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Author: Baltrūnaitė, Laima

Source: Folia Zoologica, 59(4) : 278-284

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/fozo.v59.i4.a2.2010

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Folia Zool. – 59 (4): 278–284 (2010)

Winter habitat use, niche breadth and overlap between the red fox, pine marten and raccoon dog in different landscapes of Lithuania

Laima BALTRŪNAITĖ

Nature Research Centre, Akademijos 2, LT-08412 Vilnius, Lithuania; e-mail: laima@ekoi.lt

Received 8 January 2010; Accepted 23 April 2010

Abstract. Winter habitat use, niche breadth and overlap between the native and invasive species of medium sized predators, the red fox, pine marten and raccoon dog in particular, were studied in three landscapes with different habitat structure in Lithuania. Meadows were preferred by foxes but avoided by raccoon dogs and pine martens. Pine martens intensively used various forest habitats, whilst raccoon dogs tended to prefer swamps. The habitat niche breadth (Hurlbert's standardized niche breadth) varied with respect to both the species and the study site. The habitat niche overlap was larger between raccoon dog and pine marten than that between raccoon dog and red fox. Our results suggest a low impact of the invasive raccoon dog on red fox and pine marten in studied landscapes.

Key words: medium-sized predators, invasive species

Introduction

The mammalian invasive species such as the raccoon dog *Nyctereutes procyonoides*, may have a significant detrimental impact on native mammalian species (Kauhala 1995, 1996b, Kobylińska 1996, Jędrzejewska & Jędrzejewski 1998, Kauhala et al. 1998, Borowski 2006, Kowalczyk et al. 2008, Sidorovich et al. 2008). In addition to competitive influence, invasive species may dramatically affect native species as a vector of rabies and other diseases (Kauhala et al. 2006, Holmala & Kauhala 2006, 2009). Therefore, information on relationships between raccoon dog and native species under different circumstances is of particular interest for the evaluation and prediction of invader impacts.

The natural distribution range of the raccoon dog is Eastern Asia. In 1929–1955, this medium-sized predator was introduced into the northwestern part of the former USSR. Later the raccoon dog spread to other regions of the former USSR and the neighbouring European countries. In Lithuania, the predator was first recorded in 1948, and by 1960 it occurred throughout the country (Prūsaitė et al. 1988). Recently, the raccoon dog together with native species, the red fox *Vulpes vulpes* and pine marten *Martes martes*, represent the most abundant and common medium-sized predators in Lithuania (Balčiauskas et al. 1999).

Diet studies of raccoon dog, red fox and pine marten have shown that higher food niche overlap in Lithuania is typical among the native species (Baltrūnaitė 2002, 2003, 2006). The highest food niche overlap has been observed in winter, when the abundance and availability of food decrease. Therefore, studies on habitat use in winter, a crucial season for medium-sized predators survival, may provide an important information about possible influence of invasive on native predators.

Referring to previous results, we hypothesized that in Lithuania the partitioning of food and habitat resources may result in weak competitive impact of the racoon dog on native species. This hypothesis is in accordance with the trend of abundance increase in all the studied species of medium-sized predators currently observed in Lithuania.

The aims of this study are 1) to analyze the habitat use in individual species in landscapes with different habitat structure, and 2) to estimate the niche breadth

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and overlap between these species.

Study Area

The study was performed in three study sites with area 120–150 km^2 located in the Varėna (54°06' N; 24°18' E), Anykščiai (55°33' N; 24°48' E) and Molėtai (55°09' N; 24°19' E) districts of Lithuania (southern, north-eastern and eastern part of the country, respectively), representing different landscapes: sandy plains, clay plains and hilly morainic uplands, referred below as Sands, Clays and Moraines, correspondingly. During the study period 1999–2002, the mean annual temperature was 7.7°C (-1.5°C in January and 18.9°C in July; Archive of Lithuanian Hydrometeorological Service).

