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Source: *The American Naturalist*, (-Not available-), p. 000
Published by: The University of Chicago Press for The American Society of Naturalists
Stable URL: http://www.jstor.org/stable/10.1086/682004
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VOL. 186, NO. 2 THE AMERICAN NATURALIST AUGUST 2015

Intraspecific Niche Variation Drives Abundance-Occupancy Relationships in Freshwater Fish Communities

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Submitted November 19, 2014; Accepted March 4, 2015; Electronically published May 29, 2015

Online enhancement: appendix. *Dryad data:* http://dx.doi.org/10.5061/dryad.56360.

ABSTRACT: A positive relationship between occupancy and average local abundance of species is found in a variety of taxa, yet the mechanisms driving this association between abundance and occupancy are still enigmatic. Here we show that freshwater fishes exhibit a positive abundance-occupancy relationship across 125 Swedish lakes. For a subset of 9 species from 11 lakes, we estimated species-specific diet breadth from stable isotopes, within-lake habitat breadth from catch data for littoral and pelagic nets, adaptive potential from genetic diversity, abiotic niche position, and dispersal capacity. Average local abundance was mainly positively associated with both within-lake habitat and diet breadth, that is, species with larger intraspecific variation in niche space had higher abundances. No measure was a good predictor of occupancy, indicating that occupancy may be more directly related to abundance or abiotic conditions than to niche breadth per se. This study suggests a link between intraspecific niche variation and a positive abundance-occupancy relationship and implies that management of freshwater fish communities, whether to conserve threatened or control invasive species, should initially be aimed at niche processes.

Keywords: amplified fragment length polymorphism (AFLP), conservation, distribution, habitat generalism, local-regional scale, stable isotopes.

Introduction

A striking macroecological pattern in various organism groups, from microbes to coral reefs, plants, and animals, is that species of high abundance (density) have wider distributions (occur at more sites) than less abundant species (Brown 1984; Gaston et al. 2000; Tales et al. 2004; Borregaard and Rahbek 2010; Frisk et al. 2011). Understanding the mechanisms that drive distribution and abundance of species across the landscape is crucial for conservation, particularly in situations of environmental change and pest control or invasive species (Gaston et al. 2000). Why some species are abundant while others are rare, or why some are found around the globe while others are restricted to specific habitats, is not only a central theme in ecology but also has important management applications.

The phenomenon of positive abundance-occupancy relationships (AORs) is important to understand, as it suggests a link between processes acting at local and regional (landscape) scales. However, the mechanisms linking dynamics at local and regional scales and the AOR are still enigmatic. Here, we divide hypotheses for the AOR into three main categories (sensu Gaston et al. 2000; Borregaard and Rahbek 2010): (1) the AOR is affected by niche differentiation in resources (bionomic niche) or environmental use (scenopoetic niche), resulting in structural differences in vital rates in relation to resources and the environment (Brown 1984; Hanski et al. 1993; Holt et al. 1997); (2) the AOR is affected by population dynamics mediated by dispersal or movement of organisms among sites (Hanski and Gyllenberg 1997; Freckleton et al. 2005); and (3) the AOR is affected by sampling artifacts, including range position (Gaston et al. 2000).

The first group of hypotheses addresses the idea that species have different population growth rates at different sites because of structural niche differences. Following the niche concepts of Hutchinson (1978) adopted for stable isotopes by Newsome et al. (2007), different species may differ in diet, resource use, or species interactions, that is, “the bionomic niche.” Alternatively, species differ in environmental use related to physiochemical and abiotic conditions, that is, “the scenopoetic niche.” Some species may be more abundant and widespread than others because they can use either more abundant and widespread resources or environments (Hanski et al. 1993; Holt et al. 1997) or a wider array of resources and environments (Brown 1984). One example of this may be where abundant and widespread

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DOI: 10.1086/682004

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species differentiate into various resource or environmental specialists (Bolnick et al. 2007), thereby occupying a broader niche range. The second group of hypotheses state that dispersal-mediated rescue or mass effects are more likely to occur in common species, elevating their occupancy or range distribution. Rare species, in contrast, are more susceptible to inbreeding effects, genetic drift, lowered adaptive potential, and stochastic extinction (Hanski and Gyllenberg 1997; Freckleton et al. 2005; Sæther et al. 2011). Finally, sampling artifacts may also explain the AOR. For example, if species have denser populations at the center of their range than at the range edges and if only part of the range is sampled, the AOR may be affected (Gaston et al. 2000; Eckert et al. 2008). These hypotheses are not mutually exclusive, and AORs may be driven by a combination of factors and mechanisms, providing links between processes acting at local and regional scales (Freckleton et al 2005; Verberk et al. 2010).

