Macroecological signals of species interactions in the Danish avifauna

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The role of intraspecific and interspecific interactions in structuring biotic communities at fine spatial scales is well documented, but the signature of species interactions at coarser spatial scales is unclear. We present evidence that species interactions may be a significant factor in mediating the regional assembly of the Danish avifauna. Because >95% of breeding species (n = 197) are migratory, we hypothesized that dispersal limitation would not be important and that breeding distributions would largely reflect resource availability and autecological habitat preferences. Instead, we detected a striking pattern of spatial segregation between ecologically similar species at two spatial scales with a suite of null models that factored in the spatial distribution of habitats in Denmark as well as population size and biomass of each species. Habitat utilization analyses indicated that community-wide patterns of spatial segregation could not be attributed to the patchy distribution of habitat or to gross differences in habitat utilization among ecologically similar species. We hypothesize that, when habitat patch size is limited, conspecific attraction in concert with interspecific territoriality may result in spatially segregated distributions of ecologically similar species at larger spatial scales. In the Danish avifauna, the effects of species interactions on community assembly appear pervasive and can be discerned at grain sizes up to four orders of magnitude larger than those of individual territories. These results suggest that species interactions should be incorporated into species distribution modeling algorithms designed to predict species occupancy patterns based on environmental variables.

null models | assembly rules | interspecific territoriality | conspecific social attraction | allee affect

The study of species interactions has been at the forefront of ecological research for 75 years (1–4), but the range of spatial scales at which interactions may be discerned in natural communities is imperfectly known. Species interactions affect the fine-grained spacing of individuals in a wide range of organisms including plants (5, 6), marine invertebrates (7–9), social insects (10), fish (11), lizards (12), and mammals (13). The evidence is particularly good for birds, where aggressive interactions may result in interspecific territoriality in which individuals defend territories against both conspecific and heterospecific individuals (14–16). At what point along the spatial continuum from individual territories to continental landscapes does the signature of species interactions cease to be visible?

Interspecific competition can have a pervasive influence on the distribution, abundance, and foraging behavior of birds on small islands (17–19), and it has been hypothesized that local competition among species could "scale up" to generate competitively driven distributional patterns on larger islands (20). However, interspecific competition has a more subtle and ecologically limited effect in mainland avifaunas (14–16, 21). The extent to which interspecific competition influences the geographic distribution of species in continental landscapes has never been resolved. Because large-scale field experiments on avian communities are unfeasible, evidence of interspecific competition has been sought in binary presence/absence matrices of species occurrences on islands (20, 22) and in

continental mainland regions (23). Inferences of community assembly rules from statistical analyses of presence/absence data are controversial. Even with the use of sophisticated null-model analyses, it is not possible in most systems to discriminate spatial patterns generated by species interactions from those caused by historical effects, dispersal barriers, and especially those resulting from habitat selection, the intrinsic preferences that species show for particular habitats (24). Large-scale distributional signals of species interactions, if they exist in continental avifaunas, originate at the scale of individual territories. Although habitat selection manifests itself at a wide range of grain sizes (24, 25), the effects of intraspecific and interspecific interactions in continental landscapes previously have been detected only at small grain sizes (14–16, 21, 24, 26–29). In this paper, we present evidence that both intraspecific and interspecific interactions may influence the large-scale spatial distribution of breeding birds in Denmark.

Denmark consists of the Jylland Peninsula and an archipelago of land-bridge islands, most of which are visible from the mainland. The contemporary breeding avifauna (197 species) is largely migratory, and only a handful of species (<5%) can be classified as sedentary residents, although juveniles of even these species disperse widely (30). A majority of migratory species also have breeding populations in Sweden and Norway that transit Denmark during migration. Thus, the breeding distribution of birds in Denmark largely reflects resource availability, habitat selection, and the outcome of species interactions, rather than dispersal limitation, historical contingency, or evolutionary processes (none of the species in this assemblage are endemic to Denmark).

To disentangle the effects of species interactions from those of habitat selection in the Danish avifauna, we analyzed the breeding distributions of birds at two spatial grains—from a gridded matrix of 5-km × 5-km cells (n = 2003) and a larger-scale aggregation of 10-km × 10-km cells (n = 620) (Fig. 1 and Fig. S1). Cells of the smaller grain size (25 km^2) are roughly equivalent in area to the breeding territories of the largest raptors (e.g., *Bubo bubo*) but are three to four orders of magnitude larger than the breeding territories of songbirds, which numerically dominate the Danish avifauna. We then quantified the areas of principal terrestrial and aquatic habitats occurring in each cell at the two spatial scales (Table S1). These complementary databases were used to analyze the co-occurrence patterns of species and the observed and expected values of habitat utilization and electivity at two nested levels of assemblage organization: (*i*) foraging guilds within the avifauna and (*ii*) sets of congeneric or closely related species within foraging guilds. This hierarchical framework groups species into guilds of ecologically similar species, with congeneric species within foraging guilds exhibiting the greatest similarity in foraging behavior and morphology.
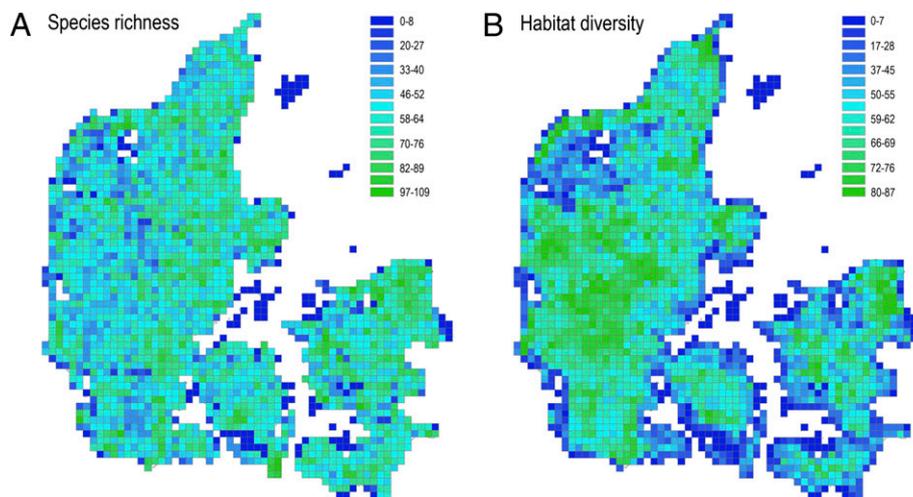
Fig. 1. Species richness of Danish breeding birds (*Left*) and spatial variation in habitat diversity (HD) (*Right*) of grid cells at a grain size of 5 km × 5 km (25 km^2). The HD score is the product of relative grid cell area and the probability that two points randomly chosen within a grid cell represent different habitat types (54). The HD score was used to parameterize null models of random species colonization independently. Species richness ranged from 1 to 109 species per cell (16, 60). The best-fitting power function was S = 27.93681(HD)$^{0.1916}$, r^2 = 0.1171. See Fig. S1 for comparable figures at the 10-km × 10-km (100-km^2) grain size.

We crossed this spatial and guild classification with analyses of four null models of species co-occurrence: a standard "fixed-fixed" null model (which preserves row and column sums of the observed binary presence/absence matrix) and three additional models that used information on habitat availability, population sizes, and biomass to modify marginal probability distributions (Table S1, S2, and S3 and Figs. S2 and S3). Finally, we conducted null-model analyses of habitat utilization and electivity (31, 32) at both grain sizes for the foraging and congeneric guilds. The resulting suite of 24 sets of null-model analyses (two guild categories × two grain sizes × six null models) permits us to address two fundamental questions about the distributional patterns of Danish breeding birds: (*i*) Do species in foraging and congeneric guilds exhibit nonrandom patterns of spatial aggregation or segregation? (*ii*) Can nonrandom distributional patterns at different spatial scales be accounted for by the availability and selection of habitat?

Results

Co-Occurrence Patterns Within Foraging Guilds. Species within most foraging guilds exhibited segregated distributions (Fig. 2, *Left* and Table S4). Summed across all of the foraging guilds, null models, and spatial grain sizes (24 guilds × 2 grain sizes × 4 null models = 192 analyses), 69.8% of tests indicated statistically significant segregated distributions, 18.2% showed random distributions, and

12.0% indicated statistically significant aggregated distributions. In a comparison of patterns at the two grain sizes, a greater fraction of tests indicated segregated distributions in 100-km^2 cells (74 segregated, 6 aggregated) than in 25-km^2 cells (60 segregated, 18 aggregated). In a comparison of the different null models, combining results from both scales of resolution, all four indicated relatively high frequencies of segregated patterns: fixed-fixed model (29 segregated, 0 aggregated); habitat model (33 segregated, 9 aggregated); population model (36 segregated, 6 aggregated); and biomass model (36 segregated, 7 aggregated). The habitat model showed the greatest difference in patterns between 100-km^2 cells (22 segregated, 1 aggregated) and 25-km^2 cells (11 segregated, 8 aggregated).

