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LETTER

Scale of population synchrony confirms macroecological estimates of minimum viable range size

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Abstract

Global ecosystems are facing a deepening biodiversity crisis, necessitating robust approaches to quantifying species extinction risk. The lower limit of the macroecological relationship between species range and body size has long been hypothesized as an estimate of the relationship between the minimum viable range size (MVRS) needed for species persistence and the organismal traits that affect space and resource requirements. Here, we perform the first explicit test of this assumption by confronting the MVRS predicted by the range-body size relationship with an independent estimate based on the scale of synchrony in abundance among spatially separated populations of riverine fish. We provide clear evidence of a positive relationship between the scale of synchrony and species body size, and strong support for the MVRS set by the lower limit of the range-body size macroecological relationship. This MVRS may help prioritize first evaluations for unassessed or data-deficient taxa in global conservation assessments.

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extinction risk assessments, freshwater fish, geographic range, IUCN red list, population time-series

INTRODUCTION

Extinction risk estimates are essential for prioritizing conservation actions (Joseph et al., 2009). Geographic range size, the area across which a species occurs, consistently emerges as a key correlate of extinction risk in vertebrates (Cardillo et al., 2008; Gaston, 1994; Lee & Jetz, 2011), with species occupying smaller geographic ranges being often associated with a higher extinction risk due to lower total population sizes (e.g. Purvis et al., 2000). Geographic range size is also considered as a proxy of extinction risk in the IUCN Red List of Threatened species (criterion B), where minimum thresholds on range area are set to define threat levels (e.g. Collen et al., 2016).

However, occupying small geographic ranges does not necessarily imply that species will face similar extinction risk. The geographic range necessary for long-term persistence likely depends on species traits that determine their populations' local and regional abundance (Gaston & Blackburn, 1996a). Body size is associated with many species attributes that influence geographic ranges (e.g. population density, individual home range size and dispersal capacity; Schmidt-Nielsen, 1984; Tamburello et al., 2015). In particular, the energetic constraints shaping the relationship between body size and metabolic requirements (Jetz et al., 2004; Swihart et al., 1988) cause larger species to have higher individual resource allocation and hence lower population densities, which can be compensated by broader geographic ranges (Brown & Maurer, 1987; Damuth, 1981). Consequently, large species with small ranges are more likely to become extinct, because of low effective population sizes and high vulnerability to catastrophic events associated with demographic and environmental stochasticity. Conversely, small-bodied species can maintain higher population abundances in smaller areas (Gaston, 1994).

The above mechanisms have been proposed to explain the triangular relationship between species' geographic range and body size. This pattern is among the earliest documented in macroecology (Brown & Maurer, 1987, 1989) and has been reported in all vertebrate groups at various geographic scales and within different biogeographic regions (e.g. Agosta & Bernardo, 2013; Carvajal-Quintero et al., 2017; Gaston & Blackburn, 1996b; Newsome et al., 2020). The range-body size relationship depicts a triangular shape defined by three boundaries in bivariate space (Figure 1a). The spatial extent of the biogeographic area studied defines the maximum range size (i.e. the upper limit), whereas physiological constraints of biological organisms define the minimum body size (i.e. the left limit). The third limit defines the

minimum range size (i.e. the lower limit) occupied by a species and thus is considered as the minimum viable range size (MVRS) necessary for a species of a given body size to maintain viable populations (Brown & Maurer, 1987, 1989). This lower boundary has been associated with a high probability of extinction and used to define the MVRS (hereafter called 'distribution-based MVRS', see Figure 1a) for species given their body size (Gaston & Blackburn, 1996a, 2000). Hence, from a conservation perspective, this boundary is of utmost importance as it potentially constitutes a viability limit below which species would display a low probability of persistence (Brown & Maurer, 1987, 1989; Gaston & Blackburn, 1996a).

Despite three decades of research, surprisingly few studies have offered empirical evidence that species extinction risk may be higher for large-bodied species with small ranges than expected based on range size alone. Furthermore, past studies assessing whether the lower boundary of the range-body size relationship could be used as a suitable predictor of threat status have focused on extinction risk categories (itself already informed by species range sizes), potentially suffering from circularity issues (Le Feuvre et al., 2016; Newsome et al., 2020; Rosenfield, 2002).