The Sands site comprised mainly forests (86.7%) including continuous pine *Pinus sylvestris* stands (71.4%) and other stands (birch *Betula* sp., black alder *Alnus glutinosa*, spruce *Picea abies*) (15.3%), and open habitats (11.9%). The Clays site structure was as follows: forests (69.6%) including spruce *Picea abies* (17.2%), deciduous (24.6%, mainly birch and also asp, black alder, grey alder *A. incana*, oak *Quercus robur*) and mixed stands (24.6%), and open habitats, mainly meadows and arable land (15.1% and 8.6%, respectively). Fragmented landscape composed of various forest and open habitats was characteristic of the Moraines site. It was comprised of forests (42.9%) including deciduous (mainly asp, birch, oak and also alders, ash *Fraxinus excelsior,* maple *Acer platanoides* and elm *Ulmus* sp.) and mixed spruce – deciduous stands (24.2% and 12.7%, respectively). Meadows (34.3%) prevailed among open habitats.

Material and Methods

The winter habitat use was assessed by snow-track count in 1999/2000–2001/2002 (Sands and Clays), and in 1999/2000–2000/2001 (Moraines). Once a year in late winter or early spring (February–March), 1–2 days after the snowfall, the chosen transect divided into 50 m long sections was walked recording habitat type and number of each predator species tracks in each section. In total, 163.3, 152.4 and 63.9 km were walked in Sands, Clays and Moraines sites, correspondingly.

For comparison of the species abundance between the studied sites, the relative abundance was estimated as track number per 1 km long transect per day. Pooled data for each species for the entire study period were analyzed by one-way ANOVAs and tested for difference using Tukey's honest significance differences test (HSD).

Current data on predator abundance in Lithuania are not available, as official surveys were terminated since 1998 (The Ministry of Environment). However, the hunting bag may be used to reveal general trends in change of predator abundance, and this method has been applied for studies of population dynamics (Carlsson et al. 2010). To reveal whether the hunting bag may be used as a proxy for abundance, the correlation between official predator survey and hunting bag (both marten species were pooled) was estimated for the period 1977–1997. The relationship was significant ($r = 0.43$, $P < 0.001$), therefore, we used the hunting bag for each species as an indicator of their abundance. Correlations (Spearman) between the individual species hunting bag as well as the hunting bag change between time periods (1990–1999 vs. 2000–2009) were assessed in order to establish general trends in predators' abundance.

The habitat selection was determined by the Chesson's electivity index, ε (Chesson 1983):

$$\varepsilon = \frac{ma_i - 1}{(m-2)a_i + 1},$$

where m is the number of habitat types, and a_i is the Manly-Chesson selection index for species i:

$$\alpha_i = \frac{n_{ri} / n_{pi}}{\sum_{i=1}^{m} (n_{ri} / n_{pi})},$$

where n_{ri} is the proportion of tracks in the habitat type, and n_{pi} is the proportion of the habitat type (Manly et al. 1972, Chesson 1978). The electivity index value ranges between -1 and +1, indicating positive selection when it is above 0 and negative when less than 0.

Significance of the habitat type selection was assessed using the log-linear analysis for frequency tables based on the null hypothesis that a species uses the habitat type in proportion to the area it occupies. The habitat type was assessed as preferred (used intensively, i.e. visited more frequently than expected), visited in proportion to habitat availability, and avoided (selected rarely, i.e. visited less frequently than expected). To account for multiple tests on non-independent data, a Bonferroni sequential test was applied (Rice 1989). For preliminary analysis, the forest habitats were classified into 15 categories: pine, spruce, mixed coniferous, soft broad-leaved (birch, asp, alders), hard broad-leaved (oak, ash, maple, elm), mixed deciduous and all variants of mixed stands. As differences between initially distinguished forest habitat types within coniferous, deciduous and mixed

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forests were mostly not significant, these habitats were further pooled into three main categories: coniferous, deciduous and mixed forest habitats. An exception was made for Sands. In this study site, coniferous forests were divided into two categories: pine stands and spruce/mixed coniferous stands, because the difference between these categories was significant, and the selection indices were opposite in these habitat types. The open habitats were grouped into four categories: clear-cuts, swamps, meadows/pastures and arable land.