Despite the established theoretical treatment of the AOR, empirical data testing specific mechanisms are scarce (Borregaard and Rahbek 2010). At present, understanding of the AOR is based mostly on correlations and statistical modeling (reviewed in Borregaard and Rahbek 2010), and causal pathways of structural and dynamic mechanisms remain to be determined. Here we first study the interspecific AOR among 22 freshwater fish species from 125 communities (lakes) in Sweden. Subsequently, from a data set of 9 fish species in 11 of these lakes, we assess specific hypotheses relating to the structural and dynamic mechanisms underlying the AOR. We test whether occupancy and abundance are both associated with (1) intraspecific variation in diet (bionomic diet breadth), (2) bionomic habitat breadth of the littoral and pelagic zones, (3) scenopoetic (abiotic) niche position, (4) dispersal limitation, (5) intraspecific genetic diversity, and (6) body size. The first three hypotheses relate to structural niche differentiation mechanisms. Hypotheses 1 and 2 suggest that species with greater intraspecific variation in diet and habitat use will both be more abundant and have higher occupancies because they have access to a larger array of resources. Although there are some abiotic differences between the pelagic and littoral zones, it is mainly the biological composition of autotrophs and herbivores and biological interactions that drive species distribution between the zones (Svanbäck et al. 2008), and indeed most species are found in both zones. Hypothesis 3 implies that some species are adapted to some abiotic conditions that are common in the landscape and therefore become both abundant and widespread. Hypotheses 4 and 5 relate to population dynamics mechanisms, that is, whether dispersal barriers have a larger effect on species that are rare or whether genetically diverse species adapt to a wider range of sites and establish stable population sizes that can adapt to local conditions. In contrast, genetically depauperate species may suffer from inbreeding depression and loss of adaptive potential and be more restricted in abundance and occupancy. Hypothesis 6 tests the importance of a morphological trait for species' abundance and occupancy (Pyron 1999; Tales et al. 2004).

Methods

Database Analysis of the AOR in Swedish Freshwater Fish Communities

Data on local abundance (catch per unit effort [CPUE]) and occurrence of different fish species in lakes was extracted from the NORS database (National Register of Survey Test-Fishing; http://www.slu.se/sjoprovfiskedatabasen) from 125 lakes (Kinnerbäck 2012). Abundance data are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.56360 (Faulks et al. 2015*b*). Lakes were sampled in a standardized manner with multisized mesh gillnets in both the littoral and the pelagic zone. Fishing was done in late summer when most fish species are active and also to avoid spawning aggregations. The method is described in detail in Appelberg (2000) and Kinnerbäck (2001). Local abundance was estimated as average CPUE (catch per net and night) in grams (biomass) at presence sites only. Occupancy was estimated as the proportion of the lakes in which a species had been sampled at least once. We excluded pike, which is not representatively sampled in gillnets. In total, we used 22 species to study the AOR on a national level.

Fish Sampling

Eleven of the sampled lakes were selected for further use in this study (tables 1, A1, A2; figs. A1–A3; tables A1, A2 and figs. A1–A3 are available online) on the basis of the following criteria: they were sampled every year, they were inhabited by more than one of the studied fish species, and they were located so that fish could be frozen and transported back to Uppsala University for further analysis. From these 11 lakes, a total of 1,590 samples from 9 species were collected during the survey in 2011 (table 1). The lakes were located in separate drainage basins (except Lake Dagarn plus Lake Övre Skärsjön and Lake Fräcksjön plus Lake Bysjön), and dispersal among them was assumed to be restricted (see the appendix for sampling location details). We extracted mean local abundance and occupancy information from the long-term monitoring database, restricted to these 11 lakes.

Scenopoetic Niche Position and Lake Connectivity

For the larger data set of 125 lakes in Sweden, lake morphometrics were supplied by the Swedish Meteorological

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and Hydrological Institute, and yearly averages of water chemistry (absorbance [water color], conductivity, total phosphorus and nitrogen concentrations, pH, and temperature) were obtained from the national database of lake chemistry data (http://webstar.vatten.slu.se/db.html). A binary variable was generated on the basis of whether a lake had been totally submerged by the Baltic Sea at some point since the last glaciation (highest coastline [HC]).

The stream order that connected each lake with the next lake downstream was assessed from topographic maps (1 : 50,000), conforming to the following criteria: each headwater was designated a first-order stream, two first-order streams combined into a second-order stream, two second-order streams combined into a third-order stream, and so on. When a stream of smaller order combined with a stream of larger order, the order of the larger stream was not changed. Lakes without outlets were given the stream order 0. The number of anthropogenic dispersal barriers between the lake and the next lake downstream (barriers 1st lake) as well as the total number of barriers to the Baltic Sea or one of the three largest lakes in Sweden (Lakes Vänern, Vättern, and Mälaren), which we consider to be the species pools, was also quantified. Data on lake morphometrics, water chemistry, and lake connectivity are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.56360 (Faulks et al. 2015*b*).

We used the species scores from a canonical correspondence analysis (CCA) as estimates of species' abiotic niche position and response to lake connectivity. Lake-specific abundances of each species were used as response variables and lake-specific average abiotic conditions and connectivity were used as explanatory variables in the CCA. Thus, CCA axes are not unique to one type of variable but may contain variation of both abiotic conditions and connectivity. The total amount of variation explained in the species-specific abundance was 35%, of which abiotic factors alone explained 15% and connectivity variables alone explained 10% (the remaining 10% was shared between connectivity and abiotic factors).

Bionomic Habitat Breadth

We estimated the (within-lake) bionomic habitat breadth of species as the relative use of pelagic and littoral zones from catch data. Both pelagic and littoral nets were used in the sampling, and for each lake and species we calculated the deviation from 50% (in each net type) as a measure of bionomic habitat breadth (HB) as a modified version of the proportional similarity index (Feinsinger et al. 1981), specifically $\mathrm{HB} = 1 - 2 \times \mathrm{abs}(0.5 - \%\mathrm{L})$, where %L is the average proportion of catches in littoral nets. Values close to 1 imply an equal use of littoral and pelagic zones, whereas values close to 0 imply specialization on either littoral or pelagic zones. For each species, we calculated HB from the average proportion of individuals caught in littoral nets among the lakes in which they had occurred over the past 5 years (2007–2011).

