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Original article

Breakdown of the species-area relationship in exotic but not in native forest patches

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ARTICLE INFO

Article history:
Received 14 September 2007
Accepted 23 November 2007
Published online ■

Keywords:
Birds
Forest specialist species
Forestry practice
Hungary
Generalist species
Habitat structure

ABSTRACT

We studied the pattern of bird species richness in native and exotic forest patches in Hungary. We hypothetized that species-area relationship will depend on forest naturalness, and on the habitat specialization of bird species. Therefore, we expected strong species-area relationship in native forest patches and forest bird species, and weaker relationship in exotic forest patches containing generalist species. We censused breeding passerine bird communities three times in 13 forest patches with only native tree species, and 14 with only exotic trees in Eastern Hungary in 2003. Although most bird species (92%) of the total of 41 species occurred in both exotic and native forests, the species-area relationship was significant for forest specialist, but not for generalist species in the native forests. No relationship between bird species and area was found for either species group in the forest with exotic tree species. The comparison of native *versus* exotic forest patches of similar sizes revealed that only large (>100 ha) native forests harbor higher bird species richness than exotic forests for the forest specialist bird species. There is no difference between small and medium forest patches and in richness of generalist species. Thus, the species-area relationship may diminish in archipelago of exotic habitat patches and/or for habitat generalist species; this result supports the warning that the extension of exotic habitats have been significantly contributing to the decline of natural community patterns.

1. Introduction

Forests are invaluable for human beings. They are important for recreation and human well being, and provide numerous ecosystem services, and are vital for the maintenance of the majority of biological diversity on Earth (Lacaze, 2000; Dirzo and Raven, 2003; Ozanne et al., 2003; Lewis, 2006). These roles need to be considered when we try to manage forests. For example, the use of wood for heating and timber in construction or paper industry needs fast growing trees, planted in a regular pattern for easy management, without other tree or scrub species. These plantations often are of non-native species and thus are inferior for recreation, and inappropriate for the maintenance of native biodiversity (Koch and Skovsgaard, 1999; Carnus et al., 2006; Gentry et al., 2006). For example, in Hungary 20% of forest cover is the black locust (*Robinia pseudoacacia*), originally from North America, and 15% is black pine (*Pinus nigra*), a European species, but not native to

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1146-609X/$ – see front matter © 2008 Published by Elsevier Masson SAS.
doi:10.1016/j.actao.2007.11.007

Hungary (Mátyás, 1997). There are similar patterns for other countries (e.g., EEA, 2006).

What are the effects of exotic (i.e. introduced or non-native) trees and forests on native wildlife? Bird species usually prefer native habitats over exotic patches (Ramos, 1996; Ortega et al., 2006). Native bushes are superior foraging sites for birds (French et al., 2005). Nesting on exotic bushes in urban parks resulted in higher rate of nest failure than nesting on native bushes (Schmidt and Whelan, 1999; Borgmann and Rodewald, 2004). Exotic forest plantations can lure settling birds into such suboptimal habitat, where nest failure is higher than in native forests (Remes, 2003).

Knowledge of the effects of exotic tree plantations on birds at the community level is limited. Several studies aimed to compare communities in native and exotic forests, using simple parameters. Species richness and abundance is less variable than species composition in native *versus* exotic forests (Hausner et al., 2002; Johnson and Freedman, 2002; Steverding and Leuschner, 2002; Bakker and Higgins, 2003), although some studies have failed to detect any differences (Donald et al., 1998; Fleishman et al., 2003; Wilson et al., 2006). The underlying mechanism of community differences between native and exotic forests may be the predation pressure on avian broods (Barber et al., 2001; Carignan and Villard, 2002), or the selective habitat preferences of species (Lerner and Stauffer, 1998). However, we have been unable to find any comparison of the species-area relationship (SAR) in exotic *versus* native forests. This is surprising, because SAR is a basic rule of ecology, stating that species richness increases with increasing sample area (Rosenzweig, 1995; Báldi and McCollin, 2003; Drakare et al., 2006). Thus, the important question is whether a fundamental ecological relationship is altered by one of the most peculiar and pervasive human activities of modern times – to introduce plant species to areas outside their native ranges. In this study we investigated if exotic forests harbour fewer species than native patches. We compared the species-area relationship of bird assemblages in native *versus* exotic forest patches in Eastern Hungary. We hypothetized that SAR will depend on forest naturalness, and on the habitat specialization of species. Naturalness probably acts via heterogeneity, which is higher in native than in exotic forests (Thompson et al., 2003; Bartha et al., 2006). Forest patches are islands for forest specialist species, but less so for generalist species, which may occur in the surrounding landscape. This may mask the general species-area relationship (e.g. Magura et al., 2001). Therefore, we expect significant SAR in native forest patches and forest specialist bird species, and weak, if any in exotic forest patches with generalist species. Further, we expect similar species richness values in small native and exotic forest patches, where no real interior habitat is available. However, different species richnesses are expected in large patches due to difference in the species-area relationships. Such finding may have important nature conservation consequences for the maintenance of biodiversity.

