of animals in the landscape. The tree and shrub vegetation surrounding the patches creates a buffer zone, limiting the impact of the open space on the inner part of the patch, ensuring stable conditions in the forest environment. The forest fauna in such patches is able to function not only inside them, but also in their edge zones, and even to opportunistically penetrate the space outside the patch (Antongiovanni, Metzger 2005). For example, the nature of the vegetation around the forest patches was a factor determining the use of space outside the patch by the Angola colobus (*Colobus angolensis palliatus* Peters) – a mammal species of the Cercopithecidae primates inhabiting the forests of central Africa. It is a species that generally favors forests. The structure of the vegetation surrounding the forest fragments (presence of high shrub, tree and fruit tree crops) provided conditions similar to that of the forest environment, enabling this species to travel even over long distances in the landscape outside the patch (Anderson et al. 2007).

The role of the vegetation surrounding the patches is particularly important for species with large territories, capable of traveling significant distances (e.g., predators), which regularly leave forest patches in search of food. For example, bats from the genus Myotis spp. travel in the landscape between forest patches and clumps of mid-field trees, where they find a rich food base (insects). In the absence of a sufficient number of such plant communities in the landscape, the bats are forced to look more intensely for food, consequently expending a great amount of energy (Tubelis et al. 2007; Umetsu, Pardini 2007; Fuentes-Montemayor et al. 2013). For this reason, an area surrounding the forest patches that is conducive to animal dispersion, for example, with a significant amount of trees and shrubs in the vicinity of the patches, is a factor that can significantly mitigate the negative effects of fragmentation (Antongiovanni, Metzger 2005). In addition to facilitating the dispersion of animals, renewing the natural vegetation near forest patches can constitute alternative environments for them (Umestsu, Pardini 2007). However, it should be noted that for animals with limited dispersal capabilities, small individual territories and strict habitat preferences, the nature of the area surrounding forest patches is not a significant limiting factor. Such animals include forest species belonging to the microlepidoptera. In their case, only the local nature (inside the patch) of the quantitative and qualitative structure of the vegetation (e.g., a large number of species and population of deciduous trees) influenced the number of species and their populations (Fuentes-Montemayor et al. 2013).

Significant contrasts in the habitat conditions between forest patches and open space often make it difficult for animals to travel in the landscape. The best example is the difference between forests and agricultural areas (Gascon et al. 1999). Agriculture has a tremendous impact on animal assemblages not only in the agrocenoses, but also in the patches they surround. This is mainly due to crop intensification and monoculture, the use of chemicals and the homogenization of the entire landscape (Opatovsky et al. 2010; Fuentes-Montemayor et al. 2012; Kosewska et al. 2014). Agricultural areas are basically an open space, which can be characterized by extremely different microclimatic conditions compared to forest assemblages. The open space includes, among others, intensive insolation, higher temperature amplitudes and lower humidity (Harper et al., 2005). As a result, the surroundings of the patches can act as a type of filter, allowing only species capable of surviving in such conditions to move about in it (Gascon et al. 1999). The presence of such a filter may be particularly unfavorable for animals whose life cycle is associated with several types of habitats. For example, amphibians use ponds for laying eggs, and the forest environment for hibernation and estivation (summer slowdown of life processes) (Joly et al. 2001). Agricultural areas hinder the movement of these animals, which adversely affects their survival (Joly et al. 2001; Fuentes-Montemayor et al. 2013). For this reason, large-sized and continuously arable fields should be avoided in the agricultural landscape. The introduction of grassy and herbaceous vegetation belts, particularly trees and shrubs, should be promoted. Their presence increases the connectivity of forest habitats (Joly et al. 2001; Ernoult et al. 2013).

The connectivity of forest patch habitats is also ensured by wildlife corridors (Červinka et al. 2013), that is, linear elements in the landscape providing a physical connection between a minimum of two patches (Beier, Noss 1998). Wildlife corridors facilitating animal dispersion in anthropogenic areas allow a comparatively stable population size of the species to be maintained in relatively spaced apart forest fragments and reduce the risk of gene pool erosion by not disrupting the gene flow (Tewksbury et al. 2002; Pardini et al. 2005). Laurance and Laurance (1999) also stated that other elements in the landscape, not considered strictly corridors as understood by Beier and Noss (1998), for example, elongated ecosystem patches with a rich vegetation structure, can also facilitate animal dispersion, thus limiting the negative impact of fragmentation (Martensen et al. 2008; Červinka et al. 2013).