Bionomic Diet Breadth

Stable isotope analysis of δ^{13}C and δ^{15}N was performed to assess species-specific diet variation in the 9 study species. Carbon levels indicate the source of food items, with pelagic food resources being more depleted in δ^{13}C than littoral resources. Fish with high δ^{13}C have consumed more benthic resources (gastropods, amphipods), while fish with low δ^{13}C have consumed more pelagic prey (zooplankton). The nitrogen value is a good indicator of the trophic level of the diet, with a higher value at a higher trophic position. Stable isotopes are integrated over a period of several months and provide a more reliable indication of resource use than one-off stomach content analysis (Quevedo et al. 2009). A piece of muscle tissue was excised from each sample and dried in an oven at 60°C for 48 h. All samples were ground, weighed on a microscale to 1 mg, and then packaged in tin foil and analyzed at the University of California, Davis, Stable Isotope Facility using the standards Pee Dee belemnite (δ^{13}C) and atmospheric nitrogen (δ^{15}N). Stable isotope data are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.56360 (Faulks et al. 2015*b*). The R package SIBER was used to calculate a Bayesian estimate of the standard ellipse area ($\mathrm{SEA_B}$) for each species within each lake (Jackson et al. 2011). This method is suitable for comparison of isotopic values at the community level, even when sample sizes can be small and variable (Jackson et al. 2011). Because values were standardized for each lake, average values of $\mathrm{SEA_B}$ across all lakes in which a species occurred could be used as an estimate of intraspecific diet breadth for that species. Thus, a higher value indicates having a larger intraspecific variation in diet, that is, consuming a range of diet items across the littoral-pelagic axis and/or over trophic positions (e.g., herbivore, omnivore, piscivore). We also tried to assess differences in diet composition, that is, ingested prey item rather than a value of resource width between individuals. However, we lacked the power to determine specific diet composition, as not all potential prey items were sampled and the isotopic signature of fish was often outside the range of signatures detected in the prey items collected (zooplankton, snails, mussels). Additionally, many fish species have ontogenetic shifts in diets (Quevedo et al. 2009; Estlander et al. 2010). To study how intraspecific diet variation depends on body size, we calculated $\mathrm{SEA_B}$ for perch and roach individuals larger and smaller than 15 cm, which is the approximate length when their diet switches from zooplankton to other prey items (Estlander et al. 2010).

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Table 1: Number of individuals analyzed (*n*), estimated intraspecific bionomic diet breadth from stable isotopes (SEA_B), bionomic habitat breadth (HB) measured as the proportion of catches in littoral nets, and expected heterozygosity from amplified fragment length polymorphism analysis (H_j) for each species in each lake

Species, variable	AG	AS[a]	BS	DN	DV	FN	FS	OS	RS	SE	SS	Total/mean
Bleak (*Alburnus alburnus*):												
n			37	26	29				11			103
SEA_B			1.19	1.31	2.81				3.86			2.29
HB			.13	.19	.24				.46			.51
H_j			.04	.04	.04				.05			.04
Bream (*Abramis brama*):												
n			15				0[b]					15
SEA_B			3.62									3.62
HB			.74				.93					.33
H_j			.29									.29
Perch (*Perca fluviatilis*):												
n	31	46	30	47	31	73	10	63	21	45	46	443
SEA_B	.87	2.83	9.23	1.4	3.44	1.47	3.11	2.19	3.28	3.44	1.95	3.02
HB	.61		.28	.31	.85	.38	.32	.91	.73	.31	.55	.95
H_j	.36	.42	.41	.32	.27	.34	.41	.27	.38	.27	.38	.35
Roach (*Rutilus rutilus*):												
n	28	31	58	56	30	62	57		60	59	58	499
SEA_B	4.68	2.35	1	4.61	.51	3.98	2.06		.49	1.35	1.76	2.28
HB	.33		.11	.32	.94	.30	.17		.22	.21	.16	.62
H_j	.14	.24	.23	.2	.15	.17	.18		.2	.2	.22	.19
Rudd (*Scardinius erythrophthalmus*):												
n		1[b]	37				31					68
SEA_B			3.2				1.93					2.56
HB			.34				.47					.42
H_j			.3				.36					.33

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Ruffe (*Gymnocephalus cernua*):												
n	18		22	44	39		13		12	31		179
SEA_B	1.29		1.32	1.8	5.67		1.1		1.54	2.07		2.11
HB	1		1	1	1		1		1	1		0
H_j	.22		.14	.18	.16		.13		.21	.12		.17
Smelt (*Osmerus eperlanus*):												
n					58		26		32			116
SEA_B					2.1		1.4		2.07			1.86
HB					.06		.01		.01			.05
H_j					.27		.22		.25			.25
Vendace (*Coregonus albula*):												
n	53			21								74
SEA_B	1.9			2.71								2.31
HB	.04			.01								.05
H_j	.38			.39								.39
Whitefish (*Coregonus megalops*):												
n					43	44			6[b]			87
SEA_B					1.22	1.75						1.48
HB					.19	.06			1.0			.83
H_j					.22	.22						.22

Note: The mean for HB is the deviation from an even catch between littoral and pelagic nets for each species determined using the proportional similarity index (see "Methods"), and the means for SEA_B and H_j are ordinary averages. AG = Lake Allgjutten; AS = Lake Älgsjön; BS = Lake Bysjön; DN = Lake Dagarn; DV = Lake Degervattnet; FN = Lake Fiolen; FS = Lake Fräcksjön; OS = Lake Övre Skärsjön; RS = Lake Remmarsjön; SE = Lake Stensjön; SS = Lake Stora Envättern.

[a] In AS, there were no pelagic nets.

