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Effects of patch size, isolation and regional abundance on forest bird communities

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Abstract

The aim of this study was to assess the impact of isolation on forest bird communities in agricultural landscapes in The Netherlands. We studied the avifauna of 235 small (0.1-39 ha) woodlots composed of mature deciduous trees in 1984– 1985. These woodlots were selected in the eastern and central/southern part of the country within 22 regions showing great differences in landscape structure, *i.e.*, degree of isolation. Multiple regression analysis indicated that woodlot size was the best single predictor of species number and probability of occurrence of most species. It turned out that the isolation variables, area of wood, number of woods, interpatch distance, and proximity and density of connecting elements, explained small but significant parts of the residual variances in species number. No single species was significantly affected by the density of connecting elements. Biogeographical differences between two groups of regions were emphasized. Evidence of four woodland- species suggested that regional abundance affected the probability of occurrence in small isolates.

Introduction

Agriculture, urbanization and other human activities dissected the habitat of many plant and animal species into small isolated patches (Burgess and Sharpe 1981). In the agricultural landscape of Western Europe, the woods have been reduced to tiny fragments surrounded by intensively used fields. Forests nowadays cover about 8% of the Dutch territory, and mainly consist of coniferous plantations. Deciduous woods are invariably small to very small, and often occur as isolated fragments in the agricultural landscape. Sometimes these woodlots and interconnecting hedgerows constitute a habitat network for species of woody vegetation. However, due to the construction of roads, amelioration of the landscape for modern agriculture and other impacts of modern land use, woodlots tend to decrease in size and the network becomes desintegrated the more woodlots and corridors are removed or fragmented. This is supposed to adversely affect the biotic diversity and conservational value of these woodlots. Quantification of the relationship between the landscape structure and the distribution and persistence of species and populations is therefore an important task for nature conservationists.

In this study, we relate the distribution of breeding forest birds to the structure of agricultural landscapes with scattered patches of forest, and focus on the possible role of the connecting network (hedgerows as corridors and woodlots as stepping stones). We use birds because they are important organisms in nature conservation and because their

habitat preferences are relatively well-known (Wiens and Rotenberry 1981, Opdam and Schotman 1986).

What evidence does exist to indicate that fragmentation of forest habitat affects the distribution of forest bird species and, by consequence, the composition of bird communities in small isolated patches? The mere fact that species number increases with patch area (as was found in almost all studies of isolated patches) cannot be used as an indication for such an effect. This is because the same relation is found for samples of increasing size taken from large forest tracts, partly due to sample statistics, partly to a possible correlation between area and habitat diversity (Connor and McCoy 1979). In species-area studies, the role of habitat diversity was often neglected. Recently, Freemark and Merriam (1986) found that both area and habitat heterogeneity were positive correlates in analysing variation in bird species number. Evidence for an ecological difference between woodlots and equivalent-sized samples from large forest tracts is presented by Howe (1984), who found similarity in species richness, but divergence in species composition. Species that were abundant in large tracts also were abundant in woodlots, but locally uncommon species were less often observed in woodlots than in control plots in large tracts. He suggested that forest interior and forest edge birds were discouraged to cross open country.

In this study, the effect of insularization on forest birds is investigated by comparing small woodlots of varying degree of isolation. Thus, an effect of isolation must be reflected by the frequency of occurrence of a bird species in samples of woodlots taken from landscapes varying in degree of fragmentation, all other things being equal. Probably due to stochastic events, the small populations in these woodlots become frequently extinct (Van Noorden 1986). If so, recolonizations by dispersal from adjacent populations are crucial to the persistence of species in such a landscape (Jones and Diamond 1976, Brown and Kodric-Brown 1977, Wright and Hubbell 1983, Wright 1985). Recolonization chance is assumed to depend on the distance between patches and the barrier-effect of the matrix of the landscape, the density of corridors, the dispersal capacity of a species and the number of possible dispersers.

The impact of isolation on the number of breeding birds in isolated patches was claimed by Lynch and Whigham (1984), Opdam *et* al. (1985) and Askins *et al.* (1987). In their studies, isolation was measured as the distance to the nearest wood or the number of woods within a certain distance. As yet, no data exist which show that the density of corridors or connecting landscape elements affects the distribution of breeding forest birds in agricultural landscapes with scattered woodlots. Since the number of possible dispersers may vary due to regional differences in abundance (Schotman unpubl. results), the response of a species to isolation (measured as a distribution pattern) may diverge among regions. This possible cause of variation was neglected in previous studies. We tried to investigate its role by dividing our samples among two regions of The Netherlands which differed in the global amount of deciduous woodland.

In this paper we present an analysis of the effect of interpatch distance, density of habitat patches in the surrounding landscape and the density of hedgerows on the distribution of breeding forest. birds in 235 deciduous woods. In our analysis, habitat differences were kept as small as possible, but variation in area and possible regional differences in abundance were maximized to measure the possible impact of these factors in relation to the effect of isolation. Woodlots were distributed over 22 regions in various parts of The Netherlands showing considerable differences in landscape structure. We studied the whole range of 'open' landscapes with few corridors and isolated woodlots to 'closed' landscapes with many corridors and wooded areas.