2. Study area and methods

The study area is located in Eastern Hungary on the Szatmár-Bereg plain (Fig. 1) (N 48°05′55″, E 22°30′22″). The plain is covered by pastures and agricultural land with scattered forest patches. The natural vegetation of Central-European plains is forest, but the millennia of human activities (e.g., cattle grazing) modified it into primarily grassland areas with small forest patches (Standovár and Primack, 2001). Roughly 80% of the region is farmland. The surroundings was similar for all studied patches, grassland and/or arable fields. Native and exotic tree species were present in the patches. We chose 13 forest patches with only deciduous native tree species (*Quercus robur*, *Carpinus betulus*, *Quercus petraea*, *Populus canescens*, *Populus alba*, with a few *Acer campestre*, *Salix alba* and *Fraxinus angustifolia*), and 14 with only deciduous exotic tree species (*Robinia pseudoacacia*, *Populus canadensis*, with few individuals of *Quercus rubra*, *Acer negundo*, *Salix matsudana*, *Amorpha fruticosa* and *Fraxinus pennsylvanica*). The age of studied forest patches was 35–70 years. Three area categories of forest fragments were established: small (<10 ha), medium (10 < 100 ha), and large (>100 ha) (Table 1). Within size class fragments with natural tree composition and those with exotic trees were distinguished. There was no significant difference between the mean area of these two groups within area category ($t_7 = 0.289$, $p = 0.781$ for small forests, $t_7 = -0.812$, $p = 0.443$ for medium forests, and $t_7 = 2.853$, $p = 0.064$ for large forests). Forest patch heterogeneity was estimated by eye as percent cover of shrubs and number of nest holes within the censused areas.

Breeding bird communities were censused in the forest patches in the breeding season of 2003. Three censuses were carried out during the season (April, May and early June), only under good weather conditions (no wind or rain), from sun rise to 9 a.m. (Moskát, 1987). We applied a standard point census technique (100 m radius, 5 min census time); all birds seen or heard were recorded. Sampling effort was standardized for all patches – since many patches were only a few hectares large, one point per patch at such patches was possible to census. We distinguished between forest specialist and habitat generalist species based on literature data (Snow and Perrins, 1998), considering local conditions.

The species-area relationship was established with the most frequently used log-log transformed model (Rosenzweig, 1995), using individual patch areas (not the categories) in the calculation. The number of forest specialist and generalist bird species between the two forest types (native and exotic) with similar size were examined by repeated measure analysis of variance (ANOVA). Forest type (native or exotic) was considered as factor and the time of the counting (April, May and June) were used as repeated measures. The data were normalized by $\log(x+1)$ transformation. When the results of the ANOVA showed that there was difference in the species richness among the forest types, this was tested by a Tukey-type multiple comparison (Sokal and Rohlf, 1981). The analyses were carried out using the SPSS-PC program (SPSS, 1999).

3. Results

Shrub cover did not differ significantly between native and exotic forest patches ($t_7 = 0.324$, $p = 0.755$ for small forests, $t_7 = 0.040$, $p = 0.969$ for medium forests, and $t_7 = 0.828$,