[b] Species is prevalent in lake, but sample size was too low to estimate SEA_B and H_j.

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Genetic Diversity

Assessment of genetic variation across the whole genome of each species was performed using amplified fragment length polymorphism (AFLP) analysis (Vos et al. 1995). DNA was extracted from a small piece of fin tissue from each sample using a modified salting-out method (Paxton et al. 1996). The restriction enzymes *Tru* and *Eco*R1 (Fermentas) were used to cut the DNA, followed by overnight ligation of adaptors. Preamplification polymerase chain reactions (PCRs) were conducted using the primers E (5′-GACTGCGTACCAATTCA-3′) and T (5′-GATGAGTCCTGAGTAAC-3′). Six selective-amplification PCR primers were used (E: ACA, ACT, ATC; T: CAG, CAC, CGT), resulting in nine primer-pair combinations. All products were analyzed on a MegaBace 1100 and subsequently scored using GeneMarker (ver. 1.85). All peaks were binned automatically and checked by eye. AFLPScore (Whitlock et al. 2008) was used to determine the scoring error rate and to select the best scoring parameters. The resulting presence/absence matrix was exported to AFLPDat (Ehrich 2006) for conversion and use in further analyses. BayeScan was used to check for the presence of loci under selection (Rusello et al. 2012). These loci were removed from downstream analyses in AFLPSurv (Vekemans et al 2002), which was used to estimate genetic diversity (H_j − expected heterozygosity) and divergence (F_{ST}) among lakes. AFLP data are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.56360 (Faulks et al. 2015*b*).

Abundance Occupancy Relationships and Hypothesis Testing

An overview of the analyses conducted is presented in figure A2. First, we tested for a positive AOR among 22 freshwater fish species from 125 lakes. As occupancy frequency may be nonlinearly related with abundance, we used the statistical model from Freckleton et al. (2005, eq. [17]) in addition to the Spearman correlation. This model approximates a population model incorporating both structural and dynamic factors. Although the association between abundance and occupancy is correlative, the model assumes that occupancy is a function of local abundances but has the advantage of explicitly testing for a population dynamic effect on AOR (Freckleton et al. 2005). We fitted mean biomass (CPUE) and proportion of lakes each species occurred in (Occ) using PROC NLIN in SAS (SAS Institute 2008):

$$\mathrm{Occ} = C(\mathrm{CPUE} - K)/[1 + g(\mathrm{CPUE} - K)], \qquad (1)$$

where C, K, and g are constants. The C/g ratio determines the asymptotic value of occurrence ($0 \le C/g \le 1$), and high g indicates that the AOR reaches its asymptote fast. The point where the AOR intersects the CPUE axis is described by K. If $K = 0$, the relationship goes through the origin, as predicted by a pure structural model where suitable sites are occupied (Freckleton et al. 2005). If $K > 0$, the AOR cuts the CPUE axis at positive values of CPUE, as predicted by a metapopulation model. This would indicate a significant dispersal, movement, or Allee effect contributing to the AOR. Below a certain abundance threshold (K), long-term extinction rates would exceed colonization rates, which prevents a species from occupying suitable patches (Freckleton et al. 2005). Thus, equation (1) tests for an influence of dynamic processes but does not reject a model that includes structural effects as one of several factors.

We use the data set of 9 species from 11 lakes to test hypotheses 1–6 regarding abundance and occupancy separately using stepwise linear regression. Mean CPUE (excluding zero values) and proportion of lakes occupied were dependent variables in separate analyses with bionomic diet breadth ($\mathrm{SEA_B}$), bionomic habitat breadth (HB), scenopoetic niche position and dispersal capacity (CCA axes), genetic diversity (H_j), and common body size (derived from http://www.fishbase.org) as explanatory variables. We used data points only where more than 10 individuals of a fish species had been sampled in a lake (table 1). If the same explanatory variable can explain interspecific variation in both abundance and occupancy, this suggests that the variable may also directly link the local and regional dynamics of species. If different variables explain abundance and occupancy, the link between local and regional dynamics of species may be indirect.

Finally, we tested the results from the subset of 9 species from 11 lakes on the larger national data set. We used the estimated local abundance (CPUE) from the stepwise regression in equation (1) to determine whether the model parameters could predict the proportion of lakes a species occurs in across a larger-scale data set.

Results

For the national data set of 22 fish species in the 125 monitoring lakes, mean local abundance (CPUE from standardized surveys) was positively correlated with occupancy (Spearman's $r = 0.70$, $P = .003$). Using equation (1), mean abundance explained occupancy frequency ($R^2 = 0.71$, $F_{2,20} = 25$, $P < .001$; fig. 1*a*), and the constant $K = -75\ \mathrm{g} \pm 81$ (SE) did not differ from 0 ($P = .4$). Perch, roach, and bream were the most common and frequently occurring species, while alpine bullhead, minnow, spined loach, and smelt were the most rare and restricted species. The AOR was also evident among the subset of 9 species from the 11 sampling lakes ($R^2 = 0.80$, $F_{2,7} = 11$, $P = .007$, $K = -162 \pm 302$) used for estimates of bionomic diet and habitat breadth as well as genetic diversity.

