The neglected role of limiting factors in large-scale abundance patterns

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Abstract

The Law of the Minimum states that species' abundance at a location is limited by one single factor. If true, abundanceenvironment plots should take polygonal shapes constrained by an upper boundary representing the maximum abundance that the species can reach across the environmental gradient. Here, we examine the generality of polygonal plots in the literature and in observational data, and assess how often they are analyzed under the theory of ecological limitation. We also present a proof-of-concept of a method to identify polygon-shaped plots. We found polygonal plots in 76% of reviewed studies and in 73% of the 300 analyzed tree and bird species. We demonstrate that polygonal shapes with upper boundaries are prevalent in abundance-environment plots; yet they are rarely interpreted considering the Law of the Minimum. A wider acknowledgement of limiting relationships would improve our ecological understanding and estimation with further benefits to theoretical and applied ecology.

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SVP designed the study, with FAM, IMC and EA. FAM gathered and processed data, with SVP and IMC. FAM, SVP and IMC analyzed the data with aid from EA. All authors discussed results, contributed equally to paper writing and approved the last version of the manuscript.

Data sources

Forest Inventory and Analysis data (USDA Forest Service 2020 available in https://www.fia.fs.fed.us/ and Stanke *et al.* 2020); eBird data (Sullivan *et al.* 2009, available in https://ebird.org/home); Environmental predictors (Sheffield *et al.* 2006, available in http://hydrology.princeton.edu/data/pgf/v3)

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Abstract

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Introduction

Species' performance depends on multiple limiting factors that determine population size at a certain location and time. However, not all factors may operate simultaneously as it is sometimes assumed. For instance, a plant species could be limited by low temperatures in winter or in the coldest regions of its distributional range, while competition for light or the scarcity of a specific nutrient could set a limit to its abundance in regions characterized by milder climates. This idea was proposed about two centuries ago by Carl Sprengel (1828), who claimed that, even if most essential nutrients are abundant in the soil, the scarcity of a single critical nutrient will limit plant growth. This observation inspired *Liebig's Law of the Minimum* (LoM hereafter; Liebig, 1840), which states that one single factor sets limits to the maximum performance a species can reach at any given point in space and time.

The LoM has been recognized to be important for explaining ecological patterns (e.g. Didham, 2006; Hiddink & Kaiser, 2005; Huston, 2002), yet it has been underexplored. If as stated by the LoM, a unique environmental factor limits the abundance of a species at each location, then the relationship between the species' abundance and a single environmental factor should take a polygonal shape characterized by points scattered on the Y axis from zero to an upper boundary, resembling an envelope (Fig 1A). These polygon-shaped patterns could take a triangle (e.g. Carroll et al., 2011), a bell (e.g. de Boer et al., 2013) or other polygonal shape (Anderson, 2008). The upper limit of the polygonal point cloud would be defined by the locations where the abundance is limited by the environmental factor under study, while points below the upper limit corresponds

to locations where other factors act as limiting for abundance. This polygon-shaped pattern contrasts with line-shaped patterns generally expected by ecologists, which would imply that abundance at each location is determined by the interaction of different factors (Fig 1B).

Although the LoM was formulated about two centuries ago, its application to interpreting polygon-shaped patterns and the analytical solution to the estimation of the upper boundary are relatively recent. In 1996, Thomson et al. linked polygon-shaped plots to the LoM and highlighted the problem of analyzing them through classical correlational approaches. Shortly after, Scharf et al. (1998) and Cade et al. (1999) recommended quantile regression models (QR hereafter) as the most suitable statistical tool to estimate the upper limits of polygon-shaped plots. Unlike standard regression models that are based on central tendency, QR can estimate the response near the upper boundary of the abundance-environment point cloud, where the measured environmental gradient is the limiting one (Cade & Noon, 2003). In the last two decades QR have been increasingly used to assess the limiting effect of abiotic and biotic factors on the performance of different organisms (e.g. Bissinger et al., 2008; Brennan et al., 2015; Fornaroli et al., 2015; Jarema et al., 2009; McClain & Rex, 2001; Vaz et al., 2007). However, despite the rising awareness of the relevance of limiting relationships in ecology, we lack a quantitative perspective on their prevalence in nature and the assimilation of this body of theory by ecologists.