Methods

Selection of sample plots

The twenty-two regions of roughly homogeneous landscape structure were selected in the eastern, central and southernmost part of The Netherlands (Fig. 1). Interpatch distance, density of habitat patches and the density of connecting landscape

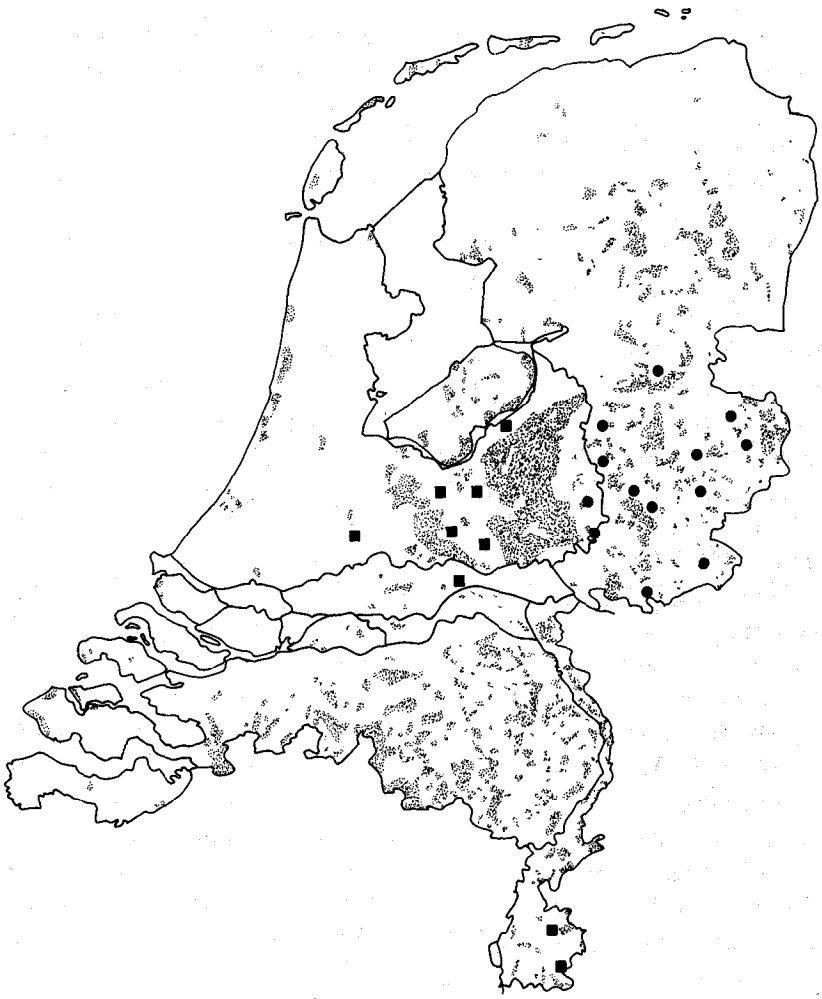

Fig. I. Location of study regions in the eastern and central/southern part of The Netherlands. Forested areas are shown in black. Squares represent central and southern regions, and circles represent eastern regions.

elements varied considerably between regions, but not within regions. The barrier effect of the landscape matrix can be regarded as constant: intensively used agricultural fields. For each region a variable number of woodlots (N= 5-18, median 11) ranging 0.1-39.4 ha in size was selected from maps at scale 1:25,000 and after a reconnaissance of the study areas. Isolation variables were calculated from these maps and a map at scale 1: 10,000 was used to digitize the area of a woodlot (Table 1). A total of 235 woodlots was selected for this study, 68 of these situated in the Gelderse Vallei and Zuid-Limburg were analysed previously (*cf.* Opdam et *al.* 1985). These two areas were divided into respectively 4 and 2 regions in order to get a similar level of variation in landscape structure and sample size within regions.

Habitat-data

Virtually all woods in The Netherlands are man-made and disturbed to some extent by sylvicultural and agricultural activities. Therefore, we selected woodlots on the basis of uniformity in tree layer, age and tree species composition as much as possible. Selected woodlots were dominated by mature deciduous tree species like oak (*Quercus robur* L.), beech (*Fagus sylvatica* L.) and ash (*Fraxinus excelsior* L.). Locally alder (*Alnus glutinosa* (L.) Vill.),

Table 1. Variables pertaining to habitat quality, patch size, isolation and biogeographic region

Habitat variables

MTC: mean tree circumference of 50 trees with DBH > 12.7 cm (cm)
CH: cover of herb layer, 3 classes: 1 = 0–10%, 2 = ll-30% and 3 = > 30%
cs: cover of shrub layer, 3 classes: 1 = < 1%, 2 = 1–10% and 3 = > 10%
NTS: number of tree species
MID: mean intertree-distance (m)
NS: number of saplings (stems with DBH 3.2 < X < 12.7 cm)
W: presence of water (ditch, brook, pond) (0/1)
N: presence of conifer trees (O/l)
SW: shape of wood (compact or oblong)
SD: standard deviation of MTC (cm)

FC: forest community. 8 types of dominant tree species were distinguished:
1 = *Fraxinus excelsior*, 2 = *Quercus robur*, 3 = *Quercus robur* + *Populus* spp. 4 = *Quercus robur* + *Betula pendula*, 5 = *Quercus robur* + various deciduous tree species, 6 = *Quercus robur* + *Pinus sylvestris*, 7 = *Fagus sylvatica* + *Quercus robur*, and 8 = *Fagus sylvatica* + *Quercus robur* + *Pinus sylvestris*.