The niche breadth and overlap were assessed using the Hurlbert's standardized niche breadth (B'_A) and the Hurlbert's measure of niche overlap (L) (Krebs 1999):

$$B'_A = \frac{B' - a_{min}}{1 - a_{min}},$$

where a_{min} is the smallest proportion of all the habitat types, B′ is the Hurlbert's niche breadth:

$$B' = \frac{1}{\sum(p_j^2 / a_j)},$$

where p_j is the proportion of tracks in the habitat j, and a_j is the proportion of the habitat j in the landscape:

$$L = \sum_i^n \left(\frac{p_{ij}\, p_{ik}}{a_i} \right),$$

where p_{ij} (or p_{ik}) is the proportion of the tracks in habitat type i utilized by species j (or k), a_i is the proportional size of habitat type i.

The range of the Hurlbert's standardized niche breadth (B'_A) varies from 0 to 1. The Hurlbert's measure of niche overlap (L) is 1 when both species utilize each resource in proportion to its availability, 0 when the two species share no resources, and > 1 when the two species both use certain resource more intensively than others and the preference of the two species for resources tends to coincide.

Results

Species abundance

The relative abundance of the red fox and pine marten was significantly lower in the Sands site compared to both other landscapes, the Clays and Moraines sites (HSD tests: $P < 0.001$), but did not differ between the Clays and Moraines sites (HSD test: $P < 0.6$) (Fig. 1). Meanwhile, the abundance of the raccoon dog significantly differed among all the study sites (HSD test: Sands vs. Clays, $P < 0.001$; Sands vs. Moraines, $P < 0.001$; Clays vs. Moraines, $P < 0.01$).

Significant positive correlation between the hunting bag of all species was observed during 20 year period, 1989–2009 (red fox and martens: r = 0.88, $P < 0.001$; red fox and raccoon dog: r = 0.85, P < 0.001; martens and raccoon dog: r = 0.88, $P < 0.001$). Comparison of the hunting bag between the two last decades clearly showed the increase in abundance for all species (t-tests: red fox (mean ± SD) 4617 ± 2919 vs 14195 ± 3304 ind. year $^{-1}$, t = 8.04, $P < 0.001$; raccoon dog: 683 ± 292 vs 4339 ± 1376 ind. year $^{-1}$, t = 6.52, $P < 0.001$; marten: 244 ± 105 vs 721 ± 295 ind. year $^{-1}$, t = 4.29, $P < 0.001$).

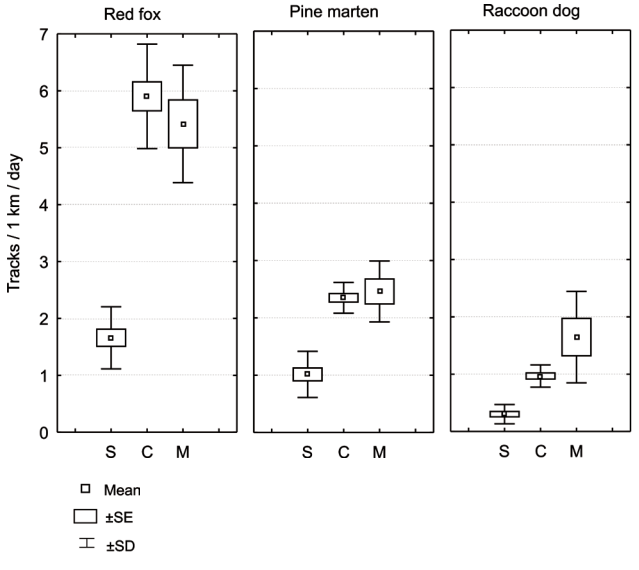


Fig. 1. *Relative abundance of red fox, pine marten and raccoon dog in Sands (S), Clays (C) and Moraines (M) sites.*