Temporal coherence or synchrony in abundances among spatially separated populations is related to species long-term persistence and extinction probability (Allen et al., 1993; Heino et al., 1997; Liebhold et al., 2004). Among the mechanisms underlying spatial synchrony patterns, the dispersal of individuals between populations is known to be a key synchronizing factor at short spatial distances, whereas correlated environmental forcing (e.g. spatially homogeneous climatic conditions) can synchronize population dynamics over greater distances (Heino et al., 1997; Liebhold et al., 2004). Synchronous population dynamics can increase species vulnerability to spatially correlated stochastic events, leading to simultaneous population extirpations and global extinction (Allen et al., 1993; Liebhold et al., 2004). Indeed, several populations simultaneously experiencing low densities are more likely to be extirpated by stochastic events because of the reduced ability of one population to rescue another through migration (i.e. rescue effect; Heino et al., 1997; Earn et al., 2000). In contrast, locally adapted populations are more likely to display asynchronous population dynamics, diversifying the species response to environmental changes and disturbances and leading to increased regional persistence and ecosystem stability (i.e. the portfolio effect; Moore et al., 2010; Schindler et al., 2010).

Population synchrony has been studied in a wide range of taxa, almost invariably documenting a decay of

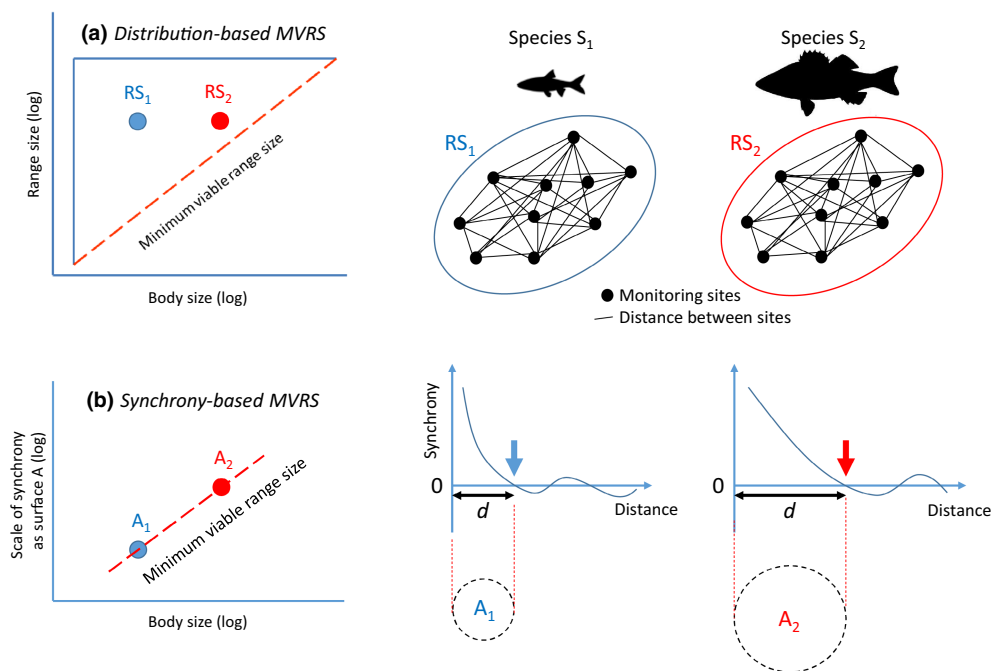


FIGURE 1 Schematic framework applied to define the distribution- and synchrony-based MVRs (minimum viable range size) for two species with different body sizes. (a) the distribution-based MVRs is defined by the geographic range size–body size triangular relationship proposed by Brown and Maurer (1987, 1989), where the two theoretical species S_1 and S_2 with different body sizes have the same range size $RS_1 = RS_2$. (b) the synchrony-based MVRs is defined by distance d , which is the scale of synchrony in population abundances from a set of monitoring sites (i.e. the maximum distance at which synchrony is still detected), then used to provide circular areas A_1 and A_2 .

synchrony with increasing geographic distance between populations (Bjørnstad et al., 1999; Liebhold et al., 2004; Ranta et al., 1995). Thus, the negative relationship between synchrony and the distance separating populations can be used to define a limit of synchrony or ‘scale of synchrony’ (Figure 1b), the maximum distance where synchrony can still be observed between populations (Bjørnstad et al., 1999). Beyond this scale of synchrony, population present compensatory mechanisms may occur, reducing the probability of local and regional extinctions (Heino et al., 1997; Liebhold et al., 2004). Hence, the scale of synchrony can be used as an independent estimate of the MVRs that a given species needs for its long-term persistence (hereafter called ‘synchrony-based MVRs’, see Figure 1b).