Four foraging guilds exhibited segregated distributional patterns at both spatial grains over all models, whereas 11 guilds exhibited a mixture of segregated and random distributions (Table S4). Eight guilds exhibited a mixture of segregated, aggregated, and random distributions, but only the dabbling ducks showed a strong pattern of aggregation (three of four models at both grain sizes). Of particular interest, the eight foraging guilds composed almost entirely of territorial songbirds (openland insectivores, terrestrial and low-stratum flycatchers, thrushes, marsh warblers, foliage gleaners, tit-like birds, corvids, passerine seedeaters) showed strongly segregated distributions in 25-km^2 cells (20 seg-
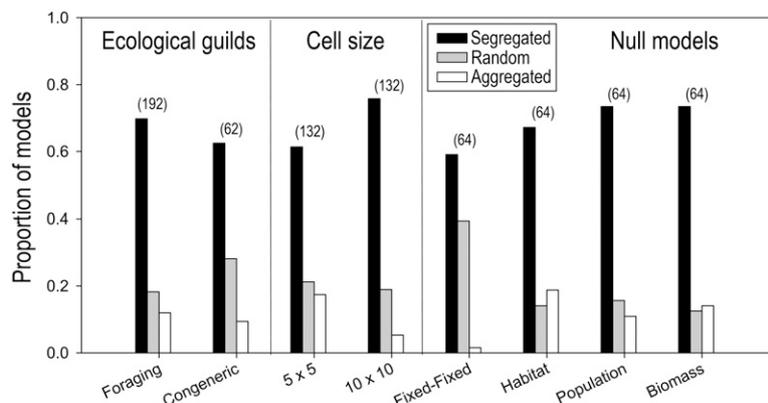
Fig. 2. Summary of null-model analyses of species co-occurrence in ecological guilds of Danish birds (Tables S4 and S5).

regated, 6 random, 5 aggregated) and 100-km^2 cells (24 segregated, 7 random, 1 aggregated).

Co-Occurrence Patterns Within Congeneric Guilds. Segregated patterns of distributional overlap in congeneric guilds of territorial songbirds provided further confirmation of patterns observed in foraging guilds (Fig. 2, *Left* and Table S5). Summed across congeneric guilds and both spatial grains (eight guilds × four null models × two grain sizes = 64 analyses), 62.5% of tests indicated statistically significant segregated distributions, 28.1% showed random distributions, and 9.4% indicated statistically significant aggregated distributions. A greater fraction of tests indicated segregated distributions in 100-km^2 cells (21 segregated, 1 aggregated) than in 25-km^2 cells (18 segregated, 5 aggregated). All null models indicated relatively high frequencies of segregated patterns: 8 segregated and 1 aggregated for the fixed-fixed model; 10 segregated and 2 aggregated for the habitat model; 11 segregated and 1 aggregated for the population model; and 10 segregated and 2 aggregated for the biomass model.

Summing across spatial grain sizes, four congeneric guilds exhibited a mixture of segregated and random distributions; the remaining four guilds showed a mixture of segregated, random, and aggregated distributions (Table S5). Overlap patterns in *Sylvia* (2 segregated, 4 random, 2 aggregated) and *Phylloscopus* (1 segregated, 5 random, 2 aggregated) were equivocal. The remaining six guilds showed strong patterns of spatial segregation: *Anthus* (6 segregated, 1 random, 1 aggregated); *Acrocephalus* (6 segregated, 2 random, 0 aggregated); *Parus* (5 segregated, 2 random, 1 aggregated); *Corvus* (8 segregated, 0 random, 0 aggregated); *Carduelis* (6 segregated, 2 random, 0 aggregated); and *Turdus* (6 segregated, 2 random, 0 aggregated).

Habitat Utilization and Electivity Within Foraging Guilds. All foraging guilds showed significantly high overlap in habitat utilization at both spatial grain sizes (48/48 tests; Table S6). Similar patterns of high overlap were observed in habitat electivity analyses of 25-km^2 cells (17/24 tests) and 100-km^2 cells (15/24 tests). Species within foraging guilds never exhibited mutually exclusive patterns of habitat utilization and electivity. These analyses suggest that the pervasive spatial patterns of segregation indicated by the four co-occurrence null models (Fig. 2) were not caused by checkerboard distributions of habitats or by gross differences among species in habitat preferences.

Habitat Utilization and Electivity Within Congeneric Guilds. Congeneric guilds are composed of species that might be expected, a priori, to exhibit the greatest degree of niche overlap based on phylogenetic similarity and niche conservatism. Congeneric guilds showed significantly high overlap in habitat utilization at both spatial grain sizes (16/16 tests; Table S7). Similar patterns of high overlap were observed in habitat electivity in 25-km^2 cells (six of eight tests) and in 100-km^2 cells (six of eight tests). The one exception was observed in *Sylvia* (five species), which exhibited high overlap in habitat utilization but mutually exclusive patterns of habitat electivity at both spatial grains. This result suggests that species of sylviid warblers occupy cells with a similar spectrum of common habitats but may differ from one another in their occupancy of grid cells containing uncommon habitats (i.e., shrublands and deciduous woodlands).

Discussion

We began the analyses with the expectation that the breeding distribution of birds in Denmark would be linked in a simple way to the availability of preferred habitat at the scale of analysis (Fig. 1) (33). The significant aggregation of dabbling ducks in grid cells containing marsh and freshwater lakes, for example, was consistent with this expectation. We were surprised, however, to discover a pervasive pattern of spatial segregation of species belonging to well-

defined foraging and congeneric guilds (Fig. 2), especially among species of territorial songbirds. Because terrestrial habitat diversity is high within 25-km^2 grid cells (9.6 of a possible 10 habitats), there is little evidence that segregated patterns of spatial overlap among widely distributed territorial species are caused by checkerboard distributions of distinctive habitat types or reflect strong differences among species in habitat preferences (Fig. 3). A lack of habitat sorting also was confirmed by the pattern of high overlap in habitat utilization and electivity among species belonging to the same foraging and congeneric guilds (Tables S6 and S7). The one exception was observed in *Sylvia* warblers, which exhibited significantly less overlap in habitat electivity. Although these findings do not rule out the possibility that subtle habitat preferences influence the pattern of spatial segregation among other guilds at coarser spatial scales, they do suggest that behavioral factors other than simple habitat selection may influence the spatial distributions of species at grain sizes several orders of magnitude larger than the areas of individual territories.

Conspecific and heterospecific attraction often result in clumped or aggregated distributions of breeding birds, most notably among colonial species such as herons, gulls, and swallows (34, 35). The occurrence of conspecific and heterospecific attraction among songbirds that defend relatively large territories (0.1–10 ha) is arguably more intriguing because the adaptive advantages of aggregated distributions for highly territorial species are less apparent. Because heterospecific attraction would yield a significant excess of aggregated distributions among pairs of species (36), the opposite of what we observed, it may be excluded as the basis for the pervasive community-wide patterns of spatial segregation.

Although logistical and ethical constraints prevented us from conducting large-scale field experiments, we hypothesize that the underlying cause of spatial segregation in territorial species at larger scales of resolution stems primarily from conspecific attraction. Several field studies have shown that patch suitability is enhanced by the presence of conspecifics, which can lead to local abundance peaks higher than expected from the distribution of habitat resources (34). The benefits of local aggregative behavior in territorial birds, including mate acquisition and public information sharing, are examples of Allee effects (37, 38), broadly defined as the positive relationship between fitness and the number of conspecifics. Allee effects, which often are manifest at low population densities, may result in conspecific aggregations at spatial scales larger than those of individual territories.