FS: forest structure; a combination of MTC and SD. 6 classes:
1 = MTC < 100 cm and SD/MTC < 0.35
2 = MTC < 100 and SD/MTC > 0.35
3 = MTC 100 < X < 125 and SD/MTC < 0.35
4 = MTC 100 < X < 125 and SD/MTC > 0.35
5 = MTC > 125 and SD/MTC < 0.35
6 = MTC > 125 and SD/MTC > 0.35

Size variables

A: area of mature deciduous wood (ha)
TA: total area of wood containing the selected site (ha)

Isolation variables

DIST: distance from nearest wood of any type larger than 20 ha, measured as the shortest distance between the edge of the selected site and the edge of the nearest woodlot (km)
AW1: area of wood of any type within a l-km radius from the centre of a woodlot (ha)
AW3: area of wood of any type within a 3-km radius (ha)
AW5: amount of wood surrounding a woodlot within a 3-5 km radius (n = 0, 20; one sector equals an area of wood of any type larger than 400 ha)
NW3: number of woodlots of any type larger than 5 ha within a 3-km radius
WB: woodlot connected to wooded banks or rows of mature trees (O/l)
DWB: density of wooded banks within a 3-km radius (m/ha)
DRT: density of rows of trees within a 3-km radius (m/ha)

GROUP: presence of woodlots and regions in the eastern and central/southern part of The Netherlands (O/l)

birch (*Betula pendula* L.) and maple (*Acer pseudoplatanus* L.) were present as Well. The shrub layer consisted of black cherry (*Prunus serotina* Ehrh.), elder (*Sambucus nigra* L.), hawthorn (*Crataegus monogyna* Jacq.) and mountain-ash berry (*Sorbus aucuparia* L.). Species composition and cover of the different layers varied considerably between plots, e.g., mixed forests have a varied shrub layer, whereas pure beech forests are mostly totally devoid of shrubs. Therefore, variation in habitat quality was measured in the field for 12 habitat variables along a transect long enough to encompass 50 trees with a DBH > 12.7 cm (Table 1). Values of these variables were used in the regression analyses on species number and single species in order to control for possible effects of, differences in habitat quality between woodlots.

Bird-data

In order to test the conjectures set out in the introduction, we wanted to have bird-data for a large number of woodlots in all the landscape types that

we studied. For practical reasons we could obtain only presence/absence data. Each woodlot was censused four times between mid-March and mid-June in 1985 except for woodlots in the Gelderse Vallei which were censused in 1984. The time spent in a woodlot was held constant at 15 minutes for woodlots up to 5 ha. These woodlots were so small that it was highly probable that any bird displaying territorial behavior would be noticed. In woodlots larger than 5 ha more time was needed to scan the whole area, approximately 30 to 45 minutes (depending on the shape of the wood). After a relevant observation on a species displaying territorial behavior was obtained, the attention was shifted to the remaining species. The presence of a species was derived from the combined four censuses on the basis of species-specific criteria described by Hustings *et al.* (1985). It was necessary to apply species-specific criteria because the chance of being recorded differs considerably between species (Kwak and Meijer 1985). For most sedentary species at least two observations made on separate visits were required, unless recording chance was low or the observation was made in the post-migration period; in this case only one record was required. The criteria were chosen such that all species were surveyed at an accuracy level of at least 90%. In this way a list of bird species was obtained for each woodlot presenting the total number of forest bird species (St). This total list was divided into two subsets comprising the number of forest-interior species (Si) (species restricted to mature deciduous woods and mainly hole-nesting birds) and the number of forest-edge species (Se) (species characteristic of woods but also occurring in scrubs, parks, plantations etc.). Rare species and species of coniferous forests were not analysed in detail.

Data analysis

Analysis was carried out on the number of species St, Si, Se and on presence/absence data of single species. The variation in these four dependent variables was analysed with multiple regression analysis using the standard statistical package Genstat (Alvey *et al.* 1982). For most size, isolation and some habitat variables we assumed non-linearity in their relation to the dependent variables. We inspected the frequency distributions of the independent variables and transformed these by taking the logarithms if distributions were skew. When we speak of isolation variables we include variables pertaining to the degree of connectivity among patches (variables WB, DWB, DRT, Table 1).

We want to analyse the effect of isolation while taking into account the effects of size and habitat variables. For statistical testing of isolation effects, woodlots within regions could not be regarded as independent samples, because isolation variables varied only slightly within regions as compared to the variation between regions. On the other hand, size and habitat variables varied strongly within regions and much less so between regions (Table 2). Therefore, a two-step approach was adopted in which the effects of size and habitat variables were analysed on a per-woodlot basis (N = 235) and the effects of isolation variables on a per-region basis (N = 22).

First, a basic model was fitted with size and habitat as independent variables. Test runs indicated that patch size reduced the variance in species number better than any of the remaining variables. Therefore, we constructed a basic model with size as a forced variable and extended it with one or more habitat variables until addition of a variable no longer significantly reduced the residual variance. In this way all significant models were inspected. We computed for the best basic model jackknife residuals and inspected them, but detected no gross outliers. We then averaged the jackknife residuals per region. The model was extended with the factor group to remove the effect of possible differences in species number between two groups of regions (see below). A second model was fitted with isolation as independent variables using the 22 mean residuals of the best basic model as input-data. Then, the equations of both models were put together in order to get an overall model in which species number is a function of size, habitat, group and isolation variables.

In the analysis on presence/absence data of single species the first step was a logistic regression

Table 2. Characteristics of all variables based on mean values per region
One-way analysis of variance on all variables shows the significance of differences in variance between-regions

	Habitat								
	MTC	SD*	FC	FS	CH	cs	NTS	MID*	NS*
mean	112.4	43.0	4.3	3.5	2.5	2.5	4.6	6.9	25.8
sd	1.4	7.8	1.1	0.5	0.4	0.3	1.4	1.1	10.8
min	95.4	32.3	2.4	2.6	1.7	1.8	2.9	5.6	11.0
max	120.5	63.4	6.5	4.6	3.0	3.0	7.8	9.4	49.4
F-value	1.923	2.439	2.709	1.350	3.160	2.749	5.551	3.135	3.419
P	**	***	***	NS	***	***	***	***	***

	Habitat			Size	
	W	N	SW	A*	TA*
mean	0‘47	0.34	1.68	5.91	9.65
sd	0.22	0.14	0.17	2.25	4.48
min	0.09	0.00	1.36	1.85	3.09
max	1.00	0.60	1.91	8.98	20.0
F-value	2.029	0.904	1.353	2.085	2.074
P	**	NS	NS	**	**

