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Research article

A test of the abundant-center hypothesis for stream fishes

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The abundant-center hypothesis (ACH) provides a conceptual model for predicting range-wide distributions of species abundance, suggesting that abundance peaks in the center of the geographic range and declines towards range edges. Empirical studies testing the ACH and its subsequent derivations predominantly occurred in terrestrial systems and reported mixed support. Moreover, none of these models consider the possibility of multiple geographic areas of elevated abundance (which we refer to as 'abundant cores'). Naturally dispersal limited species may exhibit multiple abundant cores, requiring refinement of the ACH. We used fish species abundances from 29 206 community monitoring surveys and weighted geospatial kernel density estimation to identify the number of abundant cores for 64 freshwater fish species. We regressed the number of abundant cores against range size and body size to test if larger geographic distributions and body sizes contain more abundant cores than smaller distributions and body sizes. The two predictors are surrogates for evolutionary age and dispersal ability, respectively, because older species are generally associated with larger ranges, and large-bodied fishes have greater dispersal ability than small-bodied fishes in dendritic networks. For studied species, 43 exhibited multi-core distributions, and 21 exhibited a single-core distribution. Species range size, but not body size, was significantly and positively associated with the number of abundant cores. The ACH was not a good descriptor of the abundance patterns of most stream fishes we studied, suggesting that an abundant center model may not be well-suited for freshwater fishes. Recent geo-climatic events in evolutionary time have isolated populations of the same species by a matrix of unsuitable habitat and/or hard dispersal barriers, providing the basis for multi-core distributions. Biogeographic and ecological mechanisms likely underpin observed multi-core patterns, and our work indicates that the ACH and related concepts still present opportunities for testing and refinement.

Keywords: abundant-center hypothesis, stream fish, kernel density estimation, range size

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Introduction

The abundant-center hypothesis (ACH; Brown 1984) is a foundational macroecology theory. The ACH predicts that the abundance of a species is greatest in the center of its geographic range where habitat is the most suitable and decreases towards the range edges due to decreased fitness associated with declining habitat suitability (Fig. 1A, Brown, 1984, Brown et al. 1995). Despite the intuitiveness and general acceptance of the ACH, empirical support for its predictions is mixed (Sagarin et al. 2006, Dallas et al. 2017, 2020, Santini et al. 2019). Longstanding challenges to testing this theory stem from difficulties associated with inadequate spatial sampling coverage (Sagarin et al. 2006, Santini et al. 2019, Bramon Mora et al. 2024), the inability to account for complex range geometries that preclude an obvious center (Sagarin et al. 2006), and incorporating more realistic measures of distance that include geographic barriers to dispersal (Sagarin and Gaines 2002, Sagarin et al. 2006, Tonkin et al. 2018). The minimum range size warranting the application