The effectiveness of wildlife corridors as a means of animal dispersion depends on a number of factors, including their internal vegetation structures, their width and length or the presence of environmental barriers, such as roads and rivers (Fleury, Brown 1997; Beier, Noss 1998; Haddad 1999; Laurance, Laurance 1999; Martensen et al. 2008). Vegetation structure influences the use of corridors by animals (Niemelä 2001). For example, Červinka et al. (2013) showed that the presence of shrub vegetation positively influenced the use of corridors by mustelids (Mustelidae). The presence of such vegetation provides food and shelter for animals (Ruefenacht, Knight 1995; Červinka et al. 2013). While vegetation structure significantly influences the effectiveness of corridors, the role of their width seems ambiguous. Some authors (Fleury, Brown 1997; Rodríguez-Soto et al. 2013) indicate corridor width as one of the elements determining their use by animals. According to the others (Ruefenacht, Knight 1995; Bolger et al. 2001), this feature has no effect on the use of these environmental elements. These differences result to a large extent from the individual requirements of a species in relation to the habitat conditions prevailing in them (Laurance, Laurance 1999; Červinka et al. 2013; Rodríguez-Soto et al. 2013). This is because corridor width, just like area in the case of patches, determines the relative share of internal habitats with a significant level of ecological stability. As the width of the corridors increases, the possibility of sheltering from predators and securing food increases. Wide corridors primarily enable the forest species with large body sizes and significant individual territories, such as the jaguar *Panthera onca* L., to move between patches of their preferred habitat. A large width does not exclude the use of corridors by species with less stringent habitat requirements or those preferring the edge habitats of forest patches, for example, the pygmy tarsier *Tarsius pumilus* Miller & Hollister, a Tarsiidae family mammal species from Indonesia. However, the requirements of forest stenobionts are the basis for designing wildlife corridors in the landscape. Too narrow corridors can reduce their effectiveness and result in their use mainly by opportunistic species. In addition, due to their shortage in the environment, animals may be present in significant densities in narrow corridors, which can result in intensified intra- and interspecies competition for habitat resources (Fleury, Brown 1997; Lees, Peres 2008; Brosi 2009; Červinka et 2013; Grow et al. 2013; Rodríguez-Soto et al. 2013).

Wildlife corridors between forest patches are undoubtedly a key way of enabling the dispersion of strictly forest dwelling animals. In the absence of wildlife corridors, the distance between forest patches can also significantly affect animal dispersion (Uezu et al. 2005; Martensen et al. 2008). For example, the Siberian flying squirrel, *Pteromys volans* L., a mammal species of the squirrel family Sciuridae, travels by using tree crowns. When forest patches or individual trees are separated by several dozen meters, it can soar and thus move through the landscape using the folds of the skin between its front and rear paws (Selonen, Hanski 2003). For such animals, unable to travel in open space over long distances, patches not connected by wildlife corridors, but not very far apart, can act as intermediate stopovers. This means that animals can successively move (from patch to patch) through the landscape (Magura et al. 2001). The distance between forests plays a significant role in their biodiversity. Fuentes-Montemayor et al. (2012) showed that patches located close to the other forest assemblages, especially those of a large area, were characterized by a richer qualitative and quantitative structure of animal assemblages compared to the fragments at a greater distance. The distance between habitats in a landscape is less important in the case of species with high dispersibility (those capable of traveling over large areas) and able to survive in different types of habitats. For such animals (e.g., orchid bees, Eurasian red squirrels and so on) even the lack of wildlife corridors between patches does not mean that the actual isolation of the habitats in which they live (Delin, Andre 1999; Uezu et al. 2005; Brosi 2009).