Estimating a synchrony-based MVRs is extremely data-demanding, requiring long time-series of population abundances in a number of sampling locations (see Figure 1b). These stringent data requirements have certainly hindered using the scale of synchrony approach to building a general MVRs-body size relationship. Still, a synchrony-based MVRs set by spatiotemporal population dynamics, if estimated for a sufficient number of species, could provide a comparative assessment of the validity of less data demanding distribution-based MVRs (i.e. observing similar shapes for both red lines in Figure 1a,b). Comparing these two independent approaches to estimating the MVRs may also provide novel insights into the

spatiotemporal dynamics of population abundances involved in the origin and maintenance of the range-body size macroecological pattern.

We applied this comparative framework to native riverine fishes from three biogeographic realms (Nearctic, Palearctic and Australian), where monitoring programs are sufficiently developed to provide robust and spatially extensive population abundance time-series needed to estimate the synchrony-based MVRs. We estimated the distribution-based MVRs from a global compilation of freshwater fish species distribution and body size (Carvajal-Quintero et al., 2019), and the synchrony-based MVRs from the RivFishTIME database, a global compilation of population abundance time-series (Comte et al., 2021). Our findings show a strong relationship between species body size and the scale of synchrony, thus clearly supporting the use of the distribution-based MVRs derived from macroecological range-body size relationships as a vulnerability limit to identify species with higher extinction risk. By testing for statistical associations between this macroecological boundary and species long-term probability of persistence, our findings have broad implications for the evaluation of the conservation status of poorly studied species and regions as well as forecasting species extinction risk arising from human-induced changes on species distribution ranges (Carvajal-Quintero et al., 2017; Herrera-R et al., 2020).

MATERIALS AND METHODS

Distribution-based MVRS

We collated data on the geographic range size of native freshwater fish species from three biogeographic realms, the Nearctic, Palearctic and Australian (Carvajal-Quintero et al., 2019), to quantify range-body size triangular relationships and estimate the distribution-based MVRS. These species' geographic range sizes represent the historical extent of occurrence (km^2) falling within the occupied sub-basin areas (see Carvajal-Quintero et al., 2019 for more details). The maximum observed body length (a measure of body size) for each species was sourced from FishBase (Froese & Pauly, 2020). Both range size and body size were log-transformed. To be consistent with the time-series of population abundances we used in our analysis (see below), we only included species inhabiting flowing water ecosystems (i.e. streams and rivers), excluding those with a marine or brackish life stage and those restricted to lacustrine (standing water) environments. We also excluded threatened species (i.e. those classified from 'Vulnerable' to 'Extinct' according to the IUCN Red List; IUCN, 2021) because current estimates of the range size may not reflect their complete undisturbed native range.

We estimated the distribution-based MVRS following the boundary-line procedure suggested by Blackburn et al. (1992) and used in previous studies (e.g. Agosta & Bernardo, 2013) to define linear boundaries in polygonal relationships. This method involves dividing the dataset into several body size classes, selecting the lowest (for lower boundary) y-values (in our case, range size), and applying a least squares regression line through them. Analysing various empirical and simulated datasets, Blackburn et al. (1992) suggested dividing the dataset into 6–15 body size classes, depending on the number of species, with a larger number of size classes appropriate for datasets with more species. We applied this procedure to estimate the distribution-based MVRS for all species globally, as well as separately for species in each biogeographic realm. To select the points used, we divided the range-body size plot (on a log scale) into 15 equal body size classes for the entire dataset (760 species when the three realms were considered) as well as the Nearctic realm (515 species), 12 size classes for the Palearctic realm (198 species), and eight size classes for the Australian realm (47 species). We then selected the lowest value of geographic range in each size class. To verify the robustness of this procedure, we performed a sensitivity analysis applying different numbers of body size classes (Figure S4).

Synchrony-based MVRS

The time-series of population abundances (≥ 10 years) used to estimate the synchrony-based MVRS were obtained from the RivFishTIME database (Comte et al., 2021).