	Isolation							
	DIST*	AW1*	AW3*	AW5*	NW3*	WB	DWB*	DRT
mean	1.87	30.9	220	1.66	8.7	0.64	9.8	16.3
sd	1.33	12.2	107	1.80	4.5	0.24	5.8	5.8
min	0.56	13.8	41	0.00	2.2	0.20	1.6	7.2
max	6.24	54.1	407	6.36	19.0	1.00	27.0	30.8
F-value	12.594	4.503	11.742	16.858	20.749	3.135	24.787	18.364
P	***	***	***	***	***	***	***	***

F-test; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS = not significant.
Log-transformed values were used for variables with *.

analysis which included size and habitat variables and the factor region as independent variables. Coefficients of the factor region were computed for each of the 22 regions in a regression analysis and used as input-data in a least-square regression analysis in the second step with again 22 values. In the second step two runs were executed: one which included the factor group and takes into account the possible differences in regional abundance between regions and another run without this factor, if for a species no such biogeographical difference was detected. Graphs depicting the relationship between mean jackknife residuals and mean isolation values per region indicated the presence of two distinct groups of regions which were classified as regions located in either the eastern or central/southern part of The Netherlands (for an example see Fig. 2).

Species-area relationships were initially examined by three regression functions log-log (power), semi-log (exponential) and untransformed (linear). The exponential function was used in all analyses, because of a slightly better fit over the other functions (Table 3). Some of the isolation variables were correlated to each other (Table 4).

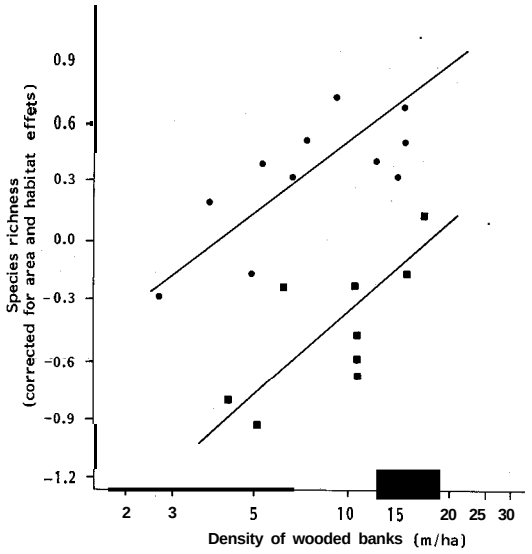

Fig. 2. Relationship between density of wooded banks (m/ha) and species richness corrected for area and habitat effects. Upper line: eastern regions, lower line: central/southern regions.

Table 3. Correlation coefficients of species-area relationships using log-log (power), semi-log (exponential) and untransformed (linear) functions for the total number of woodlot species (St), number of species restricted to mature deciduous woods (Si) and number of species restricted to woods (Se)

	St	Si	Se
S- A	0.69	0.53	0.67
S – lnA	0.85	0.75	0.76
lnS – A	0.58	0.47	0.55
lnS – lnA	0.80	0.72	0.74
DF = 233	P = 0.001 ~ 0.32		

Table 4. Correlation-matrix of eight isolation variables

	AW1	AW3	WB	AW5	DWB	DRT	DIST	NW3
AW1	1.0							
AW3	***	1.0						
WB	*	–	1.0					
AW5	–	**	–	1.0				
DWB	–	*			1.0			
DRT	–	–	–	–	–	1.0		
DIST	**	***	–	*		–	1.0	
NW3	***	***		–	–	–	***	1.0

* P < 0.05; ** P < 0.01; *** P < 0.001.

Results

Effects on species number

In all three analyses on species number (St, Si, and Se) patch size was the best single predictor of species number; 53 to 72% of the variance in species number was explained by patch size alone. Habitat variables added to a model with patch size exerted a small but significant influence on species number (Table 5). However, the small influence of habitat variation could be brought about by our selection of more or less homogeneous stands of vegetation, but also by a correlation between area and habitat diversity. Seven out of twelve habitat variables correlated significantly to the area of woodlot (Table 6). This suggests that smaller woodlots on average tend to have smaller trees (MTC), less complex and less heterogeneous forest types (FC, SD), containing less frequently conifer trees (N) and surface water (W). We think that some of the effects of area can also be attributed to habitat diversity increasing with size. Although we kept habitat characteristics as uniform as possible, we could not totally prevent this type of interdependence. The habitat variable of the best basic model could be replaced by another habitat variable without a substantial drop in the variance. *E.g.*, the variable mean trunk circumference MTC could be replaced by the variable shape of wood (SW, V^2 = 59%) in the regression analysis on the number of forest-interior species Si.

In order to test if biogeographic differences in species number were prominent after the effects of area and habitat quality were removed, we extended the model with the factor group. Addition of this factor to the best basic model resulted in a significant reduction of the residual variance in St and Si, suggesting that eastern woodlots contained consistently more species of these categories than central/southern woodlots. No such difference was found for, forest-edge species (Se). We carried out separate analyses for eastern and central/southern woodlots though, to detect possible differences between both groups (Table 5). Again, patch size was the best single predictor of species number, but the percentage variance accounted for by size alone differed somewhat between groups for all three

Table 5. Linear regression models of the number of forest bird species (St, Si, Se) containing size and habitat variables with 235 values. The factor 'group' (east or central/south) was added to the best basic model. Analysis was performed on all plots (N = 235) and for east (N = 131) and central/south (N = 104) separately. V^2 is the percentage variance accounted for by a model

Total number of woodlot species (St)