Although conspecific attraction may explain local aggregations of species at the grain sizes analyzed in this study, it cannot explain the excess frequency of interspecific segregation observed in many foraging and congeneric guilds of Danish birds. Interspecific territoriality has been documented in a number of territorial songbirds in Eurasia (21, 39–41), even among some pairs of distantly related species (42). However, spatially segregated territories
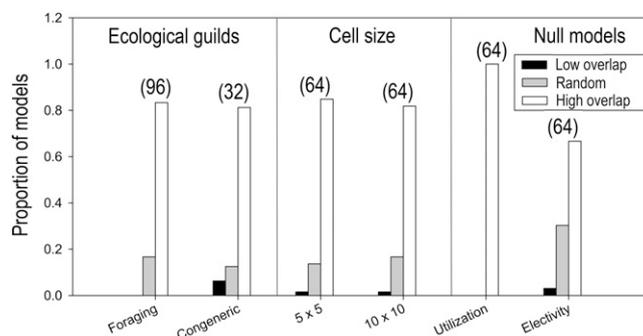
Fig. 3. Summary of null-model analyses of niche overlap in habitat utilization and electivity in ecological guilds of Danish birds (Tables S6 and S7).

occur most frequently within pairs of closely related, ecologically similar species that occupy structurally simple habitats (15, 21, 28). When interspecific territoriality occurs in heterogeneous or structurally diverse environments, behaviorally dominant species usually exclude less aggressive species from the more productive end of successional gradients, leading to local habitat segregation (14). It should be noted that similar patterns of habitat segregation commonly arise in the absence of competition through the mechanism of habitat selection in heterogeneous environments (24, 43–45). Although habitat patch size may be another determining factor for species occupancy, the minimum patch size for most northern European songbirds is relatively small (<1 ha) (46).

In the Danish avifauna, migratory species arrive to nearly empty habitat each spring. Annual mortality rates of migratory songbirds are relatively high (30), and a substantial fraction of arriving individuals are naïve yearlings with no prior breeding experience. Priority effects may come into play if several males of one species establish contiguous territories in a habitat patch before males of other species arrive. Conspecific attraction then might permit one species to dominate numerically a habitat patch so that it becomes less attractive to arriving heterospecifics, which either fail to establish territories or rapidly emigrate to other patches of similar habitat that support larger numbers of their own species. It thus is plausible that conspecific attraction combined with interspecific territoriality could result in mutually exclusive distributions of species at relatively large spatial scales. Interspecific territoriality alone would be unlikely to result in spatial segregation at the grain sizes studied here. The mechanism described above would be more likely to occur among migratory than resident species, at low rather than high population densities, and in patchy environments where patch size is relatively small. In summary, our analyses suggest that conspecific and heterospecific interactions can "scale up" to produce behaviorally driven assembly patterns at relatively large spatial grains. The next generation of coarse-grained macroecological studies may need to incorporate species interactions that occur at small spatial scales. Our results also suggest that a failure to incorporate mechanisms of species interactions may account for the mixed results of current species distribution modeling efforts that use only environmental variables to predict species occupancy (47, 48).

Methods

Geography. The deglaciation of Denmark was completed 16,000–15,500 years ago (ybp) (49), and transformation of the region into the Jylland Peninsula (i.e., mainland) and an archipelago of nearby land-bridge islands took place ≈ 8,500 ybp through the rising of the Litorina Sea (50). Present-day Denmark (~43,100 km²) presents an ideal geographic template for co-occurrence analysis of avian species at the regional scale. There are no major geographic barriers to avian dispersal (the highest point in Denmark is 173 m above sea level), and there is no evidence of in situ speciation (there are no endemic avian species or subspecies). The larger islands of Sjælland (7,016 km²), Fyn (2,977 km²), Lolland (1,241 km²), Falster (514 km²), Mors (363 km²), Als (314 km²), Langeland (284 km²), Møn (217 km²), Rømø (129 km²), Samsø (114 km²), Amager (90 km²), Ærø (88 km²), Tåsinge (70 km²), and Fanø (56 km²) were retained in our analyses. Islands with land and freshwater areas totaling <25 km² and those occurring >20 km from Jylland or the principal land-bridge islands were omitted from the analyses.

Distributional Data. The breeding distribution of the Danish avifauna was mapped at the resolution of 5-km × 5-km cells (25 km²), following the Universal Transverse Mercator coordinate system, by 750 observers during the period 1993–1996 (51) (see *SI Text* for additional sampling details). After small and distant islands and cells with <25 ha of land area were excluded from the data set, a total of 2,003 cells were available for analysis. We aggregated 5-km × 5-km cells (both complete and marginal) to create 10-km × 10-km cells (100 km²). At each grain size, we converted the distributional breeding records to a binary presence/absence (0,1) matrix in which rows represent species and columns represent cells. The matrix of 25-km² cells supported 197 breeding species. Three species recorded during the 1993–1996 censuses (*Ciconia ciconia*, *Tetrao tetrix*, and *Sylvia nisoria*) no longer breed in Denmark. Two colonial

species (*Rissa tridactyla* and *Alca torda*) that occurred in marginal coastal cells at the 25-km² grain size were omitted from the matrix when scaling it up to 100-km² cells (*n* = 620). Edge effects of peripheral cells were incorporated by taking account of the area of each cell and its habitat diversity, both of which are reduced in peripheral cells.

Habitat. The Danish environment has experienced several millennia of intensive human disturbance (52) culminating in a contemporary terrestrial landscape characterized by fine-grained patchworks of heath, hedgerow, shrubland, and woodland embedded in a matrix of pasture, meadow, and cropland. Habitats within 25-km² cells were previously classified into 12 distinctive categories defined and quantified based on remote sensing of 25-m × 25-m pixels (53): open saline water, open fresh water, urban and unvegetated ground, seasonally tilled cropland, grazed or mown grassland, marshland and bog, grassy heathland, mixed grassy and shrubby heathland, shrubby heathland, shrubby woodland, deciduous woodland, and coniferous woodland (Table S1). Cells typically contained a majority of the habitat categories present in Denmark (10.6 ± 1.0 of 12 possible habitats). We constructed a quantitative index of habitat heterogeneity (Fig. 1) based on the percent area of the common habitat categories occurring within 25-km² cells. Habitat types covering <1% (25 ha) of the cell area were omitted from the diversity index for that cell. We estimated habitat heterogeneity (HH) as:

$$HH = 1.0 - \sum_{i=1}^{12} \left(p_i^2 \right)$$

where p_i is the proportion of the total area measured within each cell that is occupied by habitat *i*. This index measures the probability that two random points chosen within a cell represent two different habitats (54). HH can range from a minimum of 0.0 (if only a single habitat type is present) to a maximum of 0.917 (if all 12 habitats are equally common). At the 100-km² grain size, we recalibrated the HH values of 13 cells (<3% of the total) from 0.00 to 0.01 so that relative probability weights could be calculated. We then multiplied HH by the cell area minus the area of open saline water to create an index of habitat diversity (HD). To minimize numerical round-off error in the HD index (which ranged from 0.01 to 83.77), 60 values <1.0 were rescaled to 1.0. Recalibration was unnecessary at the 25-km² grain size.

Indices of Species-Specific Colonization Potential. The ability of a species to colonize isolated patches of habitat is influenced by many factors including population size and dispersal behavior (53, 55). We did not attempt to model dispersal behavior per se, because the spatial scales of annual migration and natal dispersal distances of European birds are large relative to the grain size of census cells (30). Parasitism, disease, and predation also may influence the occupancy of habitat patches, but comprehensive data on these potentially important factors were unavailable.

We constructed two indices of colonization potential, one based on the estimated size of breeding populations in Denmark (51) and a second based on the biomass of each species (body mass × Danish population size). We estimated body mass as the midpoint of the mean values recorded for males and females, respectively (Table S2). Interspecific variation in avian body mass correlates with longevity (56), which in turn may be linked with a species' ability to resist local extinction through a series of failed reproductive seasons (57). Species with high biomass values in Denmark thus may exhibit enhanced abilities to colonize and persist in suitable patches of habitat. The total breeding avifauna is estimated at 1.643 × 10⁷ pairs ranging from <10 pairs (27 species) to 2,228,000 pairs (*Turdus merula*) per species. The three most abundant species (*Alauda arvensis*, *Turdus merula*, and *Fringilla coelebs*) constituted 32.5% of the total individuals, but 71 species (36%) had breeding populations >10,000 pairs (Table S2). Narrowly distributed species exhibit a strong range size–abundance relationship, but the correlation is weaker for geographically widespread species in Denmark (58). Estimates of Danish population biomass ranged from <100 g (seven species) to 6.3 × 10⁸ g (*Phasianus colchicus*).