Abundance time-series of populations obtained via field sampling are known to be potentially affected by several biases, including differences in detectability among species, sampling gear selectivity and species stocking, among others (see below). For this reason, a data filtering process was performed before analysis to maximize the robustness of our dataset to estimate the synchrony-based MVRS. First, we included only time-series sampled through electrofishing, as an effective and less selective fish sampling technique (e.g. Smith et al., 2015), excluding other techniques such as trapping or seining. These selection criteria resulted in species occurring in temperate and sub-temperate regions exclusively. Second, we only retained time-series sampled during the warm season (i.e. between April and September in the Northern hemisphere, and between September to April in the Southern hemisphere) to ensure using comparable samples that integrate two major drivers of fish population abundance, namely reproductive and movement events (Wootton, 1990). Third, non-native populations were excluded according to the global freshwater fish distribution database provided by Tedesco et al. (2017). If an occurrence was not reported for a given river basin in this database, we assigned the population nativity status (native or non-native) of the closest river basin belonging to the same country. When species were not included in Tedesco et al. (2017), we used nativity status from FishBase (Froese & Pauly, 2020) which is defined at the country level. Two species from North America (*Micropterus salmoides* and *Ictalurus punctatus*) were excluded because both are actively managed through stocking programs (Heitman et al., 2006; Siegwarth & Johnson, 1998). Fourth, to ensure reliable estimates of the synchrony-based MVRS, we applied a sample size criterion retaining only species with at least 10 locations that (1) belonged to the same monitoring program, and (2) were sampled during the same period of 10 years or more. If two monitoring programs provided time-series for the same species, we retained the group of time-series with the highest number of sampled sites (this occurred only for two species). Lastly, all abundance values greater than the 99.9th percentile were considered potential data errors and excluded. Additionally, we focused on the 20% most abundant species (based on average abundances) to ensure robust estimates of population dynamics (note that all species within the 20% most abundant had less than 50% zero counts). Indeed, including species with low abundances or many zero counts would prevent having an accurate image of population changes in time, thus providing spurious synchrony estimates. This data filtering procedure resulted in 21 species (Table S1) having sufficient and robust time-series data to maximize the reliability of estimates of the synchrony-based MVRS (eight for the Palearctic, seven for the Nearctic and six for the Australian realms).

We measured the synchrony-based MVRS for each species using the distance set by the first intercept

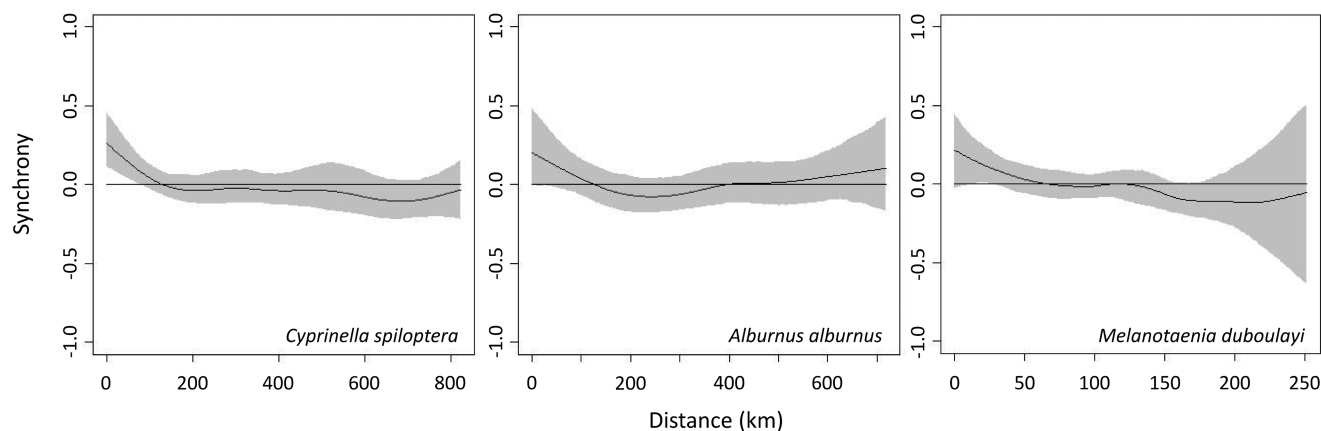


FIGURE 2 Examples of spline correlograms for three different species analysed (see Figure S2 for the spline correlograms of all species). The lines and grey areas represent the spline correlogram and 95% confidence intervals, respectively.