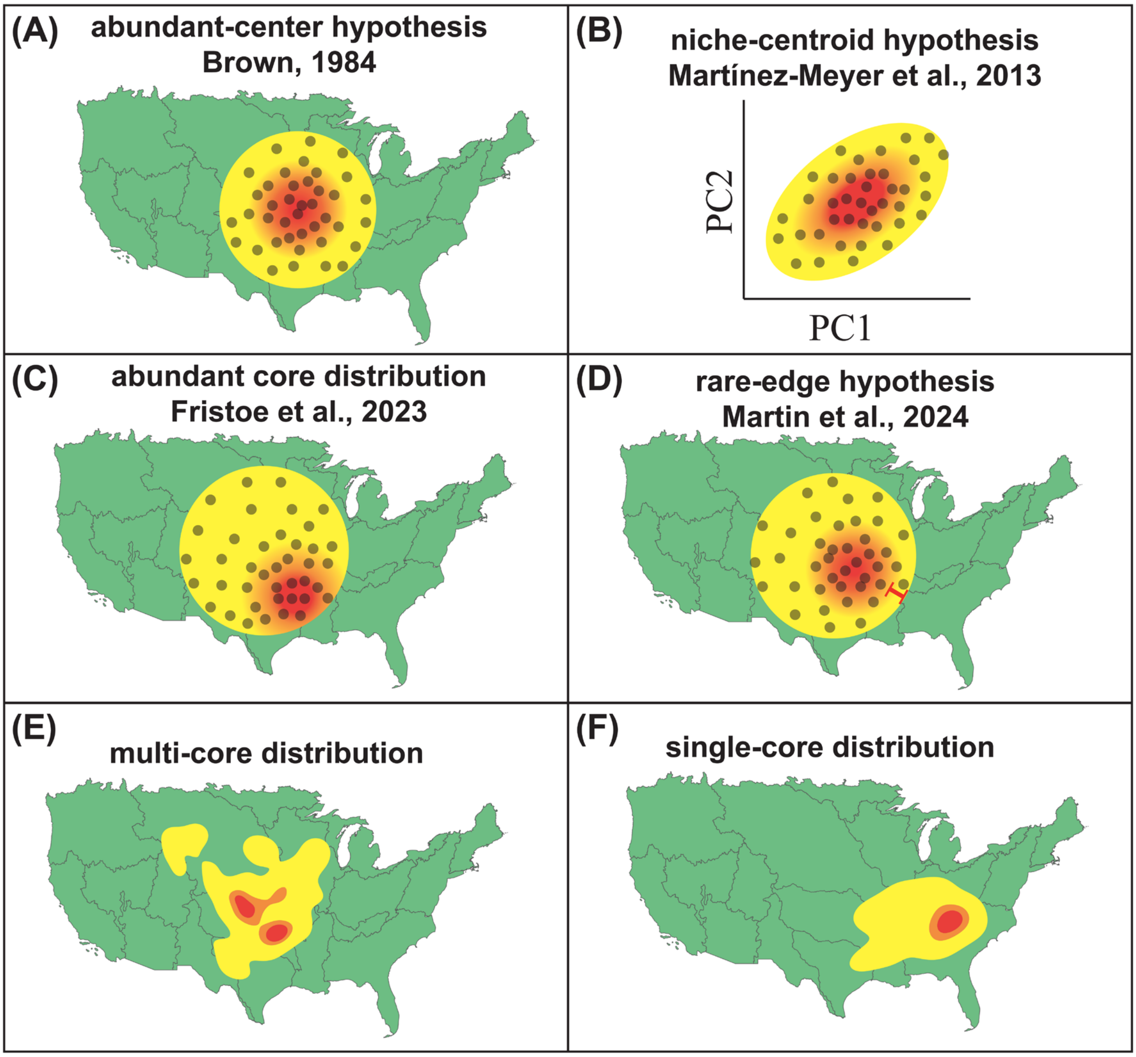

Figure 1. (A) Brown's (1984) abundant center hypothesis. (B) The niche-centroid hypothesis (Martínez-Meyer et al. 2013). (C) The abundant core distribution (Fristoe et al. 2023). (D) The rare-edge hypothesis (Martin et al. 2024). (B)–(D) are competing hypotheses proposed in the literature. In all four panels, the red region represents the abundant core and yellow indicates lower abundance and range extent. (A) represents the theoretical abundance structure in the abundant-center hypothesis (Brown 1984). The axes for the niche-centroid hypothesis (B; Martínez-Meyer et al. 2013) represent a theoretical multivariate synthesis (resulting from a principal components analysis) of a suite of environmental attributes where species are present (points). (C) depicts the abundant center distribution proposed by Fristoe et al. (2023) that states abundant cores can be located non-centrally in a species' range. (D) depicts the modification to the abundant center distribution by Martin et al. (2024), which requires a decline in abundance from the abundant core to the range edge. (E) Example of a single-core distribution in our study. (F) Example of a multi-core distribution in our study. We refer to the abundant center hypothesis and concepts proposed by Fristoe et al. (2023) and Martin et al. (2024) in the (D) as a single-core distribution (SCD), while (F) illustrates the concept of the multi-core distribution (MCD) observed in stream fishes.

of the ACH is unknown, and the relationship between habitat suitability and abundance may be weak (Dallas and Hastings 2018, Sporbert et al. 2020) or non-linear (Bramon Mora et al. 2024), further obscuring the larger ACH signal. Although the ACH remains theoretically grounded, variations in taxa, habitat types, and other factors related to distributions present opportunities to enhance the ACH into a conceptual model that produces more accurate and generalizable predictions (Fristoe et al. 2023).

Persistent challenges with applying the ACH have led to three alternative hypotheses. First, the niche-centroid hypothesis states that species are most abundant in the core of their Grinnellian niche space, which often is not aligned with the geographic center of their distribution (Fig. 1B, Martínez-Meyer et al. 2013). The niche centroid hypothesis, through Hutchinson's duality (Hutchinson 1978), allows for the ACH model in niche space that can translate into multimodal abundance distributions in geographic space. Second, Fristoe et al. (2023) suggested a distributional framework similar to the ACH, stating there is a geographic region of elevated abundance in the species range, termed an abundant core, but the abundant core can be located anywhere in the geographic range (Fig. 1C, Fristoe et al. 2023, Martin et al. 2024). Third, Martin et al. (2024) introduced the rare-edge hypothesis, which posits that the greatest abundance can occur anywhere except the range edge (Fig. 1D). The latter two hypotheses both maintain that a single peak in abundance occurs and that geography plays a critical role in shaping spatial patterns in local abundance. Although these three theoretical abundance distributions represent an evolution of the ACH to include more ecological reality (e.g. habitat characteristics, abundance over occupancy, geographic features), the latter two constrain species to a single area of high abundance and do not consider that abundance distributions may be spatially multimodal.

Patchily distributed optimal habitat and natural dispersal barriers provide another layer of ecological detail that may give rise to abundance distributions containing more than one abundant core. Terrestrial organisms historically used to develop, test, and advance the ACH (Feldhamer et al. 2012, Freeman and Beehler 2018, Fristoe et al. 2023, Martin et al. 2024) generally have fewer dispersal limitations compared to other taxa. Many species are distributed patchily across the landscape as distinct but historically connected metapopulations separated by large areas of contemporarily unsuitable habitat – a natural biogeographic phenomenon that may give rise to numerous abundant cores within a species' overall range. For instance, distributions of freshwater fishes follow watershed boundaries (resulting from biogeographic processes; Olden et al. 2010), creating dispersal limitations among watersheds regardless of habitat quality (Tonkin et al. 2018) that may present as multiple high abundance areas across a landscape of lower abundance. As a result, testing the ACH using taxa with strict limitations on dispersal can improve our understanding of macroscale abundance distributions and advance ACH ideas to better reflect and predict reality for these species.