Analysis of Ecological Guilds. We categorized the Danish breeding avifauna into two types of ecological guilds. First, we grouped 194 of 197 species into 33 mutually exclusive foraging guilds, which pool mixtures of congeneric and more distantly related species that use a similar spectrum of resources. We also analyzed a subset of eight narrowly defined congeneric guilds composed of closely related species (Table S2). To maintain statistical power in guild analyses, we focused on guilds that contained four or more species (171 species in 24 foraging guilds, and 40 species in eight congeneric guilds). For all analyses, the spatial domain included only those cells that contained at

ECOLOGY

least one guild member. This restriction guards against spurious patterns of aggregation that might arise from including empty cells that are not biologically suitable for any of the species in the guild.

Quantification of Species Co-Occurrence Patterns. We used the C-score (59) as a quantitative index of species co-occurrence. The C-score is defined as $(R_i - S) \times (R_j - S)$ where R_i and R_j represent the total number of occurrences of species i and j, respectively, and S is the number of shared occurrences. The average C-score, calculated over all unique species pairs within an ecological guild, summarizes the pattern of co-occurrence as a single metric. The larger the C-score, the fewer incidents of co-occurrence among pairs of species. However, the C-score, like most indices of segregation or aggregation, is affected both by the number of shared occurrences and by the total number of occurrences of each species. For this reason, comparison with an appropriate suite of null models is essential.

Randomization Tests. We compared the C-score observed for ecological guilds of breeding birds with scores generated by four different null models ranging in complexity from a simple constrained randomization of the binary presence/absence matrix to models that incorporated measures of habitat heterogeneity, population size, and biomass (for model details, *SI Text*). For each model, we created null avifaunal assemblages ($n = 1,000$) and calculated the C-score for each. We then compared the C-score observed for ecological guilds with the distribution of simulated C-scores to estimate the one-tailed probability. Each set of simulations was initialized with a new random number seed taken from the system clock, and all null-model analyses were conducted in EcoSim Version 7.2 (60).

Analyses of Habitat Niche Overlap. We used a null model based on the "habitat utilization matrix" (33) to determine whether species' co-occurrence patterns were associated with the coarse-grained distribution of habitats. For each species, we determined the total area of each of the 12 habitat categories in cells that it occupied. We then constructed a habitat utilization matrix in which each row represents a species, each column represents a habitat category, and the entries are the summed areas of the habitat categories in each occupied cell.

The habitat areas then were converted to percentages for each species. For each unique species pair ij, we calculated habitat niche overlap O_{ij} using Pianka's (31) overlap index as:

$$O_{ij} = O_{ji} = \frac{\sum_{k=1}^{n} p_{ik} p_{jk}}{\sqrt{\sum_{k=1}^{n} p_{ik}^{2} \sum_{k=1}^{n} p_{jk}^{2}}}$$

where p_{ik} is the proportional occupancy of cells containing habitat k by species i. If $O_{ij} = 0.0$, then species i and j occur in cells that do not share any habitat categories. In contrast, high index values indicate that species occur in cells that contain similar proportions of the various habitat categories. We then calculated the average pairwise overlap for all unique species pairs in the matrix. Habitat utilization matrices were calculated at both spatial scales for foraging and congeneric guilds. Note that the spatial scales of our analyses are relatively large compared with the scale at which avian habitat selection occurs. The metrics describe overlap in the habitat distributions of occupied sites, which is not necessarily identical with overlap in habitat utilization.

We compared the average pairwise overlap in real assemblages of species with the frequency distribution of overlap values observed in null assemblages. The null distribution was created by reshuffling the overlap values within each row of the original species × habitat utilization matrix to generate a null distribution (1,000 randomizations) that would be expected if habitat utilization was independent among species. We then calculated the probability that the observed niche overlap was drawn from this distribution (61).

One potential problem with such niche overlap analyses is that they assume that all of the resource states, or in this case habitat categories, are equally abundant (62). This assumption is not met for the habitats of Denmark, which vary considerably in their total area. We therefore analyzed "electivity indices" of species by dividing the observed utilization values for each habitat category by the total area of that habitat in Denmark (32, 63). This scaling gives less weight to common habitats, which will tend to dominate the numerical results in the unweighted analysis.

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ECOLOGY

Supporting Information

Gotelli et al. 10.1073/pnas.0914089107

Null-Model Algorithms

Null-model analysis has been controversial, in part because the results depend on the assumptions of the specific null-model test, which often are difficult to evaluate (1, 2). Most null-model analyses have been based on a modified version of Connor and Simberloff's (3) original strategy of preserving observed row and column sums in the matrix. Although this algorithm originally was criticized as allegedly being too conservative (4), extensive benchmark tests with artificial matrices suggest it has good statistical properties (5–7). However, to ensure our analyses were robust and not unduly influenced by the performance of a single test, we used a suite of four null-model algorithms. These models all use the C-score (8) as the index for measuring species segregation or aggregation. Related indices, such as Stone and Robert's togetherness index (9) could be used also, although these indices have not yet been subject to benchmark testing.

Fixed-Fixed Model. The fixed-fixed model creates null matrices in which the row and column totals of the matrix are preserved (5). In the absence of additional biological or geographic information, the fixed row and column sums account for observed heterogeneity in site suitability and differences among species in colonization potential (3). To create such a matrix, we used an algorithm (5) which swaps the elements of randomly chosen 2×2 submatrices of the form [01 | 10] or [10 | 01]. Although the pattern of ones and zeros is randomized, each null community has the same number of species (column totals) and occupied cells (row totals) as the real avifaunal community. We created each matrix with a total of 30,000 consecutive swaps or mn swaps (where m = the number of rows in the matrix and n = the number of columns), whichever was larger. These numbers ensured that, in each randomly generated matrix, every swappable submatrix was reshuffled at least once. A unique, independent swap sequence was used for each of the 1,000 null matrices. The fixed-fixed model, when used with the C-score, has been subjected to extensive benchmark testing with artificial matrices that contain specified amounts of randomness and structure (5–7). The swapping algorithm that we have used to create null matrices is slightly less likely to detect segregation of species than is a more recent algorithm that samples all matrices with the same row and column totals equiprobably (10). However, this bias is small for large matrices of the size we have analyzed here (11).

Habitat Model. A potential weakness of the fixed-fixed model is that it does not directly simulate a random colonization process. To address this deficiency, we used a model in which the row totals of the matrix (the occurrence frequency of species) were fixed, but the column totals (the number of species per cell) were not. Most importantly, species were assigned randomly and independently to cells with the probability of occurrence set proportional to the measured index of habitat diversity (HD) for each cell.

Population Model. To reflect the natural differences in habitat diversity among cells and colonization potential among species, we constructed a population-null model in which the total number of species occurrences in the matrix was preserved, but where row and column total were allowed to vary randomly (5). The probability of an occurrence of species i in cell j was proportional to both the total breeding population size of species i in Denmark and the HD value of cell j. Thus, for the placement of the first species occurrence in the matrix, the cell most likely to be chosen would occur at the intersection of the row with the largest sum (species with largest population) and column with the largest sum (grid cell with the highest HD value). The least likely cell to be chosen would be the one with the smallest row and smallest column sum.

Biomass Model. The biomass model was identical to the population model, except that biomass (total biomass of breeding individuals in Denmark) was substituted for population size. The rational for this model is that total biomass reflects the total energy that has been sequestered by the species in Denmark, integrating the effects of both population size and body size. Because it is difficult to validate or parameterize null models for entire assemblages, our strategy was to test a suite of null models applied to different spatial scales and different levels of assemblage organization. Consistent results that emerge from such a battery of tests yield robust findings that are insensitive to the assumptions and restrictions that may apply to any particular null model or data partition.

Body masses were compiled from the *Handbook of the Birds of Europe, the Middle East, and North Africa* (12–20), with a preference for data from Danish, Dutch, and northern German populations. A priori guild assignments were made by C. Rahbek and J. Fjeldså before co-occurrence analyses were performed.

Census Data for Danish Avifauna

Species occurrence records for the 197 breeding birds of Denmark were derived from data in the Danish atlas of breeding birds in Denmark, 1993–1996 (21). Denmark was divided into 2,169 atlas-cells (5 km × 5 km). More than 99% of the cells were surveyed for breeding birds: 1,465 were well surveyed, 640 were reasonably well surveyed, 50 were incompletely surveyed, and only 14 cells were not surveyed. Atlas surveys were conducted by *ca*. 750 observers. The total number of observations (cells × species occurrences) equaled 141,865. Each cell was visited 5–10 times each year for a quantitative census of all breeding species. Field work was conducted between February and August during each of the 4 years (1993–1996).