with the x -axis (i.e. the x -intercept) of a spline correlogram (Bjørnstad & Falck, 2001). This approach uses a smoothing spline to regress synchrony in abundance against the distance between populations (see Figure 1b and Figure 2). Spline correlogram differs from commonly used spatial correlograms (and Mantel correlograms) as it estimates dependence as a continuous function of distance, rather than by grouping the observations into distance classes, providing greater precision and the capacity to adapt well to different underlying covariance structures (Bjørnstad et al., 1999; Bjørnstad & Falck, 2001). The x -intercept from the spline correlogram is the distance at which populations are not more similar than that expected by chance-alone across the region (Bjørnstad et al., 1999; Sokal & Wartenberg, 1983), and is commonly used to estimate the spatial scale of synchrony (e.g. Jones et al., 2007). Riverine organisms are distributed along hydrological networks, typically making watercourse distances a pertinent choice to describe relationships between populations in adjacent tributaries of the same drainage basin (Larsen et al., 2021). However, here we purposely used Euclidean distances to define the x -intercept for each species to provide areas comparable to the distribution-based MVRs, whose range areas are not restricted to hydrological networks. We then estimated the area under which populations of the same species will fluctuate asynchronously and thus enhance its long-term persistence, that is, the synchrony-based MVRs, based on the area of a circle with the diameter defined by the x -intercept distance. We chose a circular delineation as the most appropriate way to represent the minimal area, ensuring that we encompass the limit of population synchrony in any direction across the geographical space. Importantly, no significant correlation was observed between the convex-hull areas delineated by the coordinates of the time-series sampling sites, or the number of sampling sites, and the corresponding synchrony-based MVRs values (Figure S1). This indicates that more widespread

sampling sites, or a higher number of sampled localities, are not biasing the synchrony-based MVRs estimates towards larger or smaller values.

Lastly, we compared the distribution- and synchrony-based MVRs estimates as a function of species body size. Given the limited number of species with synchrony-based MVRs estimates by realm, we combined the three biogeographic realms, and tested for statistical differences in the regression slopes and intercepts between both MVRs regressions with an Analysis of Covariance (ANCOVA). A non-significant interaction between the covariate (body size) and the factor (the MVRs method of estimation) would provide evidence that the slopes are similar between regressions. Next, we separated the datasets by realms to visually verify that the species-specific synchrony-based MVRs estimates were congruent with the prediction intervals given by the realm-specific distribution-based MVRs. In linear regression statistics, a prediction interval defines a range of values within which a response is likely to fall, given a specified value of a predictor (and is thus different from a confidence interval). Finally, we tested the lower limit of the range body-size relationship as a limit of inherent vulnerability by checking if the species listed as threatened in the IUCN Red List (i.e. Vulnerable, Endangered, Critically Endangered and Extinct) fell within or close to the confidence interval predicted by the distribution-based MVR. To do so, we used the IUCN range maps that represent the best available estimates of species' historical native distributions before major human impacts.

All data analyses were performed in R (R Core Team, 2021). For details on the R packages used, see Supporting Information Appendix, Table S2.

RESULTS

We found that the distribution-based MVRs manifests as a triangular association between species' range size and maximum body size, with a clear lower boundary

(positive slope) demonstrating that larger species typically display larger ranges (Figure 3, Table 1). The synchrony-based MVRS estimated from the species spline correlograms (Figure S2) also resulted in a positive and significant relationship with body size (Figure 3, Table 1), suggesting that body size is a strong predictor of the spatial scale of synchrony ($R^2 = 0.60$). The two relationships showed very similar regression coefficients and confidence intervals (Table 1), a result confirmed by the finding of no significant difference between the distribution- and synchrony-based MVRS regressions along species body size (ANCOVA F -value_{1,32} = 0.79, $p = 0.380$). Besides being statistically similar, the slopes of these two relationships are not significantly different from the value of 1 (Table 1).

Repeating the analysis by realms confirmed the triangular association between species' range size and maximum body size (Figure S3) with positive-slope lower boundaries (Table S3). We also found that the



FIGURE 3 Comparison between the distribution- and synchrony-based MVRS patterns. Blue dots depict the species-specific range-body size relationship of the three realms (i.e. palaearctic, Nearctic and Australian). The blue solid line represents the regression defining the distribution-based MVRS (i.e. the lower boundary of the range-body size triangular relationship, based on the blue diamond dots), with the grey envelope showing the confidence intervals of the regression parameters, and the dashed lines the prediction interval (with a tolerance level of 0.85). The red dots show the species-specific values of the synchrony-based MVRS (see Table S1) as a function of body size and the red line the associated regression line, together with its confidence interval (grey envelope).