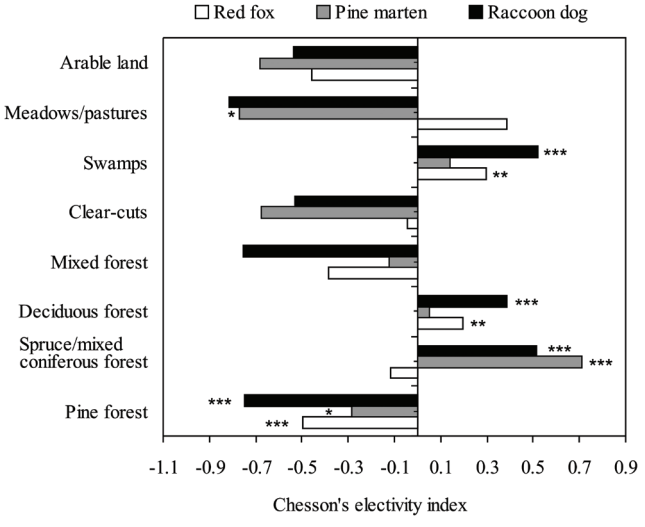


Fig. 2. *Winter habitat selection by red fox, pine marten and raccoon dog in the Sands site. Asterisks indicate significance level: * P < 0.05, ** P < 0.01, *** < 0.001.*

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Habitat use

In the Sands site, prevailing pine stands were rarely visited by all medium-sized predator species. Foxes preferred meadows, deciduous stands and swamps (Fig. 2). Pine martens frequently used spruce and mixed coniferous stands, but avoided meadows. Raccoon dogs intensively used swamps, spruce/mixed coniferous and deciduous stands (Fig. 2).

In the Clays site, meadows were the only preferred habitat for foxes. This predator rarely visited coniferous and deciduous stands, and arable land. Pine martens intensively used mixed stands. However, open habitats (meadows, arable land and clear-cuts) were avoided. Raccoon dogs visited meadows less frequently than expected. The other habitat types were used in proportion to their availability (Fig. 3).

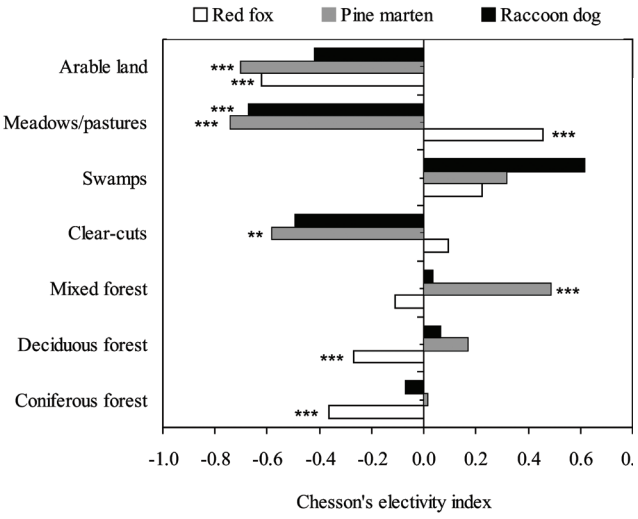


Fig. 3. *Winter habitat selection by red fox, pine marten and raccoon dog in the Clays site. Asterisks indicate significance level: ** P < 0.01, *** P < 0.001.*

In the Moraines site, red foxes visited all the habitat types in proportion to their availability. Raccoon dogs and pine martens avoided meadows. Mixed stands were preferred by pine martens (Fig. 4).

Niche breadth and overlap

Red fox and pine marten showed the broadest niche (B'_A) in the Sands site. In this landscape, the raccoon dog niche was more than two-fold narrower (Fig. 5). In the Clays site, the niche breadth was similar in red fox and pine marten, and slightly broader in raccoon dog. The niche breadth of red fox showed the highest values (0.95) in the Moraines site due to habitat type use in proportion to their availability. In

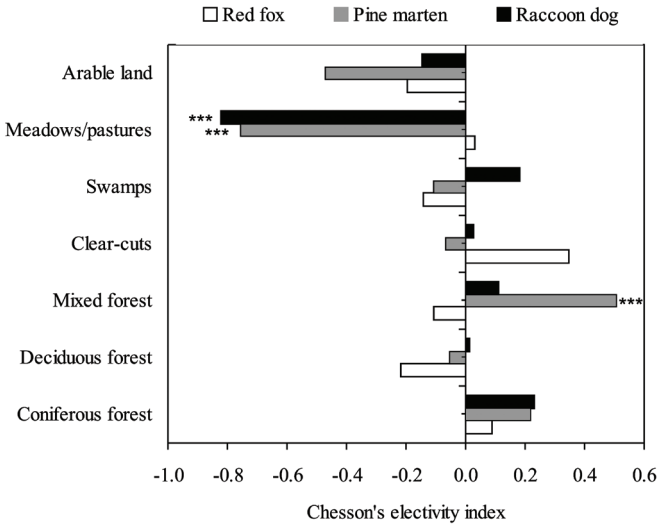


Fig. 4. *Winter habitat selection by red fox, pine marten and raccoon dog in the Moraines site. Asterisks indicate significance level: *** P < 0.001.*