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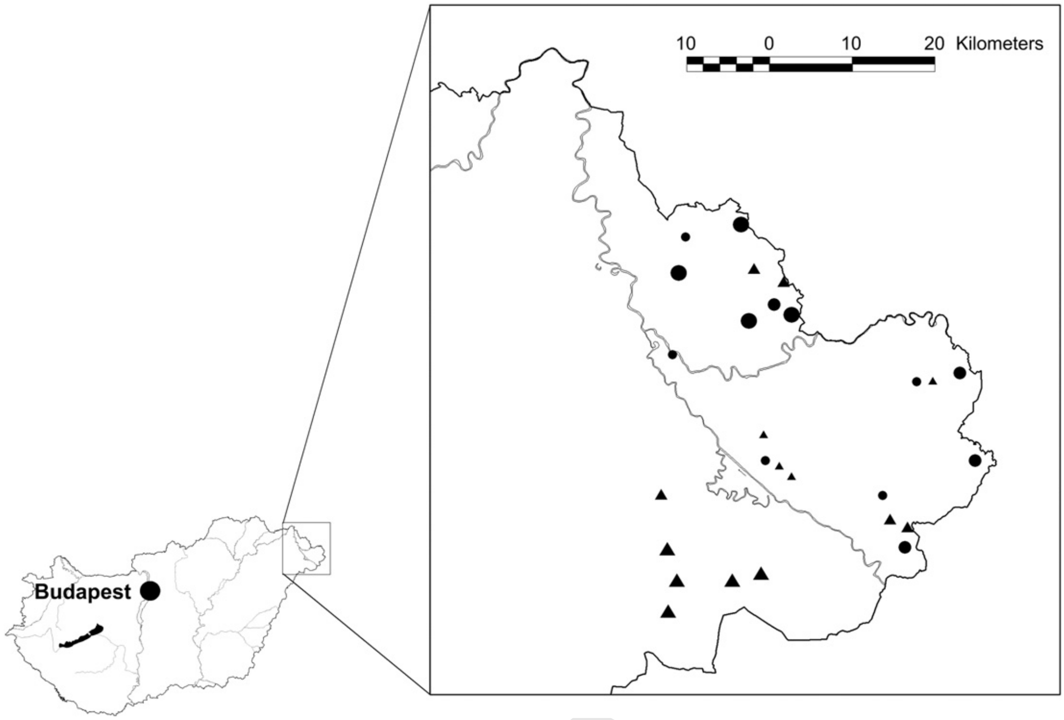

Fig. 1 – Location of the study area in Eastern Hungary. Triangles represent forest patches of exotic tree species and circles native tree species. The size of the mark represents three area categories of the patches (< 10 ha, 10–100 ha, > 100 ha).

$p = 0.435$ for large forests). There were more nest holes in native forest patches compared to the exotic patches in small and large forests, but not in the medium size category ($t_7 = 3.653$, $p = 0.008$ for small forests, $t_7 = 1.005$, $p = 0.348$ for medium forests, and $t_7 = 2.543$, $p = 0.038$ for large forests).

Altogether 41 bird species were observed during the censuses. Most species (92%) were observed in both the native and the exotic forest patches (Appendix). The species-area relationship was significantly positive in the native forest patches for forest specialist species, and positive but not significant for generalist species (Table 2). No species-area relationship were found for bird assemblages in exotic forest patches (Table 2).

Comparing bird species richness between native and exotic forest patches of similar size classes revealed that the small and medium patches were not significantly different for either forest specialist or generalist species. In large forests, however, bird species richness was significantly higher in native than in exotic forests for forest specialist species, but not for generalist species (Table 3). This relationship between the native and exotic forest patches seems to be stable, at least within season, because the interaction term of time * naturalness was on no occasion significant (Table 3). The time effect alone indicated significant decline in species number from April to June in the small forest patches (for both forest and generalist species), and for forest specialist species in medium forest patches. The number of generalist species did not change within season in medium-sized forest patches, and none of the groups declined over the season in the large forest patches (Table 3).

Table 1 – Characteristics of fragments and the number of observed bird species in three size groups of native and exotic forest patches in Eastern Hungary

	Small		Medium		Large	
	Native	Exotic	Native	Exotic	Native	Exotic
Number of fragments	5	4	4	5	4	5
Area (ha) ± s.d.	7.1 ± 1.86	6.6 ± 2.92	41.0 ± 28.94	58.7 ± 34.99	425.0 ± 206.16	130.0 ± 18.71
Number of nestholes ± s.d.	697 ± 344	55 ± 49	465 ± 447	204 ± 336	725 ± 284	172 ± 351
Cover of shrubs (%) ± s.d.	44 ± 27.9	38 ± 32.3	33.75 ± 31.5	33 ± 24.4	46 ± 35.0	28 ± 31.2
Number of observed forest specialist species	12.2 ± 1.10	10.5 ± 1.73	13.8 ± 4.99	14.0 ± 5.61	16.5 ± 1.26	12.4 ± 2.19
Number of observed generalist species	3.2 ± 1.64	3.3 ± 2.06	1.8 ± 1.50	3.0 ± 1.58	1.8 ± 0.96	4.0 ± 1.58