	Coefficient	Estimate	Std. error	CI 2.5%	CI 97.5%
Distribution-based MVRS	Intercept	5.455***	1.113	3.050	7.860
	Slope	1.343***	0.296	0.704	1.982
Synchrony-based MVRS	Intercept	5.972***	0.650	4.611	7.333
	Slope	1.043***	0.197	0.631	1.455

Note: *** $p < 0.001$.

species-specific estimates of the synchrony-based MVRS fell within the prediction intervals of the corresponding distribution-based MVRS regressions (Figure S3). These results remained unchanged when applying different numbers of equal (log-transformed) body size classes to define the distribution-based MVRS (Figure S4).

Lastly, the placement of the species listed by the IUCN threatened categories within the range size-body size space showed that the majority of species fell within or below the prediction interval estimated for the distribution-based MVRS (Figure 4). This showed the overall consistency of the distribution-based MVRS as a limit of inherent vulnerability. Note that this pattern is also observed when using only species listed with IUCN criteria A, C, D and E, excluding those listed with criteria B defined by narrow range distributions.

DISCUSSION

We report a positive relationship between the scale of synchrony and body size as well as strong evidence of congruence between the distribution- and synchrony-based MVRS approaches. To do so, we used two independent datasets and frameworks to calculate the two MVRS (one based on species occurrences shaping distribution ranges and the other on temporal dynamics of spatially-scattered population abundances). These results support previous findings of positive links between the spatial scale of synchrony and body size or other related traits (e.g. generation time, territory size) (Marquez et al., 2019; Toms et al., 2005). We also found clear support for the lower boundary of the macroecological range-body size relationship (i.e. the distribution-based MVRS) as a vulnerability limit established by the minimum viable range size required for the long-term persistence of species. These findings extend the current understanding of the processes shaping the lower boundary of the range-body size relationship, thus offering a powerful mechanistic construct to estimate, monitor and forecast the long-term persistence of species according to their geographic range and body size.

The increase of MVRS with body size observed in our comparative framework establishes a vulnerability limit whereby large-bodied species require large geographic areas to enhance their long-term viability and minimize their risk of extinction. Brown and

TABLE 1 Coefficient estimates, standard errors and confidence intervals of the linear regressions displayed in Figure 3 for the distribution-based MVRS and the synchrony-based MVRS when grouping the three realms

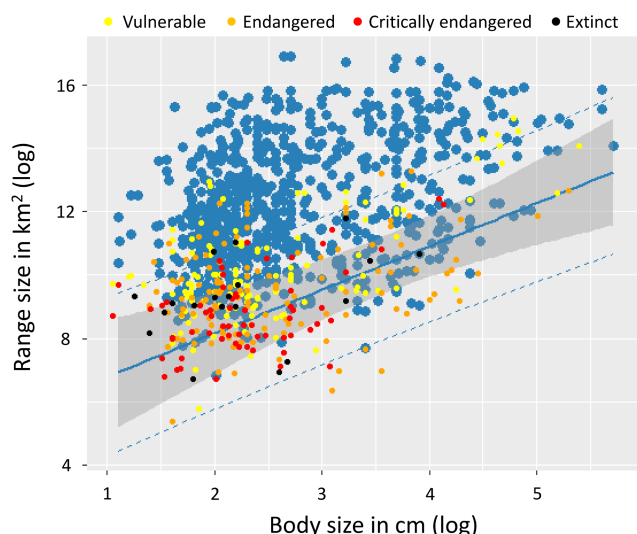


FIGURE 4 Range-body size relationship for the three realms studied (i.e. Palearctic, Nearctic, and Australian), and the corresponding distribution-based MVRs regression (blue line; see Figure 3). Species listed by the IUCN red list as threatened (i.e. vulnerable, endangered, critically endangered and extinct) are highlighted with different colours. Range sizes (in km^2) represent the best available estimates of species historical native distributions before major human impacts allowing to estimate the overall ability of the distribution-based MVRs to be used as a limit of inherent vulnerability. Note that the same pattern is observed when using only species listed with IUCN criteria a, c, d and e, excluding those listed with criteria (b) defined by narrow-range distributions. Also note that our study focuses on riverine species, not accounting for those restricted to lakes (see methods section), excluding threatened lacustrine species with narrow distributions.