Data derived from the atlas surveys were supplemented with information from census records from 2,500 large nature reserves, ongoing single-species surveys, and monitoring or research programs on rare and/or endangered species, wildfowl, and raptors. Incidental information on rare breeding species also was included from published maps on occurrences of Danish breeding birds.

The occurrence of each species in a cell was categorized as (*i*) confirmed breeding (e.g., observation of adults feeding chicks, occurrence of freshly used nests, and/or adult birds carrying food or excrement); (*ii*) probable breeding (e.g., territorial singing males observed in the breeding season, individuals observed defending territories, engaging in courtship, building nests, or carrying nesting materials); and (*iii*) presence observed (e.g., birds were observed in the breeding season but with no other evidence of breeding). In our analyses, we used only records from the first two categories to designate species occurrences.

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Fig. S1. Species richness and habitat diversity (100-km^2 grain size). Species richness of Danish breeding birds and spatial variation in habitat diversity (HD) of grid cells at a grain size of 10 km × 10 km (100 km^2). The HD score is the product of relative grid cell area and the probability that two points randomly chosen within a grid cell represent different habitat types (1). The HD score was used to parameterize null models of random species colonization independently. Species richness ranged from 10 to 117 species per cell (average = 81.45). The best-fitting power function was S = 48.17259(HD)$^{0.1468}$, r^2 = 0.4233.

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Fig. S2. Individual body mass. Distribution of body masses of the Danish avifauna (*n* = 197 species).

Fig. S3. Population biomass. Distribution of population biomass (individual body mass × population size) for the Danish avifauna (*n* = 197 species).

Other Supporting Information

Table S1 (PDF)
Table S2 (PDF)
Table S3 (PDF)
Table S4 (PDF)
Table S5 (PDF)
Table S6 (PDF)
Table S7 (PDF)

Table S1. Habitat categories.

Percent coverage and distribution of habitat types among 5 km × 5 km cells in Denmark.

Habitat Categories	% cover in cells	% cells with > 25 ha of habitat
open saline water	20.3	40.7
open fresh water	0.8	10.3
urban and unvegetated ground	7.7	93.8
Seasonally tilled cropland	38.0	95.8
grazed or mown grassland	19.0	97.0
marshland and bog	0.8	21.1
grassy heathland	2.6	67.5
mixed grassy and shrubby heathland	0.5	12.6
shrubby heathland	0.8	21.2
shrubby woodland	1.6	49.5
deciduous woodland	3.6	69.6
coniferous woodland	4.3	60.6

Table S2. Macroecological traits of the Danish avifauna.

Rows represent breeding species included in the analysis. 25 km^2 = number of grid-cell occurrences at the 5 x 5 km^2 spatial grain (n = 2003 grid cells total; 100km^2 = number of grid cell occurrences at the 10 x 10 km^2 spatial grain (n = 620 grid cells total). Territoriality = territorial or colonial status. Body mass = adult body mass in grams (averages given for sexually dimorphic species). N = estimated number of breeding pairs in Denmark. Foraging guild and congeneric guild assignments were made *a priori* by C. Rahbek and J. Fjeldså.

Common English Name	Scientific Name	25 km^2	100 km^2	Territoriality	Body Mass	N	Foraging Guild	Congeneric Guild
Little Grebe	*Tachybaptus ruficollis*	646	387	territorial	190	1750	aquatic pursuers	
Great Crested Grebe	*Podiceps cristatus*	563	321	territorial	875	4000	aquatic pursuers	
Red-necked Grebe	*Podiceps griseigena*	501	302	territorial	850	1750	aquatic pursuers	
Horned Grebe	*Podiceps auritus*	2	2	territorial	394	<10	aquatic pursuers	
Eared Grebe	*Podiceps nigricollis*	54	41	territorial	290	275	aquatic pursuers	
Great Cormorant	*Phalacrocorax carbo*	42	47	colonial	2110	38500	aquatic pursuers	
Eurasian Bittern	*Botaurus stellaris*	68	56	territorial	1225	175	wading birds	
Gray Heron	*Ardea cinerea*	226	199	colonial	1432.5	6735	wading birds	
Black Stork	*Ciconia nigra*	1	1	territorial	3000	<10	wading birds	
White Stork	*Ciconia ciconia*	8	7	territorial	3447.5	<10	wading birds	
Eurasian Spoonbill	*Platalea leucorodia*	2	2	colonial	1260	<10	wading birds	
Mute Swan	*Cygnus olor*	925	484	territorial	10750	5000	grazing waterfowl	
Graylag Goose	*Anser anser*	435	267	territorial	3465	3750	grazing waterfowl	

Canada Goose	*Branta canadensis*	26	25	territorial	4635	38	grazing waterfowl	
Barnacle Goose	*Branta leucopsis*	4	5	territorial	1585	17	grazing waterfowl	
Common Shelduck	*Tadorna tadorna*	1131	533	territorial	1152.5	2500	dabbling ducks	
Eurasian Wigeon	*Anas penelope*	7	9	territorial	642.5	10	grazing waterfowl	
Gadwall	*Anas strepera*	78	71	territorial	750	275	dabbling ducks	
Green-winged Teal	*Anas crecca*	177	147	territorial	355	300	dabbling ducks	
Mallard	*Anas platyrhynchos*	1747	603	territorial	1030	20000	dabbling ducks	
Northern Pintail	*Anas acuta*	45	46	territorial	807.5	163	dabbling ducks	
Garganey	*Anas querquedula*	97	86	territorial	327.5	275	dabbling ducks	
Northern Shoveler	*Anas clypeata*	221	182	territorial	652.5	900	dabbling ducks	
Common Pochard	*Aythya ferina*	214	159	territorial	870	500	diving ducks	
Tufted Duck	*Aythya fuligula*	358	249	territorial	657.5	900	diving ducks	
Common Eider	*Somateria mollissima*	110	119	territorial	2067.5	22000	diving ducks	
Common Goldeneye	*Bucephala clangula*	20	14	territorial	825	63	diving ducks	
Red-breasted Merganser	*Mergus serrator*	276	200	territorial	1092.5	2500	aquatic pursuers	
Common Merganser	*Mergus merganser*	35	24	territorial	1435	50	aquatic pursuers	
Honey Buzzard	*Pernis apivorus*	268	169	territorial	625	650	diurnal raptors	
Red Kite	*Milvus milvus*	39	32	territorial	1015	26	diurnal raptors	
White-tailed Eagle	*Haliaeetus albicilla*	3	3	territorial	4792.5	<10	diurnal raptors	
Marsh Harrier	*Circus aeruginosus*	391	250	territorial	585	650	diurnal raptors	
Northern Harrier	*Circus cyaneus*	7	7	territorial	438.5	<10	diurnal raptors	
Montagu's Harrier	*Circus pygargus*	33	23	territorial	315	43	diurnal raptors	
Northern Goshawk	*Accipiter gentilis*	594	331	territorial	925	675	diurnal raptors	
Eurasian Sparrowhawk	*Accipiter nisus*	1140	507	territorial	205	3750	diurnal raptors	
Common Buzzard	*Buteo buteo*	1498	524	territorial	805	5000	diurnal raptors	
Osprey	*Pandion haliaetus*	10	10	territorial	1530	<10	diurnal raptors	
Eurasian Kestrel	*Falco tinnunculus*	1215	529	territorial	115	2050	diurnal raptors	
Eurasian Hobby	*Falco subbuteo*	3	3	territorial	210	<10	diurnal raptors	