Table 2 – Equations of the species-area relationship of forest specialist birds in patches of native and exotic trees in Eastern Hungary. Equations are given for forest specialist and generalist species separately. Asterisks indicate significant relationship

	Equation	R	n	p
Native forests				
Number of forest specialist species	$Y = 0.82 + 0.09X$	0.66	13	0.02*
Number of generalist species	$Y = 0.46 - 0.01X$	−0.07	13	0.84
Exotic forests				
Number of forest specialist species	$Y = 0.76 + 0.09X$	0.40	14	0.16
Number of generalist species	$Y = 0.47 + 0.03X$	0.10	14	0.73

4. Discussion

We studied bird communities in a landscape with patches of natural and exotic tree species. The majority of the landscape was farmland (arable fields and grasslands), with scattered forest patches, including the studied patches. Although it is known that different landscape matrix influences species diversity even in similar forest patches (Lindenmayer et al., 2002; Watson et al., 2005), here we had the same landscape type as matrix. Therefore, we supposed that the matrix effect was similar for all patches, thus, did not bias the results.

There was no difference in bird species composition of natural *versus* exotic forest patches. In a study of birds in tree plantations *versus* native shrub patches in the Negev, Israel, Shochat et al. (2001) found only a small overlap of bird species. Probably the difference between exotic and native patches in our study was not large enough to exclude bird species, only to influence the frequency of occurrence. The communities showed different responses to area; the species-area relationship explained the number of bird species (i.e. significant positive species-area relationship) in native forests, but not in exotic forest patches. A similar pattern was found by Shochat et al. (2001) for native scrub fragments *versus* planted forests; bird species richness depended on area in the former, but not in the latter. Santos et al. (2006) compared native oak and mature pine plantations in Spain, and they found similar bird species richness in native and plantation archipelagoes, and different species-area relationship, just in this study. However, all species-area regression models were significant in their study (Santos et al., 2006).

The difference between native and exotic forests was more pronounced, if species were classified according to their specificity to the forest habitat. Species richness of generalists was not related to forest area at all. The species – area relationship of forest specialist bird species was not significant in exotic forest patches, but was significant (positive) in native patches. The clear difference between the response of specialist and generalist (including exotic) species to fragmentation was described for several taxa, including birds (McCollin, 1993; Germaine et al., 1998), plants (Abbott, 1992; Bakker and Higgins, 2003) and invertebrates (Magura et al., 2001; Ostergard and Ehrlen, 2005; Ouin et al., 2006). More generally, species traits are known to confound the SAR (Ewers and Didham, 2006).

There may be two potential mechanisms to explain the presence of SAR in native, but not in exotic forest patches. First, there is usually a basic difference between exotic and native forests in spatial heterogeneity; native forests are more heterogeneous (Mátyás, 1997; Thompson et al., 2003). We also found some indications of such a trend (more nest holes in native forests), although others were in our case not statistically significant (shrub cover). Habitat heterogeneity and species richness have a positive correlation (Tews et al., 2004), thus, the more heterogeneous and complex habitat structure of native forests may promote forest specialist bird species rather than generalist species (MacNally et al., 2000). Second, native forests are more island-like patches, because their complex structure is more different from the surrounding landscape, than the exotic forests with a simple structure. Therefore, forest specialist species are probably restricted to the native forest ''isolates'', with the subsequent SAR, while exotic forests might not function as isolates. This landscape effect may also be responsible for the absence of a SAR in some cases (Estades and Temple, 1999; Wethered and Lawes, 2003; Lövei et al., 2006).

Increased habitat fragmentation results in the relative increase of edge habitats due to the increase of edge/core ratio. Edges are favored by generalist and/or early successional species (Harris and Silva-Lopez, 1992; Imbeau et al., 2003; Lövei et al., 2006), therefore we expected a reverse relationship for generalist species with forest area: as forest area increases the proportion of edges, and the generalists species, is decreasing. Although these were significant neither for native ($R = -0.1$) nor for exotic ($R = 0.1$) forests, the trends of the regression coefficients (Table 2) support this hypothesis.