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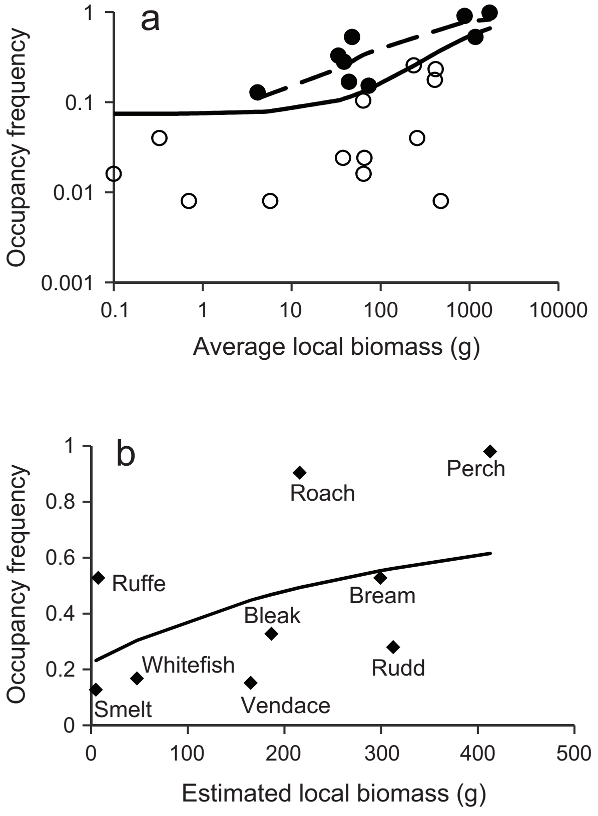

Figure 1: Average local biomass estimated as gram per catch per unit effort for all lakes in which a species occurs and the proportion of lakes in which they occur. *a*, Twenty-two freshwater species in 125 lakes across Sweden. Filled circles and the dashed line show species analyzed for bionomic niche breadth and genetic diversity in this study (see *b*), whereas open circles and the solid line show species not further analyzed here. *b*, Observed occupancy for the subset of 9 fish species for which local abundance was estimated from the best linear model of intraspecific variation in resource use and bionomic habitat breadth. The line shows the best fit to equation (1).

Scenopoetic Niche Position and Lake Connectivity

The most common of the 22 species (perch, roach, and ruffe) were close to the centroid in the CCA, meaning that environmental and connectivity variables explained little variation in their abundance. Along the first axis (explaining 16.8% of variation), cyprinids other than roach (i.e., bream, rudd, and bleak) were associated with eutrophic lakes with high connectivity. At the opposite end, several salmonid species (e.g., grayling, trout, and char) were associated with lakes at higher altitudes and low connectivity (fig. 2). The second axis (explaining 8.3% of the variation) differentiated between species with respect to temperature, size, and water color. Species with higher scores along the second CCA axis (mean scenopoetic niche position in warm, shallow, and small lakes) tended to have higher occupancy frequencies ($r = 0.39$, $P = .08$). Otherwise, species scores along the two first axes were not associated with average local abundance or occupancy in the national data set ($r < 0.3$, $P > .2$).

Parameter Estimates

Estimates of intraspecific bionomic diet and habitat breadth as well as genetic diversity of the 9 species from the 11 selected lakes are shown in table 1. Bionomic diet breadth ranged from $\mathrm{SEA_B} = 1.48$ (whitefish) to $\mathrm{SEA_B} = 3.62$ (bream), and bionomic habitat breadth ranged from $\mathrm{HB} = 0$ (ruffe) to $\mathrm{HB} = 0.95$ (perch; table 1). At least 70 AFLP loci with an average error rate of approximately 15% were used for estimates of genetic diversity in each species. Mean genetic diversity was highest in vendace ($H_j = 0.39$) and lowest in bleak ($H_j = 0.04$).

There was generally low covariation between different parameters across species. $\mathrm{SEA_B}$ and HB ($r = -0.01$, $P = 1$) and $\mathrm{SEA_B}$ and H_j ($r = 0.3$, $P = .4$) were not correlated, but $\mathrm{SEA_B}$ tended to be associated with scenopoetic niche position along the second CCA axis ($r = 0.62$, $P = .07$). H_j showed no association with HB ($r = 0.26$, $P = .4$) or scenopoetic niche position ($r < 0.5$, $P > .1$). Differences in intraspecific diet breadth and genetic diversity between species were not evidently an artifact of sample size. $\mathrm{SEA_B}$ and H_j were not associated with sample size across species ($\mathrm{SEA_B}$: $F_{1,25} = 0.7$, $P = .4$; H_j: $F_{1,25} = 0.8$, $P = .4$) or within species, as the interaction term between species and number of fish sampled per species and lake was nonsignificant ($\mathrm{SEA_B}$: $F_{7,25} = 0.6$, $P = .7$; H_j: $F_{7,25} = 0.7$, $P = .7$). We found significant genetic structure among lakes for all species (all $F_{\mathrm{ST}} > 0.06$, $P < .001$; table A2). The exceptions were bleak, which had insufficient levels of genetic diversity to properly assess genetic structure, and bream, for which we had samples from only one lake. There were also significant pairwise F_{ST} values in the within-basin comparisons, that is, between perch populations in Lake Dagarn and Lake Övre Skärsjön ($F_{\mathrm{ST}} = 0.05$) and perch ($F_{\mathrm{ST}} = 0.001$), roach ($F_{\mathrm{ST}} = 0.01$), rudd ($F_{\mathrm{ST}} = 0.09$), and ruffe ($F_{\mathrm{ST}} = 0.02$) populations found in both Lake Fräcksjön and Lake Bysjön ($P < .005$ for all F_{ST} values).