Maurer (1987, 1989) proposed that this limit is a consequence of constraints on individual and population traits that restrict the species' abilities to obtain resources and occupy geographic space. For example, individuals of large-bodied species require more energy, which in turn indicates that the total energy available for the species is used to support fewer individuals (Blackburn & Gaston, 2001). This results in higher food requirements per individual and lower densities (Brown & Maurer, 1987, 1989; Kleiber, 1975). Consequently, by having more extensive geographic ranges, large-bodied species ensure enough resources to fulfil their energy demands, thus reducing the high probability of extinction associated with low population density (Diniz-Filho et al., 2005; Legendre et al., 2008; MacArthur & Wilson, 1967).

Large-bodied species' high dispersal capacities allow them to occupy large geographic ranges and forage widely to cope with temporal and spatial variation in resource availability (Brown & Maurer, 1987; Hein et al., 2012; Kleiber, 1975; Radinger & Wolter, 2014). This higher dispersal can stabilize local dynamics through the influx of immigrants (Abbott, 2011). However, dispersal is a 'double-edged sword' since it can also increase

the risk of global extinction by spatially synchronizing local populations (Abbott, 2011; Liebhold et al., 2004) over greater distances (Marquez et al., 2019). Thus, occupying broad geographic ranges allows large-bodied species to avoid synchronizing dynamics caused by their high dispersal. Besides, species with broad geographic range sizes are commonly associated with wider environmental niches and habitat-generalist strategies (Cardillo et al., 2019; Slatyer et al., 2013). Large species with a broad geographic range may also be less sensitive to climate-synchronizing drivers by occupying habitats with different environmental conditions (Loreau & de Mazancourt, 2008; Pandit et al., 2016) where populations display asynchronous dynamics.

At the other end of the body size spectrum, small-bodied species have low energetic requirements per individual, allowing them to maintain viable populations at low and high densities (Brown & Maurer, 1989). This allows to enhance long-term persistence in both small and broad geographic ranges (Gaston & Blackburn, 1996a; Figures 1a, 2). However, small-bodied species occupying small geographic ranges may still be more sensitive to catastrophic events, especially for species with low population sizes (Cardillo et al., 2008; Gaston, 1994; Lee & Jetz, 2011) and/or ecological traits related to high population synchrony (i.e. specialist-habitat strategies and restricted environmental niches; Liebhold et al., 2004; Slatyer et al., 2013; Cardillo et al., 2019). Still, small-bodied species with small ranges may display highly-abundant populations and short life histories, thus reducing the probability of local extinction (Gaston, 1994; Gaston & Blackburn, 1996a) and diminishing the scale of spatial synchrony (Liebhold et al., 2004; Marquez et al., 2019).

In addition to supporting the lower boundary of the range body-size relationship as an MVRs limit, we provide empirical evidence of a positive link between species body size and spatial population synchrony. Few intrinsic factors (or species traits) have been identified as drivers of population synchrony, with extrinsic factors (such as climate) being mainly supported in the literature (Bjørnstad et al., 1999; Hansen et al., 2020; Liebhold et al., 2004). This positive relationship between body size and synchrony matches the trend reported by Marquez et al. (2019), showing that species with slow life histories are synchronized over greater distances than species with fast life histories (since body size correlates with the slow-fast continuum of life history variation; Sibly & Brown, 2007; Jeschke & Kokko, 2009).

Space use by animals is strongly related to body size and has been a focal point of ecological research, leading to the formulation of scaling rules—power law relationships between body size and animal area use (e.g. Jetz et al., 2004). The positive relationships observed here between body size and both the