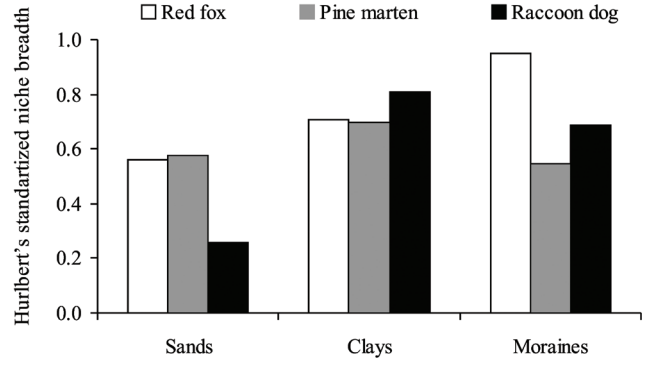


Fig. 5. *Niche breadths of red fox, pine marten and raccoon dog in Sands, Clays and Moraines sites.*

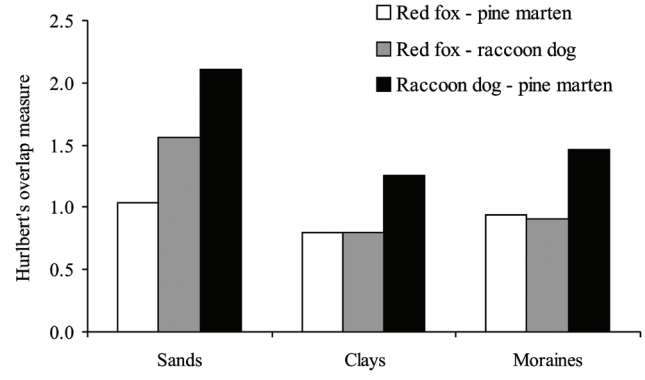


Fig. 6. *Niche overlaps between red fox, pine marten and raccoon dog in Sands, Clays and Moraines sites.*

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comparison, the niche of pine marten and raccoon dog was narrower.

Over all the study sites, the largest overlap in habitat use (L) was estimated between raccoon dog and pine marten, whereas, overlaps between raccoon dog and red fox, and between both the native predator species were lower (Fig. 6). When comparing study sites, the overlap indicators between species pairs in Sands site were higher than those in other studied landscapes.

Discussion

In this study we analyzed the winter habitat use in three species of medium-sized predators, invasive raccoon dog, and native red fox and pine marten. Winter season is of critical importance for survival of medium-sized predators, therefore, information on relations between invasive and native species during this season may be of particular importance for understanding impacts of invasive species. Although winter hibernation is characteristic for raccoon dog, its winter activity depends on day length and weather (Kauhala et al. 2006). During mild winters, raccoon dogs remain active all the year round in Lithuania. In the study period, the weather conditions were favourable for raccoon dog with respect to its activity, and that allows for comparison of the habitat use with the native species.

Our results indicate some general patterns in the predator habitat use typical for all the study sites. Meadows were preferred by foxes, but avoided by pine martens and raccoon dogs. Pine marten showed preference to forest habitats. Raccoon dogs were more frequently observed in swamps, however, no habitat type was significantly preferred in the studied landscapes. The preference and avoidance of particular habitats by these predators may vary in different landscapes with respect to habitat structure (e.g. Pulliainen 1981, Storch et al. 1990, Cavalini & Lovari 1991, Kauhala 1996a, Sidorovich 1997, Jędrzejewska & Jędrzejewski 1998, Brainerd & Rolstad 2002, Sidorovich et al. 2005, Saeki et al. 2007). Red foxes usually show preference to open areas, while pine martens prefer various forest habitats. Our results indicate some differences in the raccoon dog habitat use. The species showed avoidance of meadows and tended to avoid arable land. Drygala et al. (2008) suggested an opportunistic and flexible habitat use by raccoon dogs with no significant differences between seasons in north-eastern Germany. Holmala & Kauhala (2009) suggested fields as one of most preferred habitat in summer-autumn in southeastern Finland. This study was performed during the end of the winter season, and the pattern of habitat use may be different at that time. The avoidance of meadows and arable land by raccoon dogs might be related to varying food availability in different habitats. During winter, probability to find the food (e.g. carrion, the most important food item in winter) is usually higher in forests than in other habitats (Baltrūnaitė 2005). However, the observed pattern may also be associated with lower activity of the species during winter. The more frequent use of open habitats by raccoon dogs in the warm season may be related to the increase of food availability.