We aim to assess the generality of polygon-shaped patterns in abundance-environment relationships and to estimate the frequency to which these patterns are interpreted and analyzed in the context of ecological limitation. We hypothesize that polygon-shaped patterns are more common than it is generally recognized, and that the information contained in their upper limit is systematically neglected in ecological studies (Thomson et al., 1996). We also argue that, even when the structure of the data is identified as polygonshaped, the theory about ecological limitation is rarely discussed, and the connection with the LoM seldom established. First, we assessed the universality of polygon-shaped patterns in abundance-environment plots found in the literature. We also analyzed how frequently polygon-shaped patterns found in the literature are conceptually linked to the LoM and modeled through QR. Second, we assessed the prevalence of polygonshaped patterns in abundance-environment relationships across 186 tree and 114 bird species in North America. We used QR to estimate the number of species for which population size in the region studied is limited by water balance and energy, illustrating its application in the context of ecological limitation. Finally, we present a proof-of-concept of a procedure named *filling index* that aims to differentiate polygon-shaped point clouds from line-shaped ones.

We demonstrate that polygon-shaped patterns are pervasive in abundance-environment relationships, though they are rarely interpreted from a LoM perspective and analyzed with proper statistical tools. We hope that this work might lay the ground to help ecologists identify polygon-shaped patterns in their data and boost the incorporation of the theory of limiting factors in the area.

Materials and methods

Literature review

We searched the Web of Science for studies plotting the relationship between the abundance of an organism and an environmental factor at large geographical scales. We used the following terms: (Abundan* OR "population size" OR "population trend" OR density) AND (biogeography OR Macroecology OR "large extent" OR "large scale") on November 25th, 2020. Then, we selected literature from ecology and biogeography journals together with the multidisciplinary journal Nature (see the list of journals in Appendix S1), returning 4,700 articles (Fig 2A). From those, we conducted a title-based filtering that resulted in 744 publications (~18% of initial articles). Then, we reviewed the articles' main text in search for at least one plot relating the abundance of an organism (or an equivalent measure, such as population density) against a continuous environmental predictor. For those that showed the data points in the plot, we visually classified the shape of the abundance-environment relationship as line-shaped, polygon-shaped, or unclear – in cases where it was not possible to clearly identify the point cloud shape due to low sample sizes or representation means. We also identified the statistical method used to estimate the relationship and if there was any mention to Osted on 2 Feb 2023 — The copyright holder is the author/funder. All rights reserved. No reuse without permission. — https://doi.org/10.22541/au.167535023.30924400/v1 — This a preprint and has not been peer reviewed. Data may be prelimi

the LoM. Lastly, we recorded the taxonomic group, the habitat, and the geographical region of study.

Observational data

We analyzed two comprehensive datasets on the abundance of trees and birds to assess the prevalence of polygon-shaped abundance-environment relationships.

Tree dataset

Tree abundance data was obtained from the Forest Inventory and Analysis (FIA) program. The FIA program uses a systematic grid of permanent ground plots (approximately 1 plot per 24.28 km²) surveyed periodically across the entire United States (Burril *et al.*, 2018). We used the R package rFIA (Stanke *et al.*, 2020) to query the FIA dataset for tree species in all plots located in the continental United States, including Alaska. We obtained estimates of tree per acre (TPA) as a measure of each species' relative abundance sampled in the most recent inventory until 2016, the last year for which environmental data is available (see below). Finally, we dropped species with less than 150 observations to minimize type I error in QR (Cade*et al.*, 2005). Our final database comprised 401,033 observations belonging to 186 species (identified to the species level) and distributed in 89,369 ground plots. The database showed a range of 160 records (*Quercus incana*) to 19,763 records (*Acer rubrum*) per species.