We propose that abundance distributions of dispersal-limited species (i.e. taxa with body size limitations or physical boundaries to dispersal) can be multimodal, giving rise to more than one abundant core across the overall distribution (Fig. 1E). Conceptual multi-core distributions (MCDs) may be more descriptive of dispersal limited taxa with naturally fragmented distributions. Rather than challenge one specific hypothesis, we compare the model of the multi-core distribution to the set of existing hypotheses positing a single abundant core, which we refer to as single-core distributions (SCDs; Fig. 1F). Using stream fishes as a model system, our study objectives are to 1) quantify the extent to which stream fishes exhibit multiple abundant cores within their range and 2) investigate potential species-specific mechanisms (e.g. range size and body size) that give rise to multiple abundant cores. As independent variables, range size indirectly addresses biogeography (i.e. potential for dispersal among river basins in evolutionary time), while body size is a surrogate for dispersal potential (i.e. potential for dispersal within river basins in more recent time) (Comte and Olden 2018). We expect stream fishes will exhibit multiple abundant cores and that the number of abundant cores will be positively associated with range and body size. The larger the geographic area a species occupies, the greater the likelihood the distribution encompasses a greater diversity of habitats and contains more abundant cores or a single core that can then be subject to biogeographic mechanisms that can separate one population in two (i.e. MCD). Additionally, larger fish have greater dispersal capabilities, which may facilitate traversing longer stretches of unsuitable habitat to reach suitable habitat allowing for another abundant core, thus creating an MCD.

Material and methods

We examined distributions of a taxonomically and functionally diverse group of fishes representing eight families. The analysis was comprised of five steps: 1) species selection, 2) challenging the ACH with simple distance–abundance relationships (where lack of support here suggests that other models should be evaluated), 3) bootstrapped geospatial kernel density estimation to estimate (species-specific) abundant cores, 4) assigning species to a conceptual abundance distribution, and 5) linear modeling to test the association between the number of abundant cores in a species distribution and species' range maximum body length (Fig. 2).

Species selection

We used an extensive dataset of stream fish community monitoring surveys aggregated from 34 state agencies across the continental US (Supporting information). To reduce gear bias in sampling methodology, species were selected from backpack, barge, bank, and boat electrofishing count surveys that targeted stream fish communities in wadable streams across 36 US states from 2000–2022. Electrofishing methods are regarded as the standardized way of collecting whole communities and measuring abundance in stream fish communities