The niche breadth of all the studied species was comparatively wide (usually over 0.5). However, some differences between species in studied landscapes emerged. The breadth of the red fox niche increased with the increase in proportion of meadows in the landscape, and it was the highest in the Moraines site where the proportion of forests and open habitats was balanced. Only in that landscape the red fox used habitat types proportionally to their availability. The niche breadth in pine marten was rather similar in all the three studied landscapes, with the highest value in the Clays landscape. The niche breadth decreased with the increase in proportion of low productivity pine forests (Sands site), as well as with the increase in proportion of avoided open habitats (Moraines site). Whilst the niche of the raccoon dog was notably narrow in the Sands site due to avoidance of pine forests and preference for other habitats which share in the landscape was small. In the Clays and Moraines sites, the niche breadth was substantially wider as this species avoided only meadows and used other biotopes in proportion to their availability.

The niche overlap, between the native red fox and pine marten was small in all the studied landscapes as these species prefer different habitats, meadows and/or forests. The varying preference for meadows was responsible for the low niche overlap also between red fox and raccoon dog in the Clays and Moraines, however, it was larger in the Sands dominated by pine stands. The largest niche overlap was determined between raccoon dog and pine marten with rather similar habitat preferences over studied landscapes. Our results suggest that the impact of invasive raccoon dog on red fox may be negligible in the Clays and Moraines as these species showed spatially segregated habitat use, while the larger niche overlap between raccoon dog and pine marten may indicate a competitive impact of the invasive species. In the Sands landscape, the low habitat niche overlap was observed only between the native species whereas it was larger between the

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invasive and native species. Such a pattern suggests that, in a landscape of low productivity, the competitive impact of raccoon dog on the studied native medium-sized predators may be more important than that in productive and heterogeneous environments.

On the other hand, diet studies have shown the higher food niche overlap between the native species. In winter, rodents and carrion predominate in the diet of red foxes and pine martens, whereas, raccoon dogs mostly consume carrion, supplemented by plants, rodents, insectivorous and amphibians (Baltrūnaitė 2002, 2003, 2006). Such a pattern may indicate a stronger competition for food between native species. Furthermore, direct interference could occur between the red fox and pine marten (Storch et al. 1990, Lindström et al. 1995). The data obtained on winter habitat and food niche of raccoon dog and their overlap with red fox and pine marten suggest that the impact of the former species on native species in Lithuanian ecosystems may be comparatively low. This conclusion is in accordance with the recent trend in the increasing abundance of medium-sized predators in Lithuania. The increase in the abundance of raccoon dog did not result in a distinct decline of native species. However, the negative impact of naturalized alien species, the raccoon dog and American mink, resulting in the decrease of density of the most native predators, including the red fox and pine marten, was reported in Belarus (Sidorovich et al. 2008). Such a difference may be associated with different abundance of the raccoon dog in Lithuania and Belarus. Weak competitive interactions between the raccoon dog and native medium-sized predators were observed also in Poland (Borowski 2006). In conclusion, our data suggest that in Lithuanian ecosystems, at least currently, the competition is not severe between invasive species, the raccoon dog, and abundant native species, the red fox and pine marten. However, the raccoon dog may negatively affect the other native species such as the polecat *Mustela putorius* and badger *Meles meles*, which are less abundant in Lithuania than the studied species (Balčiauskas et al. 1999), and might be more vulnerable to detrimental impact from invasive species.

Acknowledgements

This study was partly funded by the former Lithuanian State Science and Studies Foundation. I am grateful to anonymous reviewers for valuable comments.

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