Total (N = 235)	V^2	East (N = 131)	V^2	Central/south (N = 104)	V^2
ln A	72	ln A	81	ln A	61
ln A + MTC	73	ln A + SD	82	ln A + ln TA	67
ln A + MTC + GROUP	74	ln A + MTC	82		

Number of species restricted to mature deciduous woods (Si)

Total (N = 235)	V^2	East (N = 131)	V^2	Central/south (N = 104)	V^2
ln A	58	ln A	72	ln A	52
ln A + MTC	60			ln A + ln TA	56
ln A + MTC + GROUP	66				

Number of species restricted to woods (Se)

Total (N = 235)	V^2	East (N = 131)	V^2	Central/south (N = 104)	V^2
ln A	53	ln A	63	ln A	45
ln A + CS	55	ln A + CS	65	ln A + ln TA	48
ln A + CS + GROUP	55 (NS)	ln A + SD	64	ln A + W	48

Table 6. Correlation between patch size and habitat characteristics

Variable	S W	c s	CH	W	N	F S
Corr. coef.	0.11	0.06	-0.10	0.23	0.31	0.21
P	NS	NS	NS	*	**	**
Variable	FC	MTC	SD	NTS	MID	NS
Corr. coef.	0.23	0.22	0.27	0.17	0.23	0.08
P	*	*	**	NS	*	NS

* P < 0.05; ** P < 0.01; NS = not significant.

analyses on species number (Table 5). Furthermore, some models could be extended with one size or habitat variable, but the amount of variance explained additionally was very small.

In the second step of the regression analysis we correlated the mean residuals to isolation variables per region. The factor group was incorporated as a forced variable in each model, since isolation variables hardly reduced the residual variance if no correction for geographical differences was provided. ***E.g.,*** in the analysis on Si for all regions the density of wooded banks (DWB) explained only 13% of the variation, but 76% in combination with the factor group. The factor group alone accounted for 30% and 59% of the variance in St and Si respectively (Table 7). The effect of isolation was demonstrated for St and Si, but not for Se, which implies that isolation affected mainly forest interior species, since St is the sum of Si and Se. Since we selected woodlots dominated by mature deciduous trees, we expected bird species confined to this type of habitat (Si) to be the most sensitive to isolation. The three

Table 7. Linear regression models of the number of species (St, Si and Se) corrected for size and habitat differences,containing isolation variables with 22 values (means per region). The factor group corrected for biogeographic differences in species richness between eastern and central/southern regions. V^2 is the percentage variance accounted for by a model

Total number of woodlot species (St)					
Total (N = 22)		East (N = 13)		Central/south (N = 9)	
	V^2		V^2		V^2
GROUP	30				
GROUP + (-)ln DIST	40				
GROUP + ln DWB	44				
GROUP + ln AW3	46	ln DWB	35	ln AW5	35
Number of species restricted to mature deciduous woods (Si)					
Total (N = 235)		East (N = 131)		Central/south (N = 104)	
	V^2		V^2		V^2
GROUP	59	ln AW5	52	ln AW3	33
GROUP + ln DWB	76	ln DWB	41	(-) ln DIST	34
GROUP + ln DWB + ln AW1	82	WB	60	ln AW5	60
GROUP + ln AW3 + ln DRT (-)	82	WB + ln DWB	74		
GROUP + ln DWB + ln DIST (-)	83				
Number of species restricted to woods (Se)					
Total (N = 22)		East (N = 13)		Central/south (N = 9)	
			V^2		
No significant models		ln DRT	38	No significant models	
		ln DIST (+)	46		

best Si models for all regions contained variables pertaining to different aspects of the landscape structure, ***i.e.,*** interpatch distance (DIST), density of connecting elements (DRT and DWB) and amount of wood (AW1 and AW3) (Table 7). Regression analysis on separate groups revealed that within a more homogeneous data-set fewer isolation variables were selected: for eastern woodlots proximity (WB) and density of wooded banks (DWB) and amount of woods (AW5) alone or in combination explained 41 to 74%, whereas for central/southern woodlots amount of wood (AW3 and AW5) and interpatch distance (DIST) explained 33 to 60% of the mean residual variance.

Forest-edge species inhabit different seral stages in woodland succession and from the regression analysis on all regions it is not likely that isolation contributed to the observed variation in species number (Se). Regression analysis on separate groups indicated that isolation did not affect the number of forest edge species (Se) of central/southern woodlots, but only of eastern woodlots; models with interpatch distance (DIST) and density of tree rows (DRT) explained 38–46% of the residual variance (Table 7).

Effects on single species

So far, species were treated as equals with respect to area, habitat requirements and dispersal capacity. However, species-specific differences are plausible. We conducted separate species analysis to sort out species-specific relations with patch size and isolation. The results indicate that all responses of species to patch size were more or less of a different nature (Fig. 3). Twenty-six out of 32 species were significantly related to patch size (χ^2 test, df = 1, $P < 0.05$). Abundant species not showing a correlation with patch size were chaffinch (*Fringilla coelebs* L.), woodpigeon (*Columba palumbus* L.) and blackbird (*Turdus merula* L.).