Bird dataset

Bird abundance data was obtained from eBird, which is an online repository based on amateurs' records. Observations are reviewed by experts and are then aggregated to produce abundance estimates (Sullivan et al., 2009). We compiled all records falling within continental United States including Alaska, and excluded those i) with georeferencing errors, ii) not identified to the species level, iii) without abundance information available. We used a second filtering process to further homogenize the quality of observations. First, to reduce variation in birds' detectability, we only kept records with less than 5 hours of observation, less than 5 km of traveled distance, and 10 or fewer observers (as recommended in Strimas-Mackey et al., 2020). Second, we only considered data ranging from 1969 to 2016, which is the greatest recording effort period (Appendix S2) for which we have environmental data available (see below). Third, we used BirdLife species distribution maps (BirdLife International and Handbook of the Birds of the World, 2016) to exclude sightings of birds recorded outside their home and breeding areas (for example, in migratory routes). Fourth, we only kept those species that presented at least 150 records to minimize type I error in QR (Cade *et al.*, 2005). Lastly, we estimated relative abundances as the species' local abundance divided by the minutes of observation (i.e., abundance weighted by sample effort) and excluded outlier records (i.e., relative abundance values 100 times greater than the observed value in the 75th quartile). Our final dataset contained 49,835 records belonging to 114 bird species (an average of 437 records by species, with a minimum of 152 records for the species Passerculus sandwichensis and a maximum of 1,758 records for the species Zenaida macroura).

Environmental predictors

To estimate the limiting effect of environmental gradients on species maximum abundances, we used growing degree days (GDD – °C) to measure energy available; and the difference between precipitation and potential evapotranspiration (P-PET; Zang et al., 2020) as a proxy for water balance. To calculate these variables, we obtained temperature and precipitation data in raster format from the Global Meteorological Forcing Dataset for land surface modeling (Sheffield et al., 2006, available in http://hydrology.princeton.edu/data/pgf/v3) spanning from 1965-2016. For details on how we processed the environmental predictors, see Appendix S3.

Quantile regressions

We ran QR specified at upper quartiles to estimate the influence of GDD and water balance on the maximum abundance of each species. Parameter τ was defined for each species to be proportional to its prevalence across the study region (i.e., number of ground plots with positive abundance, so that the greater the number of observations, the better the estimate of the upper limit will be), so that $\tau = \frac{40}{\text{prevalence}}$ (Villén-Pérez *et al.*, 2022). Thus, τ parameter varied from 0.75 to 0.998 (Appendix S4 and S5). To account for possible non-

linear relationships, we defined both linear and quadratic terms for the environmental predictors. Prior to the calculation of quadratic terms, we z-standardized the original variables, transforming their absolute values to a scale in which the sample mean is 0 and the standard deviation is 1. This z-standardization allows us to compare the relative contribution of each independent predictor in the estimation of the response variable (see Carrascal et al., 2016 for a similar approach), as well as to reduce the problem of multicollinearity between linear and quadratic terms (Kim, 1999). To avoid negative abundance predictions, we summed a small number to all observed abundance values (half of the smallest observed non-0 abundance) and logit-transform them prior to applying QR. Then, we back-transformed the estimated values and subtracted the small number (Orsini & Bottai, 2011; Villén-Perez *et al.*, 2020). The analyses were performed in R (R Core Team, 2019) using package *quantreg*(Koenker, 2019). After fitting models, we estimated Variation Inflation Factors (VIF; Belsey, 1991) to assess the effect of multicollinearity and only accepted models with VIF < 10 (Neter, 1996) for each of the predictors (Appendix S4 and S5). We also compared each model with the corresponding null model through Akaike information criterion (AIC) and calculated the Evidence Ratio (ER), a measure of how much more likely models including predictors were better than null models (i.e., intercept-only models; Burnham & Anderson, 2002; Symonds & Moussalli, 2011).