Hypothesis Testing of Mechanisms Driving AOR

The results from the stepwise regressions of the 9 fish species from the 11 lakes indicated that the abundance (mean CPUE) of fish species was positively associated with bionomic habitat breadth (partial $r^2 = 0.32$, $F_{1,5} = 11$, $P = .02$; fig. 3*a*) and bionomic diet breadth (partial $r^2 = 0.34$, $F_{1,5} = 9.8$, $P = .03$; fig. 3*b*). Scenopoetic niche position and dispersal ability along the first (partial $r^2 = 0.12$, $P = .11$) and second (partial $r^2 = 0.08$, $P = .09$) CCA axis showed

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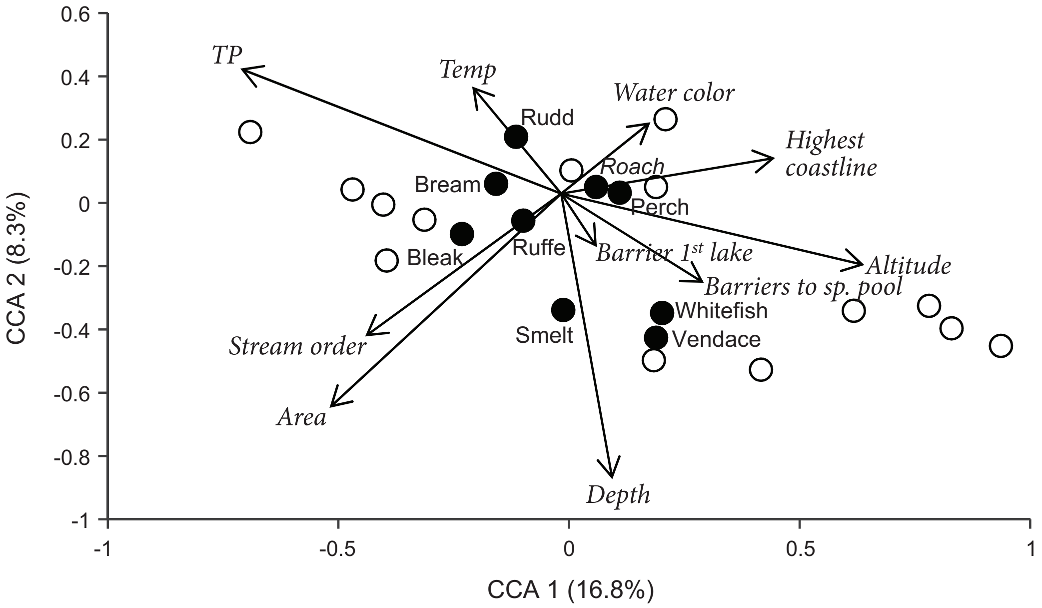

Figure 2: Canonical correspondence ordination of fish species in relation to significant environmental and connectivity variables. Circles indicate the location of species centroids. Arrows represent the vectors of statistically significant variables (for clarity, only significant variables are shown). Filled circles (with species names) show the species investigated for bionomic niche breadth and genetic diversity, whereas open circles show species not further investigated here. CCA = canonical correspondence analysis.

nonsignificant associations, whereas remaining variables did not explain any variation (partial $r^2 < 0.02$, $P > .7$). Although perch and roach had much higher local abundances than the other species, the associations remained when excluding these two species (HB: partial $r^2 = 0.44$; $\mathrm{SEA_B}$: partial $r^2 = 0.55$).

For the proportion of lakes species occurred in, there was no significant association with any investigated variable (partial $r^2 < 0.2$, $P > .1$). Despite this, the best linear model of the relationship between abundance and bionomic diet and habitat breadths (mean CPUE [g] $= -263 + 128 \times \mathrm{SEA_B} + 304 \times \mathrm{HB}$) was able to explain variation in occupancy frequency for the 9 species among all 125 lakes in the larger national data set ($r^2 = 0.77$, $F_{2,7} = 12$, $P = .006$; fig. 1*b*).

Intraspecific bionomic diet breadth was larger among large individuals for both perch ($t_{11} = 4.5$, $P < .001$) and roach ($t_{10} = 3.6$, $P = .005$; fig. A3). However, across the 9 species there was no positive relationship between common body size and $\mathrm{SEA_B}$ ($r = -0.17$, $P = .7$). But bionomic habitat breadth showed a positive trend toward increasing with body size ($r = 0.61$, $P = .08$).

Discussion

We have demonstrated a positive interspecific AOR among Swedish freshwater fish and provided evidence that structural niche mechanisms, mainly bionomic niche breadth, were responsible for this pattern. Fish species that utilized a wider range of both bionomic habitat and food resources had a higher biomass than species that specialized in either the littoral or the pelagic zone or that had a narrow diet. The importance of variation in niche space use for AOR inferred from our estimates of bionomic habitat and diet breadths were also supported by comparisons with the larger data set of 125 lakes. There was, however, no statistical support for an association between bionomic niche breadth and the proportion of lakes in which a species occurred. Thus, our results suggest that occurrence is more directly related to species abundance—for example, local extinction probabilities (Sæther et al. 2011) or, alternatively, scenopoetic niche differences—than to differences in intraspecific bionomic niche variation.