Species characteristic of conifer woods like firecrest (*Regulus ignicapillus* Temm.), bullfinch (*Pyr-*

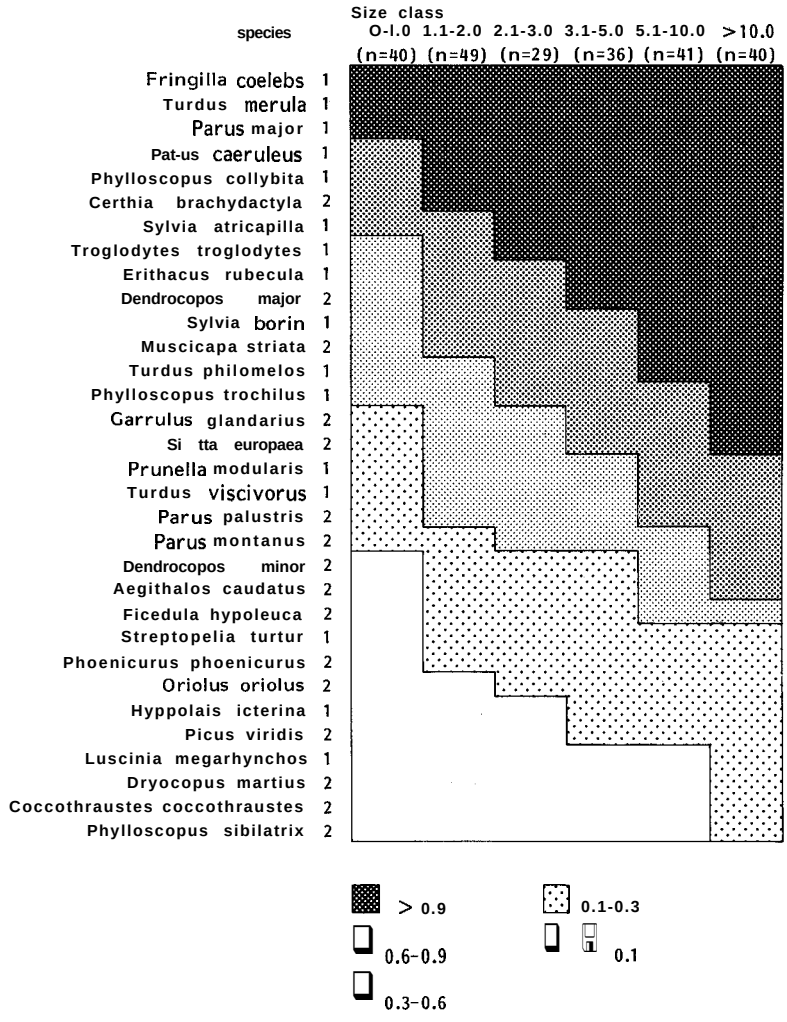

Fig. 3. Probability of occurrence over six woodlot size classes of 32 forest bird species; species of woods, scrubs etc. (l;Se) and species of mature deciduous forests (2;Si).

rhulapyrrhula L.), coal tit (*Parus ater* L.) and crested tit (*P. cristatus* L.) were present in some mature deciduous woods larger than 10 ha, obviously because conifer trees were present in patches large enough to support at least one territory. Redstart (*Phoenicurusphoenicurus* L.), golden oriole (*Oriolus oriolus* L.) and turtle dove (*Streptopelia turtur* Friv.) had an overall low probability of occurrence (0.10–0.30), regardless of patch size. Most forest-interior species showed responses to area and attained a probability of occurrence of 0.6 in woodlots exceeding 3.0 ha. Forest-edge species attained relatively high probability (Fig. 3). These differences may be related to different regional abundances, different extinction rates or different habitat requirements. Our data-set does not permit differentiation between these possible factors.

Results of the logistic regression analysis on single species indicate that 11 species were affected by certain aspects of the landscape structure (Table 8). The probability of occurrence of the green woodpecker (*Picus viridis* L.), marsh tit (*Parus palustris* L.), long-tailed tit (*Aegithalos caudatus* L.) and turtle dove decreased significantly with increasing interpatch distance (DIST). The amount of wood in the vicinity of a woodlot (AW 1, AW3 and AW5) affected the presence of the species already mentioned plus nuthatch (*Sitta europaea* L.) and golden

Table 8. Isolation variables showing significant effects on the probability of occurrence for 11 forest bird species. Results were derived from second-step regression models containing only one isolation variable. Regression coefficients were replaced by their significance levels

	GROUP	DIST	AW1	AW3	AW5	NW3	WB	DWB	DRT
Green woodpecker		−***	***	**	*	***	0	0	
Marsh tit	**	−**	0	0	**	*			
Nuthatch		−0	*	**	**	*	*		
Pied flycatcher	**				*				
Golden oriole	***		0			0			−*
Long-tailed tit		−**		*					
Turtle dove		−*		0			−**		0
Wren	−*						**		
Robin			**				*		
Tree-creeper			*						
Great spotted woodpecker							**		

t-test: 0 P < 0.10; * P < 0.05; ** P < 0.01; *** P < 0.001.

oriole. The number of woods (NW3) was correlated with AW1, AW3 and DIST (Table 4) and, not surprisingly, also correlated with the relative frequency of green woodpecker, marsh tit and nuthatch. Proximity of wooded banks (WB) was particularly relevant to great spotted woodpecker (*Dendrocopos* ***major*** L.), turtle dove, wren ***(Troglodytes troglodytes*** L.) and robin ***(Erithacus*** *rubecula* L.). Especially for the latter two species wooded banks may also constitute appropriate habitats. The density of wooded banks (DWB) was not selected in any single species model. This suggests that the degree of connectivity among woodlots does not influence the distribution of single forest-interior species in agricultural landscapes. This is contrary to the results of the analysis on species number Si (Table 7). However, logistic regression on presence/absence data is a weaker statistical tool than regression analysis on a continuous variable. The density of tree rows (DRT) was selected at $P < 0.05$ in the model of only one species (golden oriole).

In a biogeographical context woodland birds may show larger population sizes in certain regions as compared to others. A comparison between eastern and central/southern regions revealed that 16 out of 42 forest bird species showed a higher frequency of occurrence in either eastern or central/southern regions (Table 8). In eastern regions 9 species characteristic of mature woods were more frequent, whereas 7 more common and less typical woodland species were more frequent in central/southern regions. The results are not conclusive for firecrest, bullfinch and nightingale ***(Luscinia megarhynchos*** Brehm), because of their low incidence (present in respectively 6, 9 and 11 woodlots) and sampling of inappropriate habitat. Means and variances of patch size for both groups of regions were identical (ANOVA, $F = 0.00$, $P < 0.001$).