Scale dependence in abundance-environment relationships

Since FIA is a systematic survey program, we considered the absence of a species' record in a plot as a true absence. Thus, we analyzed whether there is scale-dependence in tree abundance-environment relationships, that is, whether models for species with wide geographical or environmental range are better than models for species with narrower environmental or geographical range. To do that, we calculated Spearman correlations between model's [?]AIC and species' area of occupancy, extent of occurrence, and environmental breadth. The area of occupancy was estimated as the number of plots occupied by the species divided by the total number of plots in the database (89,369 plots). The extent of occurrence was calculated as the minimum convex polygon of all occurrences (MCP - IUCN, 2019) and given as the proportion of the extent occupied by each species divided by the total available geographical space. Finally, we calculated the environmental breadth as the proportion of the environmental space occupied by the species in relation to the total available environmental space by applying the Schoener's D index (Schoener, 1974; Broennimann *et al.*, 2012; Ronquillo *et al.*, 2020).

Filling index

To assess if abundance-environment plots show a polygon-shaped point cloud characterized by an upper boundary, we developed a procedure named*filling index*. This tool can be applied to any point cloud representing the relationship between two variables. Polygon-shaped point clouds are expected to present a continuum of points from zero-abundance to the upper boundary, i.e., a polygon filled with points (Fig 1A). Conversely, line-shaped patterns are expected to show empty space between the point cloud and the bottom of the plot - the X axis (Fig 1B). Overall, polygon-shaped point clouds are expected to have larger filling of the space, from zero-abundance to the upper boundary of points, than line-shaped point clouds.

To calculate the *filling index* for each plot, we first rasterize the observed point cloud, by adding a grid of 50x50 to the abundance-environment plot and identifying the cells overlapping with at least one data point (purple cells in Fig 3). Then, for each column of the raster, we identify the cells with the highest value of abundance (dark purple cells) and connect them to get the upper boundary of the data (dark purple line). Finally, we calculate the number of cells that included at least one observation in relation to the total number of cells bellow the upper boundary (i.e., sum of colored cells/sum of all cells bellow the line). The resulting *filling index* varies from 0 to 1, where a value of 1 indicates that the area below the upper boundary is fully filled and thus the plot represents a polygon.

To determine the probability of the observed point cloud being polygon-shaped, the observed *filling index* is compared with a null distribution of *filling indexes* resulting from 100 simulated line-shaped plots (Fig 3B). Line-shaped plots are generated to have the same sample size and environmental variable values (X-axis) than the observed data. Abundance values (Y-axis) are simulated to resemble the general trend of

the observed data, though following a line-shaped pattern, using the following procedure: i) we fitted a median QR ($\tau = 0.5$) to estimate the general trend of observed data; ii) we predicted the median abundance based on the observed environmental gradient ($\hat{Y}|X$); iii) we added variation to predicted median abundance (\hat{Y}) (we simulated variation under a normal distribution, with mean equals to zero and standard deviation equals to the square root of the maximum predicted abundance ($\sigma = \sqrt{\max(Y)}$)). Finally, we calculated the *filling index* of the simulated abundance-environment plot. We repeated the procedure 999 times, and then calculated the probability of occurrence of the observed *filling index* considering the distribution, i.e., probability is lower than 0.05, then we concluded that the shape of the observed pattern is significantly different from a line.

We tested the performance of the *filling index* procedure in differentiating line- and polygon-shaped patterns by applying it to simulated point clouds (Fig 3D-F and Appendix S6). To do that, we generated 100 bivariate plots with different number of observations (n=400 and n=100) and dispersal values ($\sigma = 1.1$ to simulate line-shaped patterns, and $\sigma = 2$ to simulate polygon-shaped patterns). Moreover, we tested the performance of the procedure using two alternative grid resolutions for rasterization (plots rasterized by 50x50 cells or 25x25 cells). Finally, we tested whether the *filling index* procedure described above correctly classified the simulated point clouds as line- or polygon-shaped under each sample size and grid resolution scenario (Appendix S6).

We also exemplified the application of the *filling index* with the observational data used in this study, thus assessing whether the point clouds for tree and bird species were polygon-shaped.