Black Grouse	*Tetrao tetrix*	1	1	territorial	1080	<10	gallinaceous birds	
Gray Partridge	*Perdix perdix*	1464	547	territorial	385	25000	gallinaceous birds	
Common Quail	*Coturnix coturnix*	113	91	territorial	100	38	gallinaceous birds	
Ring-necked Pheasant	*Phasianus colchicus*	1790	590	territorial	1125	280000	gallinaceous birds	
Water Rail	*Rallus aquaticus*	400	282	territorial	115.5	3500	Rails	
Spotted Crake	*Porzana porzana*	24	21	territorial	83	35	Rails	
Corncrake	*Crex crex*	12	12	territorial	155	<10	Rails	
Common Moorhen	*Gallinula chloropus*	1329	550	territorial	350	50000	Rails	
Eurasian Coot	*Fulica atra*	1604	588	territorial	775	20000	Rails	
Common Crane	*Grus grus*	9	8	territorial	5275	10	wading birds	
Eurasian Oystercatcher	*Haematopus ostralegus*	758	420	territorial	525	7500	plovers	
Black-winged Stilt	*Himantopus himantopus*	1	1	territorial	205	<10	plovers	
Pied Avocet	*Recurvirostra avosetta*	182	141	territorial	245	5000	plovers	
Little Ringed Plover	*Charadrius dubius*	227	173	territorial	38.5	300	plovers	
Common Ringed Plover	*Charadrius hiaticula*	485	317	territorial	64.5	2000	plovers	
Snowy Plover	*Charadrius alexandrinus*	11	10	territorial	47.5	55	plovers	
European Golden Plover	*Pluvialis apricaria*	5	5	territorial	175	<10	plovers	
Northern Lapwing	*Vanellus vanellus*	1805	597	territorial	217.5	40000	plovers	
Dunlin	*Calidris alpina*	69	64	territorial	47	450	scolopacids	
Ruff	*Philomachus pugnax*	41	34	territorial	140	400	scolopacids	
Common Snipe	*Gallinago gallinago*	662	385	territorial	105	2750	scolopacids	
Eurasian Woodcock	*Scolopax rusticola*	321	207	territorial	295	1750	scolopacids	
Black-tailed Godwit	*Limosa limosa*	49	38	territorial	332.5	700	scolopacids	
Whimbrel	*Numenius arquata*	115	82	territorial	987.5	300	scolopacids	
Common Redshank	*Tringa totanus*	583	338	territorial	121.5	12500	scolopacids	
Green Sandpiper	*Tringa ochropus*	34	28	territorial	80.5	55	scolopacids	
Wood Sandpiper	*Tringa glareola*	25	19	territorial	67.5	73	scolopacids	
Common Sandpiper	*Actitis hypoleucos*	4	4	territorial	48	<10	scolopacids	

Ruddy Turnstone	*Arenaria interpres*	1	7	territorial	110.5	40	scolopacids	
Mediterranean Gull	*Larus melanocephalus*	1	1	colonial	275	<10	Gulls	
Black-headed Gull	*Larus ridibundus*	386	276	colonial	280	150000	Gulls	
Common Gull	*Larus canus*	240	193	colonial	387.5	27500	Gulls	
Lesser Black-backed Gull	*Larus fuscus*	26	41	colonial	715	4400	Gulls	
Herring Gull	*Larus argentatus*	171	160	colonial	957.5	56500	Gulls	
Great Black-backed Gull	*Larus marinus*	75	86	territorial	1600	1550	Gulls	
Black-legged Kittiwake	*Rissa tridactyla*	3	0	colonial	307.5	625	Gulls	
Gull-billed Tern	*Gelochelidon nilotica*	5	5	colonial	217.5	14	Terns	
Sandwich Tern	*Sterna sandvicensis*	18	26	colonial	275	4500	Terns	
Common Tern	*Sterna hirundo*	92	86	colonial	125	1000	Terns	
Arctic Tern	*Sterna paradisaea*	157	142	colonial	109.5	8500	Terns	
Little Tern	*Sterna albifrons*	61	65	colonial	57	500	Terns	
Black Tern	*Chlidonis niger*	13	11	colonial	63	100	Terns	
Razorbill	*Alca torda*	1	0	colonial	722.5	610		
Black Guillemot	*Cepphus grylle*	6	17	colonial	377.5	1089		
Stock Dove	*Columba oenas*	255	178	territorial	302.5	900	columbids	
Common Wood Pigeon	*Columba palumbus*	1939	608	territorial	510	291000	columbids	
Eurasian Collared Dove	*Streptopelia decaocto*	1482	563	territorial	195	48500	columbids	
European Turtle Dove	*Streptopelia turtur*	32	19	territorial	153.5	118	columbids	
Common Cuckoo	*Cuculus canorus*	1755	594	territorial	110	22050		
Barn Owl	*Tyto alba*	38	32	territorial	365	63	Owls	
Eurasian Eagle Owl	*Bubo bubo*	28	24	territorial	2220	33	Owls	
Little Owl	*Athene noctua*	110	79	territorial	167.5	188	Owls	
Tawny Owl	*Strix aluco*	889	395	territorial	462.5	4500	Owls	
Long-eared Owl	*Asio otus*	644	381	territorial	257.5	1750	Owls	
Short-eared Owl	*Asio flammeus*	14	15	territorial	295	<10	Owls	
European Nightjar	*Caprimulgus europaeus*	114	77	territorial	85	550		

Common Swift	*Apus apus*	599	337	territorial	39.5	100000	aerial insectivores	
Common Kingfisher	*Alcedo atthis*	160	111	territorial	39	300		
Eurasian Hoopoe	*Upupa epops*	1	1	territorial	66.5	<10		
Eurasian Wryneck	*Jynx torquilla*	99	81	territorial	37.5	88	woodpeckers	
European Green Woodpecker	*Picus viridis*	451	218	territorial	191	775	woodpeckers	
Black Woodpecker	*Dryocopus martius*	149	96	territorial	275	225	woodpeckers	
Great Spotted Woodpecker	*Dendrocopos major*	1518	552	territorial	74	100000	woodpeckers	
Lesser Spotted Woodpecker	*Dendrocopos minor*	37	31	territorial	20	85	woodpeckers	
Crested Lark	*Galerida cristata*	38	33	territorial	44.65	63	open-land insectivores	
Wood Lark	*Lullula arborea*	145	95	territorial	30	300	open-land insectivores	
Eurasian Skylark	*Alauda arvensis*	1984	614	territorial	36.4	1360000	open-land insectivores	
Sand Martin	*Riparia riparia*	693	418	territorial	13.15	30000	aerial insectivores	
Barn Swallow	*Hirundo rustica*	1920	608	territorial	19.05	385000	aerial insectivores	
Common House Martin	*Delichon urbica*	1629	585	territorial	18.6	93500	aerial insectivores	
Tawny Pipit	*Anthus campestris*	6	6	territorial	24.5	23	open-land insectivores	*Anthus*
Tree Pipit	*Anthus trivialis*	1275	494	territorial	21.5	67000	open-land insectivores	*Anthus*
Meadow Pipit	*Anthus pratensis*	1130	546	territorial	19.25	40000	open-land insectivores	*Anthus*
Water Pipit	*Anthus spinoletta*	12	18	territorial	23.5	123	open-land insectivores	*Anthus*
Yellow Wagtail	*Motacilla flava*	350	236	territorial	17	8900	open-land insectivores	
Gray Wagtail	*Motacilla cinerea*	326	179	territorial	17.4	475		
White Wagtail	*Motacilla alba*	1893	611	territorial	20.8	111000	open-land insectivores	
White-throated Dipper	*Cinclus cinclus*	11	10	territorial	63.8	<10		
Winter Wren	*Troglodytes troglodytes*	1915	604	territorial	8.9	404000	terrestrial and low flycatching feeders	
Dunnock	*Prunella modularis*	1728	596	territorial	19	101000	terrestrial and low flycatching feeders	
European Robin	*Erithacus rubecula*	1807	594	territorial	16.7	285000	terrestrial and low flycatching feeders	
Thrush Nightingale	*Luscinia luscinia*	1084	448	territorial	25	68000	terrestrial and low flycatching feeders	
Common Nightingale	*Luscinia svecica*	4	2	territorial	20.3	<10	terrestrial and low flycatching feeders	