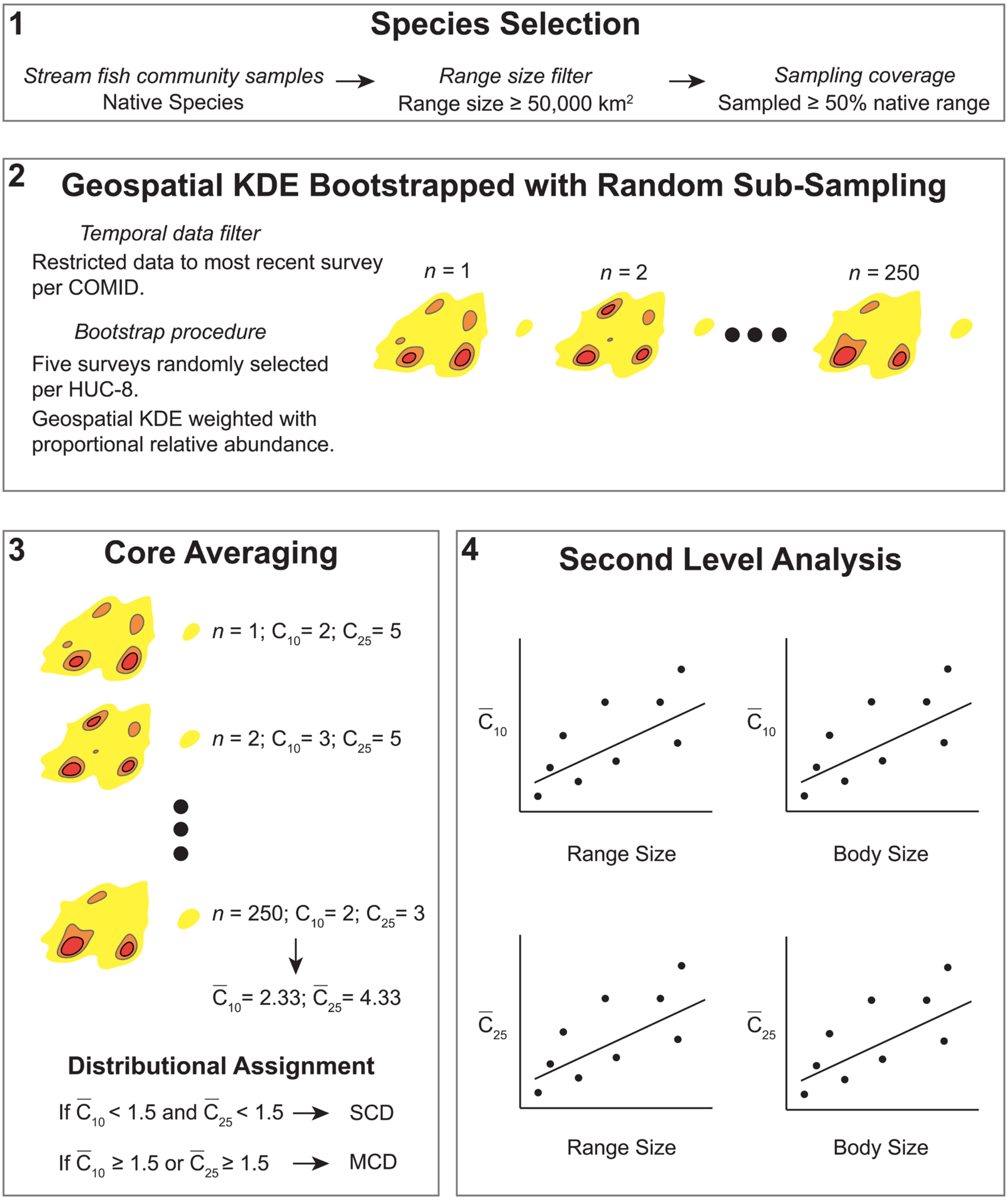

Figure 2. Workflow diagram depicting the four main steps in the analysis. In steps 3 and 4, n indicates the bootstrap iteration for the respective weighted geospatial kernel density estimates. In step 3, C_{10} and C_{25} represent abundant cores defined as the closed 10 and 25% density contours of a weighted geospatial kernel density estimate. The $\bar{C}_{10}$ and $\bar{C}_{25}$ are the average number of C_{10} and C_{25} abundant cores across all 250 iterations, respectively.

to allow for comparable measures of abundance (Yoder and Kulik 2003). Small, wadeable streams (sensu Barbour 1999 USEPA) are easily sampled in standardizable protocols that are comparably applied across the CONUS to characterize stream fish communities (Barbour 1999, Moulton et al. 2002, Bonar et al. 2009); these protocols guide all agency-based stream fish community sampling in the US. We retained 64 species that satisfied all the following conditions: 1) the species is native to the conterminous US, 2) the species native range size is at least 50 000 km^2, and 3) the species was sampled in at least 50% of its native range. We assigned native status based on NatureServe (NatureServe 2020) and the US Geological Survey Nonindigenous Aquatic Species Database (US Geological Survey 2024). Native range size was calculated from the Watershed Boundary Dataset (US Geological Survey 2023) for the US portion of the range and from Anas and Mandrak (2021) for the Canadian portion of the range as the total area (in km²) of the eight-digit hydrologic unit codes (HUC-8s; US Geological Survey 2023) and similarly sized Canadian watersheds constituting the native range. Few studies apply the ACH to stream fishes, questioning the generalizability of any given minimum range size threshold across taxa and whether this threshold is mediated by limitations on dispersal (Sagarin et al. 2006, Knouft and Anthony 2016). We chose 50 000 km² as a threshold to guarantee capturing this unknown but ecologically relevant threshold. Following Fristoe et al. (2023), we adopted the 50% coverage cutoff for balancing sampling coverage and inclusion of species. We limited our analysis to species native to the continental US within their native range to avoid potentially differing ecological drivers between native and non-native ranges. In total, the final dataset consisted of 29 206 survey locations (stream reaches) across the 36 States.

Abundant center test

Prior to testing for multiple cores, we evaluated the ACH in a manner similar to Fristoe et al. (2023) by using the distance–abundance relationship. As an index of abundance, we used proportional relative abundance, which was calculated as individual species counts divided by the total count of all species collected in an electrofishing survey. Despite finding a strong correlation of 0.77 (SE = 0.001) between proportional relative abundance and relative abundance (raw counts), the nature of combining different sampling programs necessitated the data standardization (proportions). Great circle distances from the geographic center of species distributions to sample sites (the same as used in the kernel density estimators described below) were correlated to the relative abundance at each site using Spearman's ranked correlation, ρ. Although this may be a preliminary result, this step was conducted as part of the Methods to establish the motivation for the next step, the KDE methods. For each species we used the HUC-8s and Canadian watersheds where the species was native (see above for description of native status) to establish the geographic center. Spatial data were acquired from the Watershed Boundary Dataset (US Geological Survey 2023) and the Canadian National Hydro Network (Government of Canada 2022). Watersheds were spatially joined, and the center of the distribution was calculated as the centroid of the bounding box that encompassed the entire distribution. Watersheds are irregularly shaped and result in irregularly shaped, disjunct species ranges. We explored convex hulls among others methods of center determination and found these methods did not represent better approximations of the geographic center. Strong negative correlations (ρ approaching -1) would indicate support of ACH, while weak or strong positive correlations (ρ close to 0 or approaching 1) would suggest the lack of an abundance pattern that supports ACH (Supporting information).

Kernel density estimates

We identified peaks in abundance at various magnitudes across each species' native range using geospatial kernel density estimates (KDEs) weighted with adaptive bandwidth and standardized, proportional relative abundances. We chose this approach because a single bandwidth (Fristoe et al. 2023) may not carry the same ecological relevance across taxa, and proportional relative abundance allows for robust range-wide comparisons of abundance versus standard relative abundance, which may mask the ACH signal in latitudinal gradients of total abundance. Proportional relative abundance was calculated as individual species counts divided by the total count of all species caught in an electrofishing survey, and we standardized to allow the abundance information to weight the KDEs. Specifically, we deployed the 'eks' package (Duong 2022) in R ver. 4.4.0 (www.r-project.org) to calculate two-dimensional geospatial KDEs with adaptive bandwidth, where density estimation at point **x** for data $\mathbf{X}_1, \ldots, \mathbf{X}_n$ is described by three equations,