Results

Literature review

From a total of 744 title-based selected articles, 31 showed at least one plot representing abundanceenvironment relationships. Seven of these were line charts, while the other 24 were scatterplots showing the cloud of points. However, three of them were classified as unclear (Table S7, Appendix S7). In 16 of the resulting 21 articles (76%), the point cloud in at least one abundance-environment plot clearly showed a polygonal shape. Studies with polygon-shaped patterns had larger sample sizes (ranging from 13 - 1370) than articles without them (ranging from 10 - 91). Of these 16 studies, only one used QR to estimate the relationship between abundance and the environmental factor under study (Table S7, Appendix S7). None of the articles mentioned the LoM. Polygon-shaped patterns were found in terrestrial and marine vertebrates (6 studies) and invertebrates (8 articles), as well as in freshwater and marine algae (2 articles), across different biogeographical regions (Fig S7, Appendix S7).

Species response to environmental gradients

GDD and water balance impose a limit on the maximum abundance of most North American trees (Fig 4; plots for all the species are available in Appendix S8). In 74% of tree species, including the predictors GDD and water balance were at least 100 times better supported by the data than the null model (see Appendix S4). GDD had significant limiting effects on 73 tree species (p-value < 0.05). Likewise, water balance was significantly limiting in 72 species (p-value < 0.05). Model likelihood, measured by [?]AIC, was higher for species with larger area of occupancy (Spearman r = 0.79, p<0.001), larger extent of occurrence (Spearman r = 0.52, p<0.001), and larger environmental breadth (Spearman r = 0.36, p<0.001; Fig S8, Appendix S9).

In 83% of bird species, including GDD and water balance predictors improved QR models by a hundredfold or more (see Appendix S5). GDD and water balance had a significant limiting effect on the maximum abundance of 46 and 33 bird species, respectively (see Fig 5 and Appendix S10 - S11).

Prevalence of polygon-shaped patterns in birds and trees

The *filling index* procedure showed that abundance-environment plots were polygon-shaped for 73% of North American tree and bird species. From the 186 tree species, 65% of abundance–GDD plots and 64%

of abundance–water balance plots were polygonal (i.e., the observed *filling index* was significantly higher than the line-shaped null model; Appendix S4). Moreover, 88% of bird abundance–GDD plots and 87% of abundance– water balance plots showed polygonal shapes (Appendix S5). Plot *filling index* es were positively correlated with sample size (trees: Spearman $r = 0.82 \pm 0.01$, p<0.001; birds: Spearman $r = 0.58 \pm 0.02$, p<0.001).

Performance of the Filling index Procedure to identify polygon-shaped patterns

The filling index procedure classified correctly 100% of polygon-shaped simulated plots. Its performance remained stable when applied to different sample sizes and using different grid resolutions. Likewise, the filling index procedure classified correctly an average 97% of line-shaped simulated plots with larger sample sizes, but showed a poor performance with smaller sample sizes (see Appendix S6 for details).

Discussion

The LoM as a conceptual framework to analyze abundance patterns in ecology and biogeography is promising, but largely underutilized. There is a striking contrast between the high prevalence of empirical polygonshaped patterns in abundance-environment relationships (i.e., found in 76% of reviewed studies and an average of 86% of analyzed species) and the frequency at which these relationships are interpreted from a LoM perspective (0% of reviewed studies). Such disconnect raises several questions: what challenges a more widespread use of the LoM? What are the alternatives and challenges to analyzing and interpreting polygonal abundance-environment relationships? What can be learnt by analyzing abundance-environment relationships from a LoM perspective? Our results illustrate with two environmental variables how the LOM can provide a quick way to identify the limiting effect of environmental factors for any taxa group, which has key implications for ecological inference.

For decades, ecologists have focused on abundance-environment relationships from various perspectives: population ecology (e.g. Rosenzweig & Winakur, 1969), habitat selection (e.g. Holt, 1987; Pigeon et al., 2016), or biogeographic (e.g. Dallas et al., 2017; Sagarin & Gaines, 2002). Through a literature review, we found that most abundance-environment plots are characterized by polygon-shaped patterns (76% out of 21 studies). However, the vast majority of these relationships were not approached statistically as limiting relationships (only one study used QR). Moreover, none of these studies discussed the limiting ecological relationships implicit in their polygon-shaped patterns considering the LoM. The implications are clear. Ecologists have very often ignored limiting responses in the distribution of abundance (Konrad *et al.*, 2008; Greenberg*et al.*, 2015; Stralberg *et al.*, 2018) by implicitly assuming the simultaneous influence of different environmental factors in each given site rather than acknowledging that the maximum reachable abundance would be locally limited by only one of these factors.