The SAR is a fundamental rule of ecology, but it still suffers from several biases (Báldi and McCollin, 2003). Here we demonstrated the key role of native/exotic species composition, that is the quality of habitats and the specialist/generalists character of target species on the SAR (Lövei et al., 2006). An archipelago of non-native habitats, and/or non-native species in the archipelago may lead to the breakdown of the SAR.

The age of forest patches may be relevant factor in determining species richness. In this study the age of patches were 35–70 years, that none of them were old growth. Humphrey (2005) and Santos et al. (2006), for example, showed that 100–200 year old plantations already conferring substantial benefits to many species. It is clear that for the studied forest archipelago and landscape only large (>100 ha) forest patches containing native tree species can preserve natural patterns. Such patches support forest specialist bird species during the whole breeding season. We warn, however, against using only species presence in forest patches for patch evaluation: on our study nearly all the observed species (92%) were present in both native and exotic forest patches. Therefore, simple presence-absence survey may be misleading, because it can not identify the superior value of native forests. Other studies also highlighted the subordinate role of exotic trees and bushes for nesting, foraging and community assemblage (Schmidt and Whelan, 1999; Remes, 2003; Borgmann and Rodewald, 2004; French et al., 2005). This evidence support the conclusion that the expansion of exotic trees and bushes via forestry practice and gardening will harm natural patterns and the underlying processes, hence accelerating the decline of birds in isolated forests.

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Table 3 – Results of the repeated measures ANOVA for the bird species richness in deciduous forests with similar size. Naturalness of the forests (native, exotic) comprised the factor and the time of the counting (April, May and June in 2003) were used as repeated measures. Results of the Tukey test indicate which forest category differs significantly ($p < 0.05$) from the other; for example 'Native > Exotic' indicates that the species richness was significantly higher in the native forests than in the exotic patches

Variable	Source	SS	df	MS	F	p	Tukey posteriori test
Small forests, Number of forest specialist species	*Within-Subjects Effects*						
	Time	0.130	2	0.065	18.100	0.000	
	Time × Naturalness	0.004	2	0.002	0.558	0.585	
	Error	0.050	14	0.004			
	Between-Subjects Effects						
	Naturalness	0.013	1	0.013	0.653	0.446	
	Error	0.143	7	0.020			
Small forests, Number of generalist species	*Within-Subjects Effects*						
	Time	0.150	2	0.075	4.830	0.025	
	Time × Naturalness	0.043	2	0.021	1.382	0.283	
	Error	0.217	14	0.016			
	Between-Subjects Effects						
	Naturalness	0.028	1	0.028	0.294	0.604	
	Error	0.662	7	0.095			
Medium forests, Number of forest specialist species	*Within-Subjects Effects*						
	Time	0.080	2	0.040	7.235	0.007	
	Time × Naturalness	0.005	2	0.003	0.474	0.632	
	Error	0.077	14	0.006			
	Between-Subjects Effects						
	Naturalness	0.006	1	0.006	0.072	0.797	
	Error	0.625	7	0.089			
Medium forests, Number of generalist species	*Within-Subjects Effects*						
	Time	0.006	2	0.003	0.210	0.813	
	Time × Naturalness	0.084	2	0.042	2.751	0.098	
	Error	0.213	14	0.015			
	Between-Subjects Effects						
	Naturalness	0.011	1	0.011	0.255	0.629	
	Error	0.297	7	0.042			
Large forests, Number of forest specialist species	*Within-Subjects Effects*						
	Time	0.021	2	0.011	3.024	0.081	
	Time × Naturalness	0.005	2	0.003	0.734	0.498	
	Error	0.050	14	0.004			
	Between-Subjects Effects						
	Naturalness	0.162	1	0.162	10.228	0.015	Native > Exotic
	Error	0.111	7	0.016			
Large forests, Number of generalist species	*Within-Subjects Effects*						
	Time	0.000	2	0.000	0.005	0.995	
	Time × Naturalness	0.031	2	0.016	0.458	0.642	
	Error	0.478	14	0.034			
	Between-Subjects Effects						
	Naturalness	0.077	1	0.077	1.012	0.348	
	Error	0.536	7	0.077			

Acknowledgement

We are indebted to Duncan McCollin, Béla Tóthmérész and two anonymous referees for comments on previous versions of the paper. The research was supported by a grant of the Hungarian Scientific Research Fund (OTKA research grant no. F61651, to T. M.), and the Directorate of the Hortobágy National Park. T. M. and A. B. were Bolyai Research Fellows of the Hungarian Academy of Sciences.