$$\hat{f}_H(x) = n^{-1}\sum_{i=1}^{n} w_i K_H(x - \mathrm{X}_i), \quad \text{for } i = 1,\ldots,\mathrm{n} \qquad (1)$$

$$K_{\boldsymbol{H}} = (2\pi)^{-1} |\boldsymbol{H}|^{-1/2} e^{\left(-1/2\boldsymbol{x}^{T}\boldsymbol{H}^{-1}\boldsymbol{x}\right)}, \quad \text{for } i = 1,\ldots,\mathrm{n} \qquad (2)$$

$$w_i = \frac{(x_i - \bar{x})}{\mathrm{sd}(x)} + 1, \quad \text{for } i = 1,\ldots,\mathrm{n} \qquad (3)$$

where X_i was the latitude and longitude for survey *i* projected into Albers equal area conical projection for the conterminous US, $\boldsymbol{H}$ was the adaptive bandwidth matrix calculated with the plug-in method (Duong 2022) and was the variance for the gaussian function *K*, x_i is the proportional relative abundance in survey *i*, x was the average proportional relative abundance for $i = 1,\ldots, n$, and w_i was the standardized proportional relative abundance increased by one for survey *i*. The weighted, geospatial KDE avoided imposing a center to the distribution while still allowing us to incorporate abundance data to identify abundant cores.

Stream fishes in the US are not sampled with spatial uniformity due to several factors, such as habitat availability, property access and monitoring agency logistics. To minimize possible local-scale effects from areas that were intensively sampled, we used a random sub-sampling procedure. First, we restricted the data included in the analysis to one survey per stream segment (COMID) from the National Hydrology Dataset (NHD Plus ver. 2, McKay et al. 2012). For each species, the most recent survey for each COMID was chosen, or if multiple surveys occurred on the same day in the same COMID, the proportional relative abundance was averaged among those surveys (< 3% of surveys across all species). We then bootstrapped 250 iterations (to produce 250 KDEs) to randomly subsample five surveys per HUC-8 (five distinct COMIDs), and any HUC-8s with fewer than five surveys were excluded. Each bootstrap iteration repeated the random sub-sampling, calculated the weights as the standardized proportional relative abundance, and calculated a geospatial KDE. We increased all standardized relative abundances by 1 to center the weights around one instead of zero (required for kernel density estimation). Coordinates for the geospatial KDEs were projected into Albers equal area conical projection for the conterminous US.

We used two criteria to define abundant cores: the closed 10% (C_{10}) and closed 25% (C_{25}) density contours in a single KDE, which corresponded to the smallest regions that contain the top 10 and 25% of the density estimates weighted with relative abundance. Fristoe et al. (2023) used a 10% cutoff to identify a single core, which made our work similar in that we used a relatively high-density threshold for abundant core(s). We added a 25% cutoff for two reasons: 1) to identify any abundant cores that were lower in magnitude but still represented areas of elevated abundance (because high abundance is not an absolute number), and 2) to replace distance calculations because a C_{25} abundant core could be spatially distinct from the C_{10} abundant core, creating a non-monotonic abundance gradient that excludes a single-core distribution as a possibility. In single-core distributions, there would be one C_{10} abundant core nested within a single C_{25} abundant core, because the 25% density region from a KDE must contain the 10% density region if there is only one of each.

For each species set of 250 KDEs, we calculated the average number of C_{10} and C_{25} abundant cores and subsequently rounded the average to a whole number for assignment in support of SCDs or MCDs. Species that averaged a single C_{10} and C_{25} abundant core were classified as SCDs (Fig. 1F). Stream fish with more than one abundant core, C_{10} or C_{25}, were classified as MCDs (Fig. 1E). The 'eks' package in R (Duong 2022) was used to calculate density contours with the probability contours method (Bowman and Foster 1993, Hyndman 1996) and can be considered as the quantiles of the KDE density estimates.

Predictors of abundant cores

Linear regression analyses were conducted to test for effects of range size (log km^2) and maximum total length (cm) on the average number of C_{10} and C_{25} abundant cores. Range size and total length were moderately correlated ($r = 0.44$), but the correlation was not strong enough to preclude investigating both factors. Maximum total length was assigned from the FishTraits database (Frimpong and Angermeier 2009, Supporting information). The families represented in our analysis varied in sample size, precluding more in-depth phylogenetic analyses such as eigenvector regression (Diniz-Filho et al. 1998)

Results

Abundant center test

Overall, the majority of the freshwater fish species that we studied did not display a distance–abundance relationship that aligned with the ACH. Over two-thirds of species (46 of 64) had either a positive distance–abundance relationship or no direction to the distance–abundance relationship, while only 30% of species (19 of 64) showed a negative distance–abundance relationship in support of the ACH (Supporting information). For species supporting the ACH, correlations were weak to moderate, ranging from −0.02 to −0.35. The species with positive correlations ranged from 0.06 to 0.42, which indicates that neither positive nor negative correlations were strong. Given the overall lack of negative distance–abundance relationships that would support ACH and the weak correlations across all species, this evaluation of ACH suggests that species may be exhibiting multiple cores and warrants further investigation.