Black Redstart	*Phoenicurus ochruros*	454	294	territorial	16.2	875	terrestrial and low flycatching feeders	
Common Redstart	*Phoenicurus phoenicurus*	1146	504	territorial	15.5	36000	terrestrial and low flycatching feeders	
Whinchat	*Saxicola rubetra*	895	431	territorial	16.5	14000	terrestrial and low flycatching feeders	
Eurasian Stonechat	*Saxicola torquata*	15	13	territorial	15.2	<10	terrestrial and low flycatching feeders	
Northern Wheatear	*Oenanthe oenanthe*	253	198	territorial	23.8	2900	terrestrial and low flycatching feeders	
Common Blackbird	*Turdus merula*	1977	610	territorial	96	2282000	thrushes	*Turdus*
Fieldfare	*Turdus pilaris*	352	220	territorial	104.5	3500	thrushes	*Turdus*
Song Thrush	*Turdus philomelos*	1821	595	territorial	68.5	259000	thrushes	*Turdus*
Redwing	*Turdus iliacus*	2	2	territorial	62.5	<10	thrushes	*Turdus*
Mistle Thrush	*Turdus viscivorus*	997	445	territorial	119	28000	thrushes	*Turdus*
Grasshopper Warbler	*Locustella naevia*	413	271	territorial	13.3	1000	marsh warblers	
River Warbler	*Locustella fluviatilis*	11	10	territorial	18.8	<10	marsh warblers	
Savi's Warbler	*Locustella luscinioides*	22	19	territorial	15.65	25	marsh warblers	
Sedge Warbler	*Acrocephalus schoenobaenus*	484	326	territorial	11.9	3900	marsh warblers	*Acrocephalus*
Marsh Warbler	*Acrocephalus palustris*	1198	514	territorial	12	30000	marsh warblers	*Acrocephalus*
Eurasian Reed Warbler	*Acrocephalus scirpaceus*	1304	563	territorial	11.8	53000	marsh warblers	*Acrocephalus*
Great Reed Warbler	*Acrocephalus arundinaceus*	15	15	territorial	30.35	20	marsh warblers	*Acrocephalus*
Icterine Warbler	*Hippolais icterina*	1560	587	territorial	13.3	64000	foliage gleaners	
Barred Warbler	*Sylvia nisoria*	3	3	territorial	24.35	<10	foliage gleaners	*Sylvia*
Lesser Whitethroat	*Sylvia curruca*	1704	598	territorial	11.6	160000	foliage gleaners	*Sylvia*
Greater Whitethroat	*Sylvia communis*	1920	610	territorial	14.5	358000	foliage gleaners	*Sylvia*
Garden Warbler	*Sylvia borin*	1732	588	territorial	18.25	216000	foliage gleaners	*Sylvia*
Eurasian Blackcap	*Sylvia atricapilla*	1778	588	territorial	18.95	284000	foliage gleaners	*Sylvia*
Green Warbler	*Phylloscopus trochiloides*	3	4	territorial	7.8	<10	foliage gleaners	*Phylloscopus*
Wood Warbler	*Phylloscopus sibilatrix*	629	372	territorial	10.6	16000	foliage gleaners	*Phylloscopus*
Chiffchaff	*Phylloscopus collybita*	1778	587	territorial	8.4	240000	foliage gleaners	*Phylloscopus*
Willow Warbler	*Phylloscopus trochilus*	1910	607	territorial	9.35	603000	foliage gleaners	*Phylloscopus*

Red-breasted Flycatcher	*Ficedula parva*	11	11	territorial	11	<10		
Eurasian Pied Flycatcher	*Ficedula hypoleuca*	646	372	territorial	13.65	16200		
Spotted Flycatcher	*Muscicapa striata*	1033	489	territorial	14.9	19000		
Goldcrest	*Regulus regulus*	1462	560	territorial	5.8	168000	tit-like birds	
Firecrest	*Regulus ignicapillus*	27	25	territorial	5	15	tit-like birds	
Bearded Tit	*Panurus biarmicus*	81	67	territorial	14.4	1500		
Long-tailed Tit	*Aegithalos caudatus*	579	333	territorial	9	9700	tit-like birds	
Marsh Tit	*Parus palustris*	1073	453	territorial	11.9	27000	tit-like birds	*Parus*
Willow Tit	*Parus montanus*	38	22	territorial	11.15	200	tit-like birds	*Parus*
Crested Tit	*Parus cristatus*	854	354	territorial	11.15	26000	tit-like birds	*Parus*
Coal Tit	*Parus ater*	1417	543	territorial	10.1	178000	tit-like birds	*Parus*
Blue Tit	*Parus caeruleus*	1839	597	territorial	10.85	245000	tit-like birds	*Parus*
Great Tit	*Parus major*	1943	607	territorial	18.45	745000	tit-like birds	*Parus*
Eurasian Nuthatch	*Sitta europaea*	948	409	territorial	23.9	35200	tit-like birds	
Eurasian Treecreeper	*Certhia familiaris*	863	403	territorial	9.1	33000	tit-like birds	
Short-toed Treecreeper	*Certhia brachydactyla*	200	123	territorial	8.6	1250	tit-like birds	
Eurasian Penduline Tit	*Remiz pendulinus*	87	71	territorial	10	150		
Eurasian Golden Oriole	*Oriolus oriolus*	63	53	territorial	71	88		
Red-backed Shrike	*Lanius collurio*	557	355	territorial	30.25	1750		
Great Gray Shrike	*Lanius excubitor*	18	15	territorial	67	23		
Eurasian Jay	*Garrulus glandarius*	1315	522	territorial	167.55	56000	omnivorous corvids	
Eurasian Magpie	*Pica pica*	1656	556	territorial	217.5	249000	omnivorous corvids	
Spotted Nutcracker	*Nucifraga caryocatactes*	20	18	territorial	193	30	omnivorous corvids	
Western Jackdaw	*Corvus monedula*	1308	529	territorial	234.5	82500	omnivorous corvids	*Corvus*
Rook	*Corvus frugilegus*	533	296	territorial	462.5	45000	omnivorous corvids	*Corvus*
Carrion Crow	*Corvus corone*	1767	604	territorial	506	160000	omnivorous corvids	*Corvus*
Northern Raven	*Corvus corax*	461	255	territorial	1200.5	550	omnivorous corvids	*Corvus*
Common Starling	*Sturnus vulgaris*	1909	605	territorial	80.5	660000		

House Sparrow	*Passer domesticus*	1845	592	territorial	30.35	944000		
Eurasian Tree Sparrow	*Passer montanus*	1816	587	territorial	21.7	482000		
Common Chaffinch	*Fringilla coelebs*	1969	610	territorial	22.2	1700000	foliage gleaners	
Brambling	*Fringilla montifringilla*	3	3	territorial	23.25	<10	foliage gleaners	
European Serin	*Serinus serinus*	18	18	territorial	11.95	<10	passerine seedeaters	
European Greenfinch	*Carduelis chloris*	1855	597	territorial	25.1	489000	passerine seedeaters	*Carduelis*
European Goldfinch	*Carduelis carduelis*	1249	524	territorial	16.75	34600	passerine seedeaters	*Carduelis*
Eurasian Siskin	*Carduelis spinus*	314	227	territorial	13	1000	passerine seedeaters	*Carduelis*
Common Linnet	*Carduelis cannabina*	1863	611	territorial	18.75	283000	passerine seedeaters	*Carduelis*
Common Redpoll	*Carduelis flammea*	831	413	territorial	13.1	15000	passerine seedeaters	*Carduelis*
Red Crossbill	*Loxia curvirostra*	424	257	territorial	40.75	2000		
Parrot Crossbill	*Loxia pytyopsittacus*	1	1	territorial	51.55	<10		
Scarlet Rosefinch	*Carpodacus erythrinus*	98	87	territorial	22.95	225		
Eurasian Bullfinch	*Pyrrhula pyrrhula*	1023	463	territorial	31.05	45000		
Hawfinch	*Coccothraustes coccothraustes*	577	338	territorial	54.7	13900	passerine seedeaters	
Yellowhammer	*Emberiza citrinella*	1947	601	territorial	31.65	567000		
Reed Bunting	*Emberiza schoeniclus*	1539	588	territorial	18.8	49900		
Corn Bunting	*Miliaria calandra*	1200	466	territorial	47.65	31000		

Table S3. Null models.

Classification of row and column constraints and weighting factors used in each of 4 null model algorithms. Constraints are applied to a binary presence-absence matrix in which rows are species, columns are cells, and entries are the presence (1) or absence (0) of a particular species in a particular cell.

Model	Rows Sums (species)	Columns Sums (cells)	Weighting factor
Fixed-fixed	Fixed	Fixed	None
Habitat	Fixed	Allowed to vary	Habitat diversity
Population	Allowed to vary	Allowed to vary	Habitat diversity and population size
Biomass	Allowed to vary	Allowed to vary	Habitat diversity and biomass

Table S4. Co-occurrence analyses of foraging guilds.

Each entry represents the probability value for a one-tailed test of the null hypothesis that species co-occurrence patterns are random. Tan-shaded cells indicate statistically significant segregation. Yellow-shaded cells indicate statistically significant aggregation. No shading indicates a non-significant pattern (p > 0.05 for both tails of the distribution). Number of species in each guild is given in parentheses.