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Appendix

List of observed bird species in taxonomic order from 27 forest patches in Eastern Hungary. Total number of observations during the three censuses in 2003 is given. Snow and Perrins (1998) was followed for nomenclature. Asterisks indicate forest specialist species

		Small		Medium		Large	
		Native	Exotic	Native	Exotic	Native	Exotic
Columbidae							
Columba palumbus	Woodpigeon	0	6	2	3	0	0
Streptopelia turtur	Turtle Dove	7	7	4	5	5	6
Upupidae							
Upupa epops	Hoopoe	0	0	0	0	0	2
Picidae							
*Dendrocopos major**	Great Spotted Woodpecker	7	2	3	6	8	9
*Dendrocopos medius**	Middle Spotted Woodpecker	0	0	0	0	1	0
*Dendrocopos minor**	Lesser Spotted Woodpecker	0	0	2	1	0	0
*Dryocopus martius**	Black Woodpecker	1	0	1	4	3	0
*Jynx torquilla**	Wryneck	6	4	1	3	3	9
*Picus viridis**	Green Woodpecker	0	0	1	0	0	1
Motacillidae							
Anthus trivialis	Tree Pipit	6	4	3	12	2	2
Turdidae							
*Erithacus rubecula**	Robin	12	4	8	12	8	5
*Luscinia megarhynchos**	Nightingale	10	18	4	13	3	6
*Turdus merula**	Blackbird	14	9	11	12	20	8
*Turdus philomelos**	Song Trush	1	0	0	2	3	0
Sylviidae							
*Locustella fluviatilis**	River Warbler	1	3	1	2	0	9
*Phylloscopus collybita**	Chiffchaff	9	3	8	9	12	8
*Phylloscopus sibilatrix**	Wood Warbler	6	5	6	7	12	1
*Phylloscopus trochilus**	Willow Warbler	0	1	1	0	2	0
*Sylvia atricapilla**	Blackcap	22	13	18	19	18	13
Sylvia curruca	Lesser Whitethroat	0	1	0	0	0	0
Muscicapidae							
*Muscicapa striata**	Spotted Flycatcher	0	0	1	2	2	1
*Ficedula sp.**	Flycather sp.	0	0	0	0	1	0
Aegithalidae							
*Aegithalos caudatus**	Long-tailed Tit	0	0	1	1	0	0
Paridae							
*Parus ater**	Coal Tit	0	0	0	0	3	0
*Parus caeruleus**	Blue Tit	3	2	3	6	11	4
*Parus major**	Great Tit	17	8	11	12	14	9
*Parus palustris**	Marsh Tit	0	0	0	0	0	1
Sittidae							
*Sitta europaea**	Nuthatch	1	0	4	2	3	2
Certhiidae							
*Certhia sp.**	Treecreeper	10	8	4	8	5	10
Oriolidae							
*Oriolus oriolus**	Golden Oriol	9	9	4	12	8	14
Laniidae							
Lanius collurio	Red-backed Shrike	1	2	0	3	0	4
Corvidae							
*Garrulus glandarius**	Jay	1	0	2	3	2	1
Sturnidae							
Sturnus vulgaris	Starling	21	21	17	8	10	48
Passeridae							
Passer montanus	Tree Sparrow	0	0	0	1	0	0
Fringillidae							
Carduelis carduelis	Goldfinch	0	2	0	1	0	2
*Carduelis chloris**	Greenfinch	3	2	0	2	2	7
*Coccothraustes coccothraustes**	Hawfinch	6	13	6	7	11	4
*Fringilla coelebs**	Chaffinch	29	23	28	24	33	37
Serinus serinus	Serin	0	0	0	0	0	1

Appendix (*continued*)

		Small		Medium		Large	
		Native	Exotic	Native	Exotic	Native	Exotic
Emberizidae							
Emberiza citrinella	Yellowhammer	5	2	2	7	2	10
Miliaria calandra	Corn Bunting	1	0	0	0	0	0

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Please cite this article in press as: Magura, T. et al., Breakdown of the species-area relationship in exotic but not in native forest patches, Acta Oecolo. (2008), doi:10.1016/j.actao.2007.11.007

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