Kernel density estimates

The majority of the stream fish species we investigated (43 out of 64, 67%) exhibited a multi-core distribution, while about a third (21 species, 33%) of species were classified as a single-core distribution (for all species results, Supporting information). The average number of C_{10} abundant cores ranged from 1.00–5.12, and the average number of C_{25} abundant cores ranged from 1.02–5.64. For species with MCDs, about half averaged between two and three C_{10} abundant cores ($n = 19$), while nine species averaged between three to four abundant cores, and the remaining species ($n = 13$) had a single C_{10} core with multiple C_{25} cores. More species ($n = 24$) with MCDs averaged between two and three C_{25} abundant cores, while 19 species averaged between three and six C_{25} abundant cores. A greater number of C_{25} abundant cores indicated that at least one C_{25} abundant core did not have a C_{10} abundant core nested within it, suggesting that not all abundant cores are equal in magnitude (Fig. 3). Most species had the same or fewer C_{10} abundant cores than C_{25} abundant cores, with just a few exceptions. See Supporting information for KDEs for each species representing all 250 iterations.

Total range size had a positive association with the number of both C_{10} and C_{25} abundant cores for the stream fish we investigated (Fig. 4). The parameter estimates for the effect of (log) range size in the C_{10} and C_{25} models were 0.52 (95% CI [0.40, 0.64]) and 0.62 (95% CI [0.46, 0.78]), respectively, both reflecting significant positive relationships ($p < 0.001$; Fig. 4). Single-core and multi-core distributions were observed in species with relatively large and small ranges, thus while species with larger ranges had more cores, single-core and multi-core distributions were still observed across a wide range of the spatial extents represented in our study (Fig. 3). The effect of maximum total length was not significant in models for both abundant core cutoffs (Supporting information). We compared model residuals among families using an ANOVA, which was justified because nearly all orders were represented by a single family and most genera by only one or two species. Given these constraints, finer phylogenetic analyses based on actual phylogenetic distances were not feasible. The ANOVA revealed no significant differences in residuals for either C10 or C25 cores, suggesting that a phylogenetic correction was unnecessary.

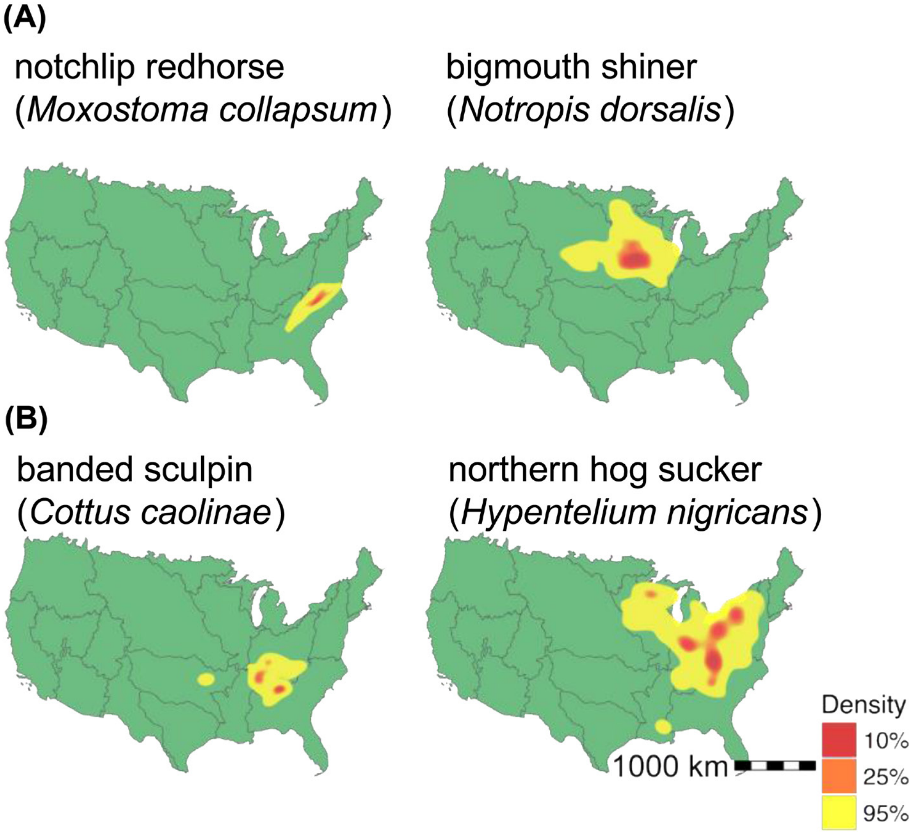

Figure 3. (A) Kernel density estimate (KDE) results from two single-core distributions representing a smaller (left) and larger (right) range size for notchlip redhorse *Moxostoma collapsum* and the bigmouth shiner *Notropis dorsalis*, respectively. (B) KDE results from two multi-core distributions representing a smaller (left) and larger (right) range size for the banded sculpin *Cottus carolinae* and the northern hog sucker *Hypentelium nigricans*, respectively. All coordinates are projected with Albers equal area conical projection for the continental US.

Discussion

We present clear evidence in support of multiple abundant cores in distributions of broadly occurring freshwater fish species based on a continental investigation. Although some stream fishes exhibited a single abundant core, many of the studied species showed clear evidence for MCDs. Additionally, most stream fish species did not exhibit significant declines in abundance as distance from the geographic center increased. While some species with MCDs supported the ACH, the correlations were weak ($\rho < 0.25$). Thus, despite an overall decline in abundance from center to edge, the KDEs showed that the underlying patterns of abundance are still heterogeneous with spatially discrete regions of elevated abundance. Because our study design randomly sampled within spatial units to avoid overrepresenting areas of greater initial electrofishing, we have increased confidence in the KDE results and estimates of cores.