In order to test if regional abundance influences the probability of occurrence over size classes, four species were selected occurring with different frequencies in eastern and central/southern regions ($P < 0.001$) and at the same time significantly affected by patch size ($P < 0.001$). We assumed that the regional abundance parallels the overall frequency of occurrence of a species (Hanski 1982, Van Noorden 1986).

We constructed logistic regression models containing the variables size, group and their interaction (size x group) and compared the residual deviances of the respective models (Ter Braak and Looman 1986). The interaction of both variables would indicate if the rate of increase in the probability of occurrence over the size classes is significantly different between eastern and central/southern groups. The results show that a species scarce in one region relative to the other was absent from or occurred with a lower relative frequency in woodlots less than 5 ha (Fig. 4). Jay (*Garrulus glandarius* L.), marsh tit and pied flycatcher (*Ficedula hypoleuca* Pallas) showed area effects in central/

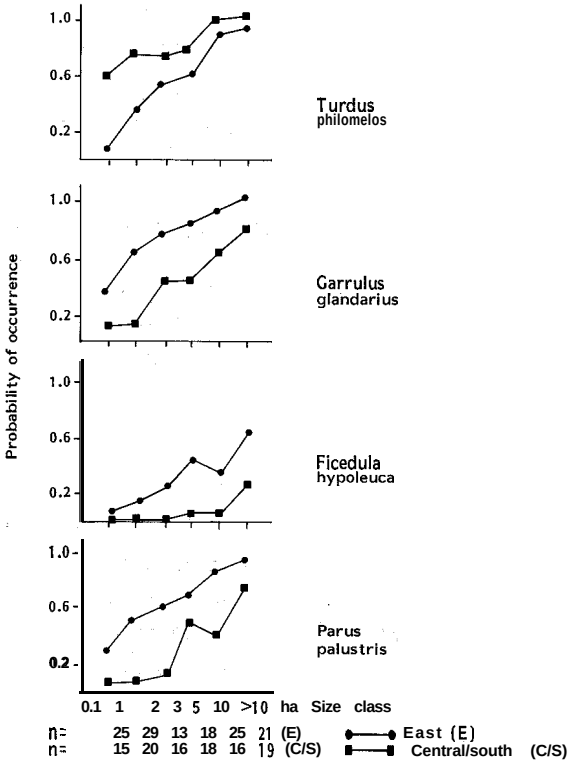

Fig. 4. Probability of occurrence over six woodlot size classes of four forest bird species in the eastern and central/southern part of The Netherlands.

Table 9. Relative frequency of occurrence of forest bird species being significantly more frequent in either eastern regions (E) (top) or central/southern regions (C/S) (bottom)

East	E	C/S	P
Lesser spotted woodpecker	0.27	0.17	*
Nightingale	0.09	0.02	*
Garden warbler	0.82	0.69	*
Redstart	0.22	0.08	**
Bullfinch	0.07	0.00	**
Pied flycatcher	0.28	0.07	***
Marsh tit	0.64	0.32	***
Golden oriole	0.23	0.04	***
Jay	0.74	0.43	***
Central/south	**E**	**c/s**	**P**
Wren	0.82	0.93	*
Icterine warbler	0.08	0.18	*
Spotted flycatcher	0.72	0.84	*
Blackcap	0.74	0.89	**
Firecrest	0.00	0.06	**
Songthrush	0.58	0.79	***
Tree sparrow	0.18	0.48	***

(χ^2 test: df = 1; * P = 0.05; ** P = 0.01; *** P = 0.001)

southern regions, whereas they occupied even the smallest woodlots in eastern regions. Even in woodlots larger than 10 ha, differences in probability of occurrence between both groups of regions still remained. On the other hand, the songthrush (*Turdus philomelos* L.) being more numerous in central/southern regions of The Netherlands than the other species, attained similar probabilities in woodlots larger than 5 ha. However,. in all cases we could not reject the null hypothesis that the rate of increase in the probability of occurrence over the size classes is similar for both groups (χ^2 test $P < 0.5$).

Discussion

bistribution of forest birds in isolated woodlots: influences of many factors

During the last decade several studies have focussed on the composition of breeding bird communities of habitat islands in agricultural landscapes (Moore and Hooper 1975, Galli *et al.* 1976, Forman *et al.* 1976, Helliwell 1976, Martin 1981, Whitcomb *et al.* 1981, Lynch and Whigham 1984, Opdam *et al.* 1984, 1985, Howe 1984). These studies provide a test of the factors that influence the distribution of breeding forest birds species in fragmented landscapes. These studies are not quite comparable, because of (1) the strong emphasis on one or few factors while neglecting or not quantifying others, (2) the specific habitat that was investigated being shelterbelts, second growth forest, forest remnants or mosaics of different habitat types, (3) the great variation in size-range of the woodlots studied and (4) lumping too many species without appreciating species-specific responses. It seems impractical to take into account all possible factors. Careful sampling-design may allow the scrutiny of specific factors and assess their specific influences, but this is not a common practise (e.g., many studies use confounded variables).