We identify three major challenges that may hinder a more widespread application of the LoM perspective to understand ecological patterns. First, we uncover researchers' biases towards using standard regression models that estimate measures of central tendency responses (Lancaster & Belyea, 2006). This tendency could be due to researchers not being concerned with inspecting the shape of bivariate relationships between abundance and environmental factors, which would also explain why 23% of 31 reviewed studies did not show a point cloud in their plots. Alternatively, researchers may have explored abundance-environment plots, found polygonal point clouds, and assumed that fitting the central tendency amidst the point cloud would characterize accurately the relationship and that deviations from the mean response are the consequence of sampling error (Lancaster & Belyea, 2006). This assumption overlooks the ecological significance of the upper limit in the cloud of points (Thomson *et al.*, 1996), which is explicitly accounted for by QR.

To overcome this bias, we encourage ecologists to thoroughly inspect their abundance-environment plots (Thomson *et al.*, 1996) with the novel *filling index* procedure provided here (the access code and a database example in Appendix S12). Although this method is presented here as a proof-of-concept and may require further evaluation, it has proven to be useful in detecting polygon-shaped point clouds in the simulated data. To our knowledge, this is the first procedure that identifies polygonal patterns with upper boundaries (but see an alternative approach not focused on the upper limit in Milne et al., 2006). When ecologists come

across polygon-shaped patterns, they should consider the role of limiting factors together with the theory and the techniques associated to it, since a misinterpretation of polygon-shaped data (i.e. estimating central tendency rather the maximum limit of abundance) could lead to incorrect inferences about abundanceenvironment relationships. We expect that this tool, together with the empirical evidence unveiled here, will manifest the pervasiveness of limiting relationships in ecology and promote the usage of the LoM framework. Progressively adopting in a data exploration stage, the practice of assessing the shape of point clouds may help ecologists correct the bias found in the literature towards expecting line-shaped patterns and a using regression techniques based on mean estimates.

A second barrier as to why the LoM perspective is not adopted is the general dismissal of the theory behind limiting relationships in ecology and biogeography. Polygonal relationships and QR are not linked to the LoM even in research acknowledging the limiting nature of different predictors on abundance. We recognize that several alternative methods can accommodate non-stationarities in the importance of different factors along gradients, in the magnitude and direction of effects along gradients or across geographical spaces (i.e. Geographically Weighted Regression – GWR; Fotheringham et al., 2002; Generalized Additive Models for Location, Scale and Shape – GAMLSS; Rigby & Stasinopoulos, 2005; Rollinson et al., 2021). These particularities may be better fit to respond to a different set of questions. For instance, GWR is applied to assess the spatial heterogeneity in the relationship between species richness and climate variability by identifying regions in which some environmental factors are more relevant than others (e.g. Hortal et al., 2011). However, QR is the only statistical method that accounts for non-stationarity along a bivariate relationship, which is the central point of the LoM. Thus, if one aims to model the effect of an environmental gradient on a particular part of the distribution of the response variable, in our case the upper quantiles or the maximum abundance of a species, QR seems best equipped to provide accurate answers (Kneib, 2013).