Several empirical studies have proposed that niche processes can drive interspecific AORs in natural communities (e.g., Brown 1984; Freckleton et al. 2005, 2006; Verberk et al. 2010; Slatyer et al. 2013). Of particular interest as a comparison to our results are other studies of fishes (Pyron 1999; Tales et al. 2004) and aquatic macroinvertebrates (Verberk et al. 2010; Heino and Grönroos 2014). These studies demonstrate the role played by various aspects of niche processes in driving AOR, including scenopoetic niche availability and position (Tales et al. 2004; Heino and Grönroos 2014) and scenopoetic habitat breadth (Py-

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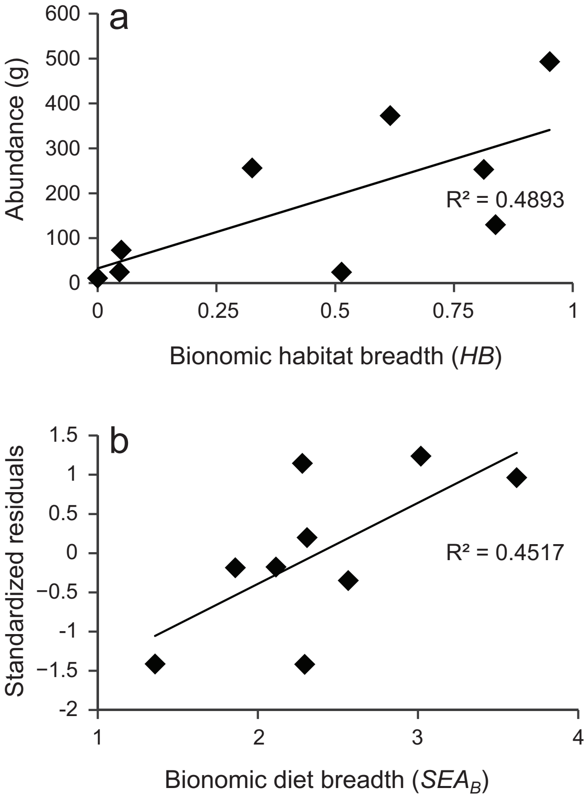

Figure 3: For the subset of data on 9 fish species in 11 lakes, there was a positive association between average local abundance and bionomic habitat breadth (HB; *a*) and intraspecific bionomic diet breadth (SEA_B; *b*) estimated from stable isotopes. In *b*, local abundance is controlled for HB by showing the relationship with the standardized residuals of *a*.

ron 1999; Verberk et al 2010). However, the conclusions of these studies are based on scenopoetic niche estimates from abundance and occupancy data and not strictly independent estimates of niche space use. Here we used estimators of (bionomic) niche space use and genetic diversity derived independently from local abundances and lake occupancy, yet we still found support for the importance of niche processes with respect to the AOR, albeit mainly bionomic niche processes rather than scenopoetic.

The main explanation for the general AOR emerging from this study is that freshwater fishes with high intraspecific bionomic niche variation—that is, those that use both the littoral and the pelagic zone and have a variable diet (e.g., omnivory, molluscs, insects, and crustaceans)—additively contribute to high average local abundances. One potential explanation for this is that fish populations as well as populations of other taxa (reviewed in Bolnick et al. 2003) with a broader niche use are composed of heterogeneous but relatively specialized individuals (Lister 1976; Svanbäck and Persson 2004). The most abundant species here, perch and roach, show ontogenetic shifts in diet and habitat use (Quevedo et al. 2009; Estlander et al. 2010), which may be an important trait for a population to achieve high abundances and may also stabilize dynamics (Hin et al. 2011). In addition, these two species and whitefish often coexist as different morphs (body shapes) in littoral and pelagic habitats (Svanbäck and Persson 2004; Svanbäck et al. 2008; Gagnaire et al. 2013). Bream, which is mainly confined to the littoral zone but shows a wide diet breadth, displays plasticity in gill raker size depending on the prey composition (Hoogenboezem et al. 1993). Thus, a common feature of the locally more abundant species here is their ability to divide resources among individuals within a population to use a larger bionomic niche space and decrease intraspecific competition, likely facilitating higher local abundances.

There was an evidently stronger association between bionomic niche breadth and abundance than between bionomic niche breadth and occupancy. Intuitively, the link between niche breadth and occupancy is expected to be stronger than that for local abundance (Grinnell 1917; Gaston et al 1997; Borregaard and Rahbek 2010). For example, a species could be a locally abundant specialist if the resource is also locally abundant yet restricted across the landscape (Lawton and Pratchett 2012). In our 11 studied lakes, perch had the widest bionomic niche and was found in most lakes, but for the remaining species occupancy was independent of bionomic niche variation, suggesting that occupancy may depend on some other mechanism. But as no other variable explained significant variation in occupancy and both observed and estimated abundance from the abundance regressions explained significant variation in occupancy, abundance per se may be an important determinant of species occupancy. For example, British birds show a positive interspecific AOR, seemingly related to structural effects (Freckleton et al. 2005). But less abundant bird species show considerably higher local extinction rates (Sæther et al. 2011), which lowers occupancy.

Alternatively, in the larger data set of 125 lakes, species more common in warmer, smaller, and darker lakes tended to have higher occupancy, indicating an influence of scenopoetic niche position. Heino and Grönroos (2014) also suggested that scenopoetic niche position was important for the occupancy of stream invertebrates but not for local abundance. Moreover, we had no estimates of scenopoetic niche breadth, but we note that the species close to the centroid in the CCA (perch, roach, and ruffe, whose distributions are weakly correlated with lake conditions) all had higher observed occupancy than that expected on the basis of their estimated biomass from bionomic niche breadth. This could indicate an importance of scenopoetic niche

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breadth for occupancy; however, this would not really change the conclusions of this study, as we argue that intraspecific niche breadth is the main driver of positive AOR.