A gamut of potential factors thus influences the

distribution of forest birds, acting on different levels, *i.e.*, on the population, species and community level. On the population level population density and variability and regional abundance are potential factors operating on the distribution of forest birds. Species-specific traits like dispersal-capacity, trophic status, size and habitat requirements and site-tenacity act on the species level. Some authors (e.g., Ambuel and Temple 1983) stress the role of interspecific competition, predation and brood-parasitism in shaping the composition of bird communities. Apart from all these factors implying ecological relationships, chance may be involved as well. Apart from these functional aspects, features of the sample site and surrounding landscape, like habitat structure, floristic composition, interpatch distance, connectivity, and habitat quantity affect the distribution of birds on the species, population, as well as on the community, level. All these factors may be operational to a greater or lesser extent in each setting depending on the structure of the data-set. In this study we kept habitat variation small and maximized variation in landscape structure. Consequently, habitat factors were weak predictors of bird parameters, but the impact of landscape structure was demonstrated clearly, after accounting for effects of patch size and geographical trends. Species-specific differences were unambiguous. The amount of variation in species number not explained by the models could have been caused, at least partly, by factors on the community level and by methodological variance.

The number of bird species in woodlots was strongly associated with patch size (St, Si and Se alike), a result consistent with most previous studies on the avian composition of habitat islands. Multiple regression analysis suggested that of the habitat variables only structural heterogeneity (SD), variation in trunk diameter (MTC) and cover of shrub layers (CS) explained significant but small parts of the variances in species number (Table 6). Moreover, a weak and partial correlation between patch size and habitat characteristics (Table 4) suggested that differences in habitat quality might have been masked by patch size to some extent. However, in the uniform series of woodlots that we have intentionally chosen, habitat differences played a minor role in determining the composition of bird communities. These results corroborate the findings of an earlier study reported by Opdam et al. (1985), but contradicts the conclusions drawn by Lynch and Whigham (1984) who contend that the occurrence of many species is better predicted from structural and floristic characteristics of woods than from patch size and isolation. In this study the probability of occurrence of any bird species except one (tree sparrow) was better predicted from patch size than from habitat variables.

Isolation

Isolation clearly had an effect on the number of species and the composition of forest bird communities of woodlots, in particular the number of forest-interior species (Tables 7 and 8). Colonization of vacant sites by these species is probably hampered by interpatch distance and the nature of the interstitial habitat, whereas woods in the vicinity may function as stepping stones for as well as sources of potential colonizers.

The importance of corridors connecting habitat islands in a functional way so that species can move among them, was pointed out by MacClintock *et al.* (1977) and Merriam (1984) among others. A high density of corridors or connecting elements means a high connectivity. In our case corridors consisted mainly of wooded banks and tree rows. The mean density of connecting elements varied between regions from 1.6 to 27.0 m/ha for wooded banks and from 7.2 to 30.8 m/ha for tree rows. We failed to show for any single species that a high connectivity means a high frequency of occurrence, but the number of forest-interior species (Si) was significantly affected by the density of connecting elements. For forest-interior birds, these may serve at least two functions, (1) an additional feeding habitat for the birds in the adjacent woods, both during the breeding season and during winter and (2) a corridor for dispersing birds. The habitat function has been poorly documented, but we failed to find any publication discussing the corridor function. Bull *et al.* (1976) observed significant changes in the bird community structure after

a reduction of the density of hedgerows from 90 to 60 m/ha, but they did not differentiate between the habitat and corridor functions.

Species of mature deciduous woods like nuthatch, marsh tit and green woodpecker, are characterized by a strong site-tenacity and low dispersal capacity. Interpatch distance, patch density and the density of the corridor network influenced the probability of occurrence of such a species in isolated woodlots. Edge-species were not sensitive to the degree of isolation. Interpatch movements by dispersers are apparently sufficient to compensate for local extinctions within a very short time.

Regional abundance

Regional abundance influenced the probability of occurrence of a species in woodlots of different sizes as was shown for four forest bird species (jay, marsh tit, pied flycatcher and songthrush). These species were underrepresented in small woodlots in regions where those species were scarce relative to other regions. No less than 59% of the residual variance in the number of forest-interior species (Si) was explained by this biogeographic factor. The importance of a distinction between eastern and central/southern regions reflects the differential distribution patterns of these species within The Netherlands as a whole. These patterns are to some extent related to the landscape structure. ***E.g.,*** the landscape in eastern regions has a higher density of wooded patches composed of mature deciduous trees and a higher degree of connectivity among woodlots than in central/southern regions. Populations of site-tenacious species are then larger in these more stable and better connected landscapes versus open landscapes with few isolated patches. On a larger spatial scale, this parallels the effects of the landscape structure described above.

We conclude by suggesting that the distribution of forest birds in a patch or a landscape (as a group of patches) is the result of the following processes:

-the dispersal flow through the surrounding landscape, which is governed by (1) the combined effect of local and regional patch density and (2) the resistance of the landscape (the barrier effect), determined by the density of patches (stepping stones) and corridors, and perhaps also by specific barriers like highways and urban areas. Patches may serve as reproduction habitat and as transitional habitat at the same time.

-population dynamics of the population in the patch or the metapopulation in the landscape, resulting from a fluctuating birth and death rate. These populations are viewed as sinks to the dispersal flow, but if birth rate exceeds death rate, a sink turns into a source for its surroundings.

In this system various spatial scales interact. The dispersal flow, either at landscape scale or at a regional scale, may compensate for negative population trends, either by supplying individuals to occupy the vacant territories in the patches or by recolonization of empty patches. (Meta)populations will eventually become extinct if the dispersal flow becomes so weak that recolonization is not frequent enough to compensate for extinctions (Hanski 1985). This may happen as a result of alterations in the density of patches and corridors in the surrounding landscape. Because species will differ in tendency to disperse and to cross unattractive habitat types, the minimal required dispersal flow in a given mosaic of patches will differ among species. To landscape ecologists it is a great challenge to predict quantitatively the dynamic distribution of a species from the spatial arrangement of a set of habitat patches and the landscape structure of the surrounding region.

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