Our findings support mounting evidence that the ACH is insufficient for stream fishes (Dettmers et al. 2001, Comte and Grenouillet 2013, Knouft and Anthony 2016, Dallas et al. 2020) and that recent SCDs do not make adequate predictions to understand often-fragmented distributions of dispersal-limited taxa. For species with MCDs, the number of abundant cores increased with range size, which is intuitive as larger range sizes implicitly carry the potential for more abundant cores than smaller ranges. Abundant cores can be theoretically attributed to the spatial aggregation of suitable habitat that provides a species with the resources (e.g. food, reproductive habitat) needed for sustaining a population over a large spatial extent. As range sizes increase, species encounter a wider variety of habitats across a gradient of favorability. Thus, for a widely distributed species, there is an increased likelihood of encountering another spatial aggregation of suitable habitat capable of supporting a local population with biotic (e.g. competition) or abiotic (e.g. substrate type, physiological barrier) factors limiting abundance between cores, which parallels the niche-centroid idea (Martínez-Meyer et al. 2013) and Hutchinson's duality. However, it is important to note that we only tested the ACH in geographic space and not niche space; therefore, we cannot discount the possibility of Hutchinson's duality in stream fish abundance that may adhere to the ACH in niche space. While this approach is beyond the scope of the present study, this remains a clear next step for better understanding how the ACH may or may not be useful for riverine fishes.

Biogeographic and ecological mechanisms likely underpin the observed multiple core patterns. Specifically,

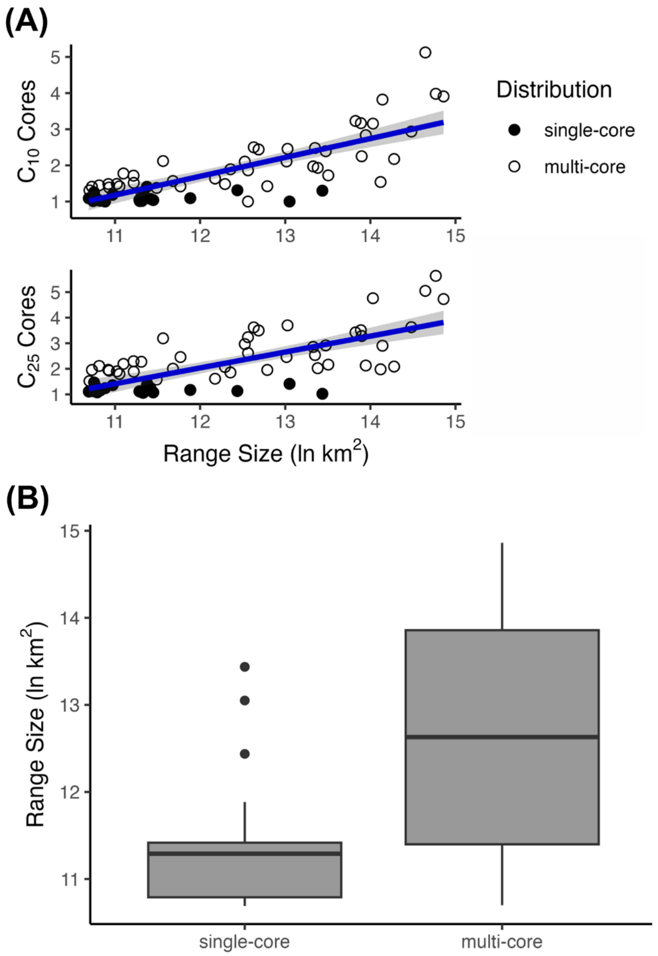

Figure 4. (A) Partial effects plots for range size from both linear regressions. (B) Boxplots of range size for multi-core and single-core distributed fishes. Both the C_{10} and C_{25} cores are used to categorize a species into single- or multi-core distributions.

biogeographic events created an initial setting of species, habitats, and ecological processes that have continued to change and influence the distributions we see today. For some species, geo-climatic events in recent evolutionary time have isolated populations by a matrix of unsuitable habitat and/or hard dispersal barriers, providing a basis for multi-core distributions. Multiple biogeographic mechanisms such as stream capture, glaciation and marine embayment can fragment and restructure river habitats and separate a single population into multiple while temperature shifts allow species distributions to expand and contract latitudinally (Griffiths 2010). Local maxima in abundant cores may then derive from environmental gradients relevant to stream fish abundance that follow the hierarchical and longitudinal structure of dendritic networks (Erős et al. 2017). For stream fish species, the orientation and connectivity of watersheds drive the patterns of correlated habitat variables, contrasting the spatial autocorrelation of habitat expected underlying the ACH in terrestrial species in the traditional sense and shifting it to the longitudinal dendritic network. For example, species adapted for small streams typically avoid large river habitats, resulting in expected declines in abundance from upstream to downstream and suitable habitats existing only at the periphery of watersheds, which in turn creates patchy patterns of abundance dependent on the spatial orientation of watersheds and connectivity among habitats. Thus, species-specific abundance is expected to change longitudinally within dendritic networks along key habitat gradients (e.g. stream size, temperature, flow regime, etc.; Altermatt and Fronhofer 2018), making the assembly of isolated populations of a fragmented distribution into range-wide patterns of abundance likely to reflect a multi-core distribution. Ultimately, biogeographical and ecological mechanisms – and their interactions – make multiple abundant cores likely, but also complex processes to document and understand.