4. Implications for landscape management

Assessing the impact of forest habitat fragmentation on fauna assemblages is primarily based, thus far, on factors acting at the scale of a single patch (mainly surface area and degree of patch isolation). The area of the forest fragment plays a significant role in shaping the structure of the animal assemblages, which is why it is important to define the forest in its natural and legal contexts. According to the FAO (2012b), the minimum area of a forest is 0.5 hectares, and according to national legislation (Act of 1991), a forest is "land with a compact area of at least 0.10 ha (...)". The minimum area of 0.1 ha has also been assumed for regulations on qualifying a piece of land for afforestation (MRiRW 2017). Taking into account the already mentioned requirements of forest species and the interaction of the factors discussed above, it should be stated that this area is too small for the vegetation it contains to be considered a forest in functional terms. From an ecological point of view, such a patch will not be characterized by the species structure characteristic of large forest assemblages (Cabrera-Guzmán, Reynoso 2012), and therefore, the most valuable in terms of the natural environment. Assuming that a forest is something more important than just a cluster of trees, it seems that the area should be larger. According to Bücking (2003), only patches with an area of 1.0 ha should be thus considered, assuming that they have a compact shape (square, circle) and an inner zone that is not influenced by the surrounding open space. This happens when the edge effect only reaches two heights of the tree stand. However, its impact can be many times greater – several hundred meters (Hofmeister et al. 2013). In such a situation, only patches exceeding a dozen hectares are able to provide forest fauna with a stable inner zone, and in the case of patches having a developed boundary with open space, this area can be much larger (Schneider-Maunoury et al. 2016). Therefore, the smallest surface area of forest patches and those having a developed boundary with the open space should receive the attention of conservation activities. One should strive to maximize the surface area and decrease the edges of the patches by planting trees in the adjacent areas. An important issue in relation to the forest islands is the ecotone zone. Many forest fragments have a sharp and abrupt boundary with an open space. In order to eliminate the edge effects, ecotone zones should be propagated, with a rich spatial structure of vegetation achieved by developing the shrub and herbaceous plant layers (Magura 2002).

In addition to the features of the forest fragments themselves, assessing the ecological consequences of the process of forest habitat fragmentation should also take into account the wider scale, that is, their entire surroundings – the landscape. Elements such as: the number of patches, their distance from large forest complexes, the presence of wildlife corridors, the nature of the space around the islands and how it contrasts with the forest environment are factors that have a significant impact on the structure of animal assemblages. Martensen et al. (2008) even stated that for animals, a significant negative consequence of forest fragmentation is not so much reduced surface area and their insular character, but the difficulties in dispersing in a landscape lacking the features conducive to the animals' use. The survival of a species of animals in the landscape is even more probable if the patches of forest habitat are better connected to each other, creating a functional network (Laurance, Laurance 1999). Therefore, landscape modifica-tion may be one of the basic tools in mitigating the effects of forest fragmentation (Beier, Noss 1998; Haddad 1999). These activities should involve the promotion of wildlife corridors in the landscape, clumps of natural renewal, in-field and roadside trees and shrubs, as well as individual trees. These elements facilitate the movement of animals in anthropogenic space (Anderson et al. 2007; Umetsu, Pardini 2007). From this point of view, even the smallest patches covered with trees are important in the environment. When planning new renewals, it is important to consider both the features of a single patch, as well as its location in relation to the neighboring patches and large forest complexes, and the nature of the habitat in the surrounding environment. In this context, it is also important to educate the private forest owners about the characteristics of the forest patches. A higher level of biodiversity means less exposure to harmful natural and anthropogenic influences (Brockerhoff et al. 2008). These private forest owners should therefore be vitally interested in enriching the agricultural environment with structures that make it more animal-friendly, facilitating their mobility between individual patches.

Protecting biodiversity is among the most important activities undertaken to preserve natural resources (Kleiner et al. 2009). As mentioned, forests are considered a refuge for biodiversity (Brockerhoff et al. 2008). The development of anthropogenic space in the future may constitute a specific justification, and at the same time a challenge for conservation activities aimed at protecting and preserving biodiversity. It's very likely that the role of forests as a refuge for biodiversity will gain in importance. The problem of the permanent loss of forested areas on almost all of the continents still remains. Over the past few centuries, the global forest area has been reduced by almost half. It is deforestation and the transformation of forest assemblages from originally large and expansive areas into a number of variably sized and isolated patches suspended in the anthropogenic landscape that will probably pose the most serious threat to biodiversity in the future.

Conflict of interest

The authors declare that there are no potential conflicts of interest.

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Authors' contributions

R.B. – concept, literature review, writing the manuscript; A.K. – literature review, writing the manuscript; J.B. – concept, writing the manuscript, text corrections.

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