distribution- and synchrony-based estimates of the MVRS provided slope values close to 1. Previous studies reporting on the lower boundary of the range-body size relationship do not usually provide regression coefficients to compare with (see e.g. for freshwater fish Pyron, 1999; Rosenfield, 2002), neither does the only study we are aware of that explored the relationship between the scale of synchrony and body size (Toms et al., 2005). However, this slope value is similar to a pattern commonly observed between body mass or size and individual home range size on a log scale, usually indicating a home range scaling also close to 1 (e.g. Minns, 1995; Jetz et al., 2004 and see Tucker et al., 2014 and Tamburello et al., 2015 for examples on fish species). The body size-dependent energetic requirements have been suggested to explain both patterns, the body size scaling of individual home range size and the species' minimum viable geographic range size (Brown & Maurer, 1987; McNab, 1963). The increase of energetic demands and individual space needs with body size (Jetz et al., 2004; Kleiber, 1975) may scale up from individuals to populations and species resulting in similar slope values. Home range studies, and the finding of an allometric scaling close to 1 with body size, have been historically biased toward terrestrial species (but see Minns, 1995 and Tamburello et al., 2015), and it is unclear whether the factors driving home range size are the same for species in other environments. Our results for riverine fishes suggest that similar forces may be acting in both terrestrial and riverine ecosystems.

Beyond the theoretical importance of our results, the validation of the lower limit of the range-body size relationship has important applied implications. Perhaps most notably, this limit could help with the main challenges faced by extinction risk assessments (see Bachman et al., 2019; Cazalis et al., 2022 for more details in red listing challenges). For example, through the Barometer of Life initiative (Stuart et al., 2010), the IUCN is increasing the number of assessed species to evaluate the conservation status of global biodiversity and provide a more robust basis to inform conservation decisions. However, budgetary limits require the IUCN to prioritize efforts to improve its assessments' coverage, updating and consistency (Cazalis et al., 2022; Rondinini et al., 2014). Although our approach could not be directly integrated into new species assessments, as it does not conform to the Red List criteria already set (Cazalis et al., 2022), it would be possible to use the lower limit of the range-body size relationship as a "low-data approach" to rapidly identify potentially imperilled species (i.e. species below the distribution-based MVRS limit) and prioritize first assessments and reassessments of conservation status, and data collection for data-deficient taxa. The usefulness and validity of this "low-data approach" to prioritize species are

supported by recent studies showing that most species listed as threatened or extinct by the IUCN lie along the distribution-based MVRS (Le Feuvre et al., 2016; Newsome et al., 2020). We confirm this finding for freshwater riverine fish species, highlighting the inherent low viability of species near or below this boundary to range size reductions (e.g. habitat loss or climate change; Carvajal-Quintero et al., 2017).

Our study shows a strong congruence between a species-level macroecological pattern (i.e. the distribution-based MVRS) and a pattern arising from the temporal dynamics of populations on ecological time scales (i.e. the synchrony-based MVRS). Although we show clear congruence between the distribution- and synchrony-based MVRS, it is based on a limited number of species. Evidence for this similarity is limited to riverine fishes from temperate biogeographic realms, suggesting the need for additional investigations in other climatic and geographic contexts. Long-term climatically unstable regions (i.e. temperate) harbour lower proportions of small-ranged species because those species usually have narrow climatic niches and poor dispersal capacity, two factors that increased their extinction risk under past climate changes (Blanchet et al., 2013; Sandel et al., 2011). Besides, the higher resource availability and climatic stability of tropical ecosystems should allow for the maintenance of species with smaller range sizes, compared to their temperate counterparts, thus suggesting a different distribution-based MVRS pattern, at least in terms of the intercept parameter. This question remains to be formally tested. The triangular shape of the macroecological range - body size relationship has been widely documented across multiple vertebrate taxa (e.g. Newsome et al., 2020) and our empirical validation of the lower bound as a vulnerability limit is based on freshwater fish data across the world. Testing the validity of this limit in other major vertebrate groups offers exciting research opportunities to test the broader generality of our findings.

AUTHOR CONTRIBUTIONS

JC-Q, PAT and FV conceived the study. JC-Q and PAT implemented the statistical analysis and wrote the initial draft. All authors contributed to the final version of the manuscript.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

No new data were collected and used for this study. We obtained species body sizes and geographic range sizes from FishBase (<https://www.fishbase.in/>, Froese & Pauly, 2020) and Carvajal-Quintero et al. (2019), respectively; whereas the time series of species abundances come from the RivFishTIME database (Comte et al., 2021), which is publicly available through the iDiv Biodiversity Portal: <https://doi.org/10.25829/ividiv.1873-10-4000>. The data used to calculate the range-body size relationship and the code used to subset data and analyses is on Zenodo (<https://doi.org/10.5281/zenodo.6520116>).

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SUPPORTING INFORMATION

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