Within roach and perch, it was larger individuals in particular that contributed to the intraspecific bionomic diet breadth, highlighting the importance of large-sized individuals for an ecologically diverse population. But across species there was no association between bionomic diet breadth and body size; for example, the large-bodied whitefish showed little variation in diet. Perhaps it is easier for larger fish to utilize both littoral and pelagic zones, as there was a weak association between body size and bionomic habitat breadth. But then the relatively large-bodied bream was almost entirely restricted to the littoral zone. Thus, in line with some previous studies showing a weak or contradictory impact on AOR (Pyron 1999; Tales et al. 2004; Heino and Grönroos 2014), body size itself cannot explain a positive AOR.

One potential mechanism behind AORs that has not previously been explicitly considered is genetic diversity. Genetic diversity is a fundamental aspect of biodiversity, providing the basis for organisms to adapt to their environment and maintain evolutionary potential. Low genetic diversity may be associated with inbreeding depression and loss of adaptive potential (Frankham 1995; Hughes et al. 2008). Consequently, genetic diversity may constrain abundances and could therefore provide a link between population dynamic processes and positive AOR. Genetic diversity can also be dependent on population abundances, where larger effective population sizes maintain and generate diversity, while diversity is lost because of drift in small populations (Amos and Harwood 1998; Montgomery et al. 2000). The rarest species had to be excluded from this study for methodological reasons, but including more rare species may provide better evidence of genetic constraints on species abundance. The lack of a population dynamic term in the AOR of the larger national data set (22 species in 125 lakes) and the weak associations between genetic diversity and abundance or occurrence among species do not mean that population genetic processes, including gene flow, are of no importance. In contrast, dispersal limitation may restrict the occurrence of all species (Mazaris et al. 2010). The sampling locations used in this study were lakes isolated in separate drainage basins, and analysis of genetic differentiation across all fish species confirmed that dispersal among these lakes is restricted. Hence, we acknowledge that to more effectively assess the effect of dispersal on AOR a finer-spatial-scale experimental design would be required. However, dispersal ability seemed to have little effect on the AOR. In fact, the species that were positively associated with dispersal barriers (e.g., salmonids) and that should have relative high dispersal capacity generally showed low occurrence and abundance. Thus, dispersal limitations seem to exclude some common species rather than constrain rare species. Additionally, the species used for genetic analysis had higher occupancies than noninvestigated species (fig. 1*b*), so there is potential for bias in our analysis, as rare species, which are harder to obtain samples of, may be more constrained by genetic or population dynamic processes.

It is also possible that genetic diversity at specific loci may be more important for population abundances than diversity estimates of the whole genome. Habitat and diet use are associated with genetic differentiation at particular loci in some species (e.g., sticklebacks [Jones et al. 2012] and whitefish [Gagnaire et al. 2013]). However, the mechanisms for intraspecific niche differentiation in other common species studied here (e.g., perch, roach, and bream) tend to involve phenotypic plasticity (Hoogenboezem et al. 1993; Svanbäck and Eklöv 2006; Faulks et al. 2015*a*). If niche space use is little dependent on genetic variation, then genetic diversity is not likely to constrain abundances and occupancies.

The final mechanism thought to influence AOR is sampling artifacts. The sampling method used in the biodiversity surveys, gillnets, passively catch fish; thus, mobile species are more likely to result in both higher CPUE and detection frequency than more sedentary species (Prchalova et al. 2011). However, as these lakes have been sampled for more than 40 years, we find it unlikely that a species would be completely undetected. On the other hand, differences in mobility may cause some variability around the AOR observed here. But mobility may also be an important trait, as movements between pelagic and littoral zones may be a prerequisite for a wide bionomic habitat use, and thereby these species have a higher CPUE. Sampling artifacts due to differences in range position are unlikely to have an effect in this study. Lakes were distributed evenly across Sweden (fig. A1), and most species are common over much larger parts of Eurasia than considered here (Nielsen and Svedberg 2010). In addition, the distributional ranges of freshwater fish across Sweden are determined not by latitude but more by the historic highest coastline, which is a more longitudinal separation (Otto 1998). Thus, although we cannot rule out range position effects, we do find them unlikely to have confounded the variation in the estimates of niche space use adopted here.

This is the first study to show that bionomic niche space use arising from intraspecific ecological differentiation can explain positive interspecific AORs for a particular group of taxa using abundance-independent estimates of intraspecific variation. Thus, fish species that have a broad bionomic niche due to intraspecific variation seem to have more available resources, making them more abundant, and as they can use a wider array of bionomic resources, they also occupy more lakes. In addition, the macroeco-

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logical pattern of abundance and occurrence suggests that structural differences in species niches are sufficient to explain the positive AOR. The reason for species rarity is often idiosyncratic (Gaston 1994), and we cannot rule out genetic constraints on abundance and occupancy for some fish species. Despite this, our results do indicate that conservation management for threatened freshwater fish species should prioritize activities aimed at restoring and/or improving natural niche processes, such as habitat and resource availability. The same approach is likely to apply to the management of invasive species. For example, although rare in Sweden, one of the most invasive freshwater fish around the world, Eurasian carp (*Cyprinus carpio*), displays wide bionomic niche use (Sibbing 1988) similar to the most abundant and widespread species in this study. Finally, this study has mainly considered relatively stationary fish species, and these conclusions may not apply to species for which barriers to dispersal (such as dams) are a direct threat. Thus, further studies of AORs and the mechanisms driving them can be important to identify general management tools for freshwater fish communities.

Acknowledgments

We thank the staff at the Institute of Freshwater Research, Swedish University of Agricultural Sciences, for collection of samples, especially A. Kinnebäck, who helped us organize the fish sampling. Funding for this project was provided by the Carl Tryggers Foundation and the Swedish Research Council. We thank G. Engström, R. Kozma, and Y.-F. Liao for assistance in the laboratory.

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