Foraging Guild	Fixed-Fixed Model 5 × 5	Fixed-Fixed Model 10 × 10	Habitat Model 5 × 5	Habitat Model 10 × 10	Population Model 5 × 5	Population Model 10 × 10	Biomass Model 5 × 5	Biomass Model 10 × 10
aquatic pursuers (8)	0.042	< 0.001	< 0.001	< 0.001	< 0.001	0.006	< 0.001	< 0.001
wading birds (6)	0.145	0.423	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
grazing waterfowl (5)	0.372	0.567	< 0.001	< 0.001	0.049	0.001	0.049	0.003
dabbling ducks (7)	< 0.001	< 0.001	> 0.999	> 0.999	> 0.999	> 0.999	> 0.999	> 0.999
diving ducks (4)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
diurnal raptors (12)	< 0.001	<0.001	> 0.999	< 0.001	0.997	0.164	> 0.999	0.001
gallinaceous birds (4)	< 0.001	0.291	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
rails (5)	0.131	< 0.001	0.933	< 0.001	0.788	< 0.001	0.002	< 0.001
plovers (8)	< 0.001	< 0.001	> 0.999	< 0.001	> 0.999	0.037	0.960	< 0.001
sandpipers (11)	< 0.001	0.013	< 0.001	< 0.001	< 0.001	0.001	0.626	0.261
gulls (7)	< 0.001	< 0.001	< 0.001	< 0.001	0.007	< 0.001	0.256	0.991
terns (6)	0.833	0.210	< 0.001	< 0.001	0.002	< 0.001	< 0.001	< 0.001
pigeons (4)	0.031	0.020	0.022	< 0.001	< 0.001	0.002	< 0.001	< 0.001
owls (6)	0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
woodpeckers (5)	0.079	0.926	0.761	> 0.999	0.104	0.327	0.001	0.001
aerial insectivores (4)	0.109	0.214	0.976	< 0.001	> 0.999	< 0.001	> 0.999	< 0.001
openland insectivores (9)	0.009	0.780	0.021	< 0.001	0.033	< 0.001	< 0.001	< 0.001
terrestrial & low strata flycatchers (10)	< 0.001	< 0.001	0.306	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
thrushes(5)	0.002	0.191	0.089	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
marsh warblers (7)	0.755	0.941	0.953	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
foliage gleaners (12)	< 0.001	0.627	> 0.999	0.024	< 0.001	0.975	0.967	0.918
tit-like birds (12)	< 0.001	< 0.001	> 0.999	< 0.001	0.569	< 0.001	0.783	< 0.001
corvids (7)	< 0.001	0.642	0.740	< 0.001	0.001	< 0.001	0.001	< 0.001
passerine seedeaters (7)	< 0.001	0.887	> 0.999	< 0.001	0.259	< 0.001	< 0.001	< 0.001
SEGREGATED	17	12	11	22	16	20	16	20
RANDOM	7	12	5	0	4	2	3	2
AGGREGATED	0	0	8	2	4	2	5	2

Table S5. Co-occurrence analyses of congeneric guilds.

Entries as in Table S4.

Ecological Guild	Fixed-Fixed Model 5 × 5	Fixed-Fixed Model 10 × 10	Habitat Model 5 × 5	Habitat Model 10 × 10	Population Model 5 × 5	Population Model 10 × 10	Biomass Model 5 × 5	Biomass Model 10 × 10
Anthus (4)	0.326	0.995	< 0.001	< 0.001	0.001	< 0.001	0.001	< 0.001
Acrocephalus (4)	0.578	0.142	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Sylvia (5)	0.017	0.020	0.605	0.430	0.981	0.942	0.951	0.808
Phylloscopus (4)	0.189	0.712	> 0.999	‡*<0.001*	0.779	0.213	0.976	0.283
Parus (6)	< 0.001	< 0.001	> 0.999	< 0.001	0.569	< 0.001	0.783	< 0.001
Corvus (4)	< 0.001	< 0.001	< 0.001	‡*<0.001*	< 0.001	< 0.001	< 0.001	< 0.001
Carduelis (5)	< 0.001	0.245	0.164	‡*<0.001*	< 0.001	< 0.001	< 0.001	< 0.001
Turdus (5)	0.002	0.191	0.089	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
SEGREGATED	5	3	3	7	5	6	5	6
RANDOM	3	4	3	1	2	2	1	2
AGGREGATED	0	1	2	0	1	0	2	0

‡Entries in italics indicate three models for which it was not possible to generate 1000 randomizations because the constraints were very difficult to achieve, and the simulation usually aborted after thousands of unsuccessful trials. These p-values were estimated from the standardized effect size, based on 10 successful replications of each model.

Table S6. Habitat utilization and electivity in foraging guilds.

Cell entries represent the average pairwise values of niche overlap for species in ecological guilds (number of species in parentheses). The left-hand column presents habitat utilization overlap values whereas the right-hand column represents electivity overlap values, which are scaled to account for the areas of different habitats in Denmark. Yellow shading indicates statistically significant overlap in habitat utilization or electivity (p < 0.01 for most analyses). Unshaded entries indicate a pattern that was not statistically significant. None of the foraging guilds exhibited significant segregation in habitat utilization or electivity.

Ecological Guild	Grain size	Utilization Overlap	Electivity Overlap
aquatic pursuers (8)	5 × 5	0.852	0.800
	10 × 10	0.887	0.776
wading birds (6)	5 × 5	0.860	0.585
	10 × 10	0.797	0.615
grazing waterfowl (5)	5 × 5	0.882	0.873
	10 × 10	0.852	0.911
dabbling ducks (7)	5 × 5	0.937	0.903
	10 × 10	0.938	0.905
diving ducks (4)	5 × 5	0.768	0.618
	10 × 10	0.793	0.797
diurnal raptors (12)	5 × 5	0.913	0.764
	10 × 10	0.942	0.866
gallinaceous birds (4)	5 × 5	0.936	0.835
	10 × 10	0.905	0.834
rails (5)	5 × 5	0.980	0.831
	10 × 10	0.99	0.889
plovers (8)	5 × 5	0.725	0.725
	10 × 10	0.667	0.658

sandpipers (11)	5 × 5	0.897	0.704
	10 × 10	0.857	0.729
gulls (7)	5 × 5	0.843	0.730
	10 × 10	0.900	0.755
terns (6)	5 × 5	0.806	0.694
	10 × 10	0.820	0.810
pigeons (4)	5 × 5	0.978	0.862
	10 × 10	0.927	0.883
owls (6)	5 × 5	0.936	0.836
	10 × 10	0.916	0.864
woodpeckers (5)	5 × 5	0.970	0.863
	10 × 10	0.978	0.902
aerial insectivores (4)	5 × 5	0.997	0.984
	10 × 10	0.986	0.987
openland insectivores (9)	5 × 5	0.786	0.785
	10 × 10	0.866	0.820
terrestrial & low strata flycatchers (10)	5 × 5	0.890	0.853
	10 × 10	0.931	0.874
thrushes(5)	5 × 5	0.978	0.880
	10 × 10	0.925	0.926
marsh warblers (7)	5 × 5	0.965	0.850
	10 × 10	0.954	0.902
foliage gleaners (12)	5 × 5	0.884	0.870
	10 × 10	0.907	0.841
tit-like birds (12)	5 × 5	0.984	0.934
	10 × 10	0.974	0.937
corvids (7)	5 × 5	0.988	0.954
	10 × 10	0.984	0.960
passerine seedeaters (7)	5 × 5	0.944	0.931
	10 × 10	0.980	0.958

Table S7. Habitat utilization and electivity in congeneric guilds.

Each row represents a different guild. Entries as in Table S6 except that tan shading indicates significantly

lower niche overlap than expected by chance.

Congeneric Guild	Grain size	Utilization Overlap	Electivity Overlap
Anthus (4)	5 × 5	0.657	0.711
	10 × 10	0.772	0.724
Acrocephalus (4)	5 × 5	0.973	0.902
	10 × 10	0.982	0.951
Sylvia (5)	5 × 5	0.911	0.836
	10 × 10	0.893	0.810
Phylloscopus (7)	5 × 5	0.743	0.811
	10 × 10	0.830	0.825
Parus (6)	5 × 5	0.986	0.939
	10 × 10	0.968	0.933
Corvus (4)	5 × 5	0.994	0.966
	10 × 10	0.976	0.976
Carduelis (5)	5 × 5	0.992	0.968
	10 × 10	0.990	0.984
Turdus (5)	5 × 5	0.978	0.880
	10 × 10	0.925	0.926