We recognize several limitations of our analysis. Large-scale analyses often require the aggregation of data collected for various purposes under different sampling protocols, which can complicate inference. To minimize human bias (e.g. variability in sampling protocols), we filtered our data to electrofishing surveys sampling entire communities and limited the temporal window of samples considered. Aggregating data can result in heterogeneous sampling densities, and we avoided modeling trends in sampling density instead of abundance by repeating random selection of samples in discrete spatial units. Stream fishes are shown to exhibit asynchrony in metapopulation abundance (Larsen et al. 2021), which limits our scope of inference to the current abundance distributions, not the net abundance distributions that accounts for fluxes in abundance through time. Our analysis had incomplete spatial coverage of some native ranges, yet we required sampling from at least half of the native range along with minimum area limits, similar to Fristoe et al. (2023). We did not have the local abundance data needed for the Canadian portion of species' ranges and did not have data to analyze many widely distributed stream fish species with Nearctic distributions; however, with appropriate data these species represent an opportunity to further investigate the number of abundant cores in stream fish distributions. For species that were included and widely distributed in the US and Canada, we had good coverage of the US portion of the range allowing for restricted, but useful inference. The ecologically relevant range size and coverage both remain important aspects of macroscale distributions to explore in future studies under ACH based frameworks.

The ACH has functioned as a good hypothesis-generating model but still has many avenues for improvement. Explicitly including habitat variables instead of implicitly assigning patterns to surrogate abiotic gradients (e.g. latitude) and encompassing a wider range of factors influencing biogeographic history provide interesting paths forward to advance hypotheses based on the ACH. For taxa with greater limitations on dispersal, relevant habitat variables may supersede or be poorly reflected by surrogate abiotic gradients such as latitude or longitude even at larger spatial scales and could allow future investigations to gain a better mechanistic understanding of why abundance distributions form the way they do (Jackson et al. 2001). Biogeographic factors present another avenue to explore mechanistic processes governing the formation of abundance distributions. For example, species age could account for variation in observed macroscale abundance distributions due to the intrinsic link between species age and range size (Johnson 1998, Guo et al. 2024). For North American freshwater fishes, older species have in principle had more opportunities to disperse across and among continents as major geological events have dis- and reconnected river networks, and therefore are more likely to be subject to range-wide heterogeny in abundance and exhibit multiple cores. For example, many upland-adapted species were distributed across a contiguous mountainous region in eastern North America, but are now separated by large areas of unsuitable habitat (lowland fluvial valleys) that fragmented the uplands through glaciation and embayment during the Pleistocene. Moreover, many species have experienced natural introduction events and range expansions into previously disconnected basins through interbasin stream capture. Meanwhile, more recently evolved species have had fewer opportunities to naturally access currently disconnected river networks and therefore may be more likely to be restricted to small ranges with a single core. In the upper Mobile basin, endemic species were isolated and speciated during Pleistocene embayment events and could hypothetically experience natural introductions and range expansions into the upper Tennessee/Mississippi or Atlantic slope drainages, given sufficient time for new stream capture events to occur. Therefore, we emphasize that we do not intend to attribute these patterns to species' dispersal abilities within watersheds (i.e. based on their physical capabilities) but rather simply to whether or not they could have been present during natural interbasin transfers. We recognize that the influence of biogeographic processes and habitat variables may be difficult to separate mechanistically from anthropogenic impacts on species distributions and habitats (Utz et al. 2010, Su et al. 2021). Moreover, freshwater fishes may be unique in how biogeographic events have shaped their abundance distributions, as most species, including freshwater species, have some form of terrestrial or aerial dispersal.

Taxa with anthropogenically driven introductions present a challenge to ACH-based thinking (Sakai et al. 2001). Under the ACH, such species should be low in abundance at the new range edge, yet this is not always the case (Firn et al. 2011, Hartman and Larson 2023). For instance, plant species can achieve similar abundances in both introduced and native ranges (Firn et al. 2011). In general, established nonnative species question if abundance distributions in a species' introduced range mirror the native range (both MCDs or SCDs), or do species exhibit native SCDs and introduced MCDs or vice versa (Bradley et al. 2019). Evaluating the relationship between abundance in native and nonnative ranges through application of ACH-based ideas could be an interesting way of advancing the science of invasion biogeography.

Ecologists continue in their search for general principles that can apply across taxonomic groups, but empirical evidence still lags behind theoretical expectations. Considering biogeographic mechanisms and habitat variables while allowing for multiple abundant cores may help to disentangle the mixed evidence supporting the ACH into single-core and multi-core distributions. We attempt to move the discussion of macroscale patterns of abundance beyond testing simply whether species are abundantly centered or not. Allowing for multi-core distributions can better integrate general factors that influence a species range and abundance such as biogeography, population connectivity/fragmentation, and evolutionary ages, while still allowing for the ACH to occur. This study fits into a growing collection of research that suggest that macroscale abundance distributions may not be as generalizable across taxa as once thought. We hope that our work promotes the broadening of perspectives by encouraging further investigation of the biogeographic drivers of multi-core distributions in widely distributed taxa with greater limitations on dispersal.

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.r4xgxd2r1 (Zink et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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