Finally, a more widespread application of the LoM is hampered by data availability. The lack of large enough abundance samples hinders capturing meaningful clouds of points and estimating their upper limit (Cade et al., 1999). For example, only 9 out of 24 reviewed studies containing at least one plot, encompass sufficiently large sample sizes (> 100 observations) to estimate upper limiting responses using QR with a reasonable Type-I Error (τ [?] 0.90; Cade et al., 2005). Moreover, we found that identifying polygon-shaped patterns were positively related with sample size in trees and birds in the USA. Our empirical examples encompass some of the best sampled organisms and regions worldwide, but the exploration of polygon-shaped patterns in other regions and taxa would require good quality abundance data sampled across large spatial (or temporal) scales (Howard et al., 2014). These data requirements may be better fulfilled by institutional programs dedicated to the systematic sampling of a group of organisms such as FIA, whose data demonstrated to be better fitted for QR models than eBird data (i.e., evidence ratios, were on average higher for trees than for birds: See Appendix S4 and Appendix S5). Systematic sampling at large spatial scales may sometimes require international coordination, but abundance data may not be costlier to collect than presence data in terms of time and number of collectors (Gibbons *et al.*, 2007). We expect that the increased availability of large-scale data on species abundances will foster the application of LoM-based approaches in the near future.

Here we found polygon-shaped patterns in most American birds and trees (Appendix S8 and S10) showing the constraints imposed by GDD and water balance in their maximum abundances (see Fig 5-6; Cade & Noon, 2003). Contrary to what ecologists may intuitively think, the LoM does not dismiss that abundance patterns depend on a range of environmental conditions and resources. In fact, it considers these multiple limiting factors, that is, the variation below the upper boundary is explained by situations when factors other than the gradient under study limit abundance. But the LoM emphasizes the maximum abundance reachable in each point of the gradient under study which is limited by it (Hiddink & Kaiser, 2005).

The potential applications of the LoM approach are manifold because knowing the maximum number of individuals of a species that a given locality or region can support is fundamental to making informed decisions on wildlife and forest management. First, it is key to predict ecological shifts driven by environmental disturbance (e.g. algal blooms; Carvalho et al., 2013), potential abundance shifts caused by climate change

(e.g. Villén-Perez et al., 2020), or it could complement forecasts of species invasions induced by any type of environmental change (e.g. Bezeng et al., 2017). Moreover, reintroduction, restoration, and rewilding programs may also benefit from accurate estimates of the maximum number of individuals potentially supported by a system (Johnston *et al.*, 2015). The LoM approach could also be applied to identify limiting factors in populations and/or determine whether a given habitat could support a viable population (See *et al.*, 2021). Finally, the LoM approach can be used to estimate the carrying capacity of managed systems such as forest plantations (e.g. Farias et al., 2021) or fishery stocks (e.g. See et al., 2021; Sweka & Mackey, 2010). Overall, the LoM approach can help both to design mitigation actions against global change impacts on biodiversity and to optimize production systems.

We advocate using QR and the LoM to model maximum potential abundances and interpret polygon-shaped patterns (see also Villen-Perez et al., 2020), acknowledging that its potential to ecology goes far beyond. For instance, it would be interesting to formally examine the role of the LoM and niche theory. Does the maximum potential abundance that species can reach at each given temperature value reflect species' fundamental niche respect to temperature (Villen-Perez et al., 2020)? If this is validated, it would set new standards in ecology, which currently assume that distribution data only inform the realized niche of the species and the fundamental niche can only be assessed experimentally (Kearney & Porter, 2009; Soberon, 2010). Distribution data may reveal more information than previously acknowledged, and the LoM approach could enable the quantification of the fundamental niche for a massive number of species and complement the experimental approaches.

Understanding abundance-environment relationships is an integral part of ecology, and it has the potential to aid at planning species conservation and habitat management (Wilson *et al.*, 2005), or for predicting responses to global change (Ehrlen & Morris, 2015). However, this is only possible when ecological data are correctly interpreted (Thomson *et al.*, 1996). Here we show that species' abundance patterns along environmental gradients often adopt polygonal shapes, with an upper limit indicating consistent limiting responses. These patterns conform to the LoM and can be analysed using QR. Despite the many decades of studying abundance-environment relationships, there is still room for a paradigm shift in how we analyze, interpret, and infer such relationships. The LoM as a conceptual framework and QR as an analytical tool offer a promising research avenue in need for further exploration.

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Conflicts of interests

The authors declare no conflicts of interest.

Figures and figure captions



Figure 1: Hypothetical relationships between abundance and environmental gradients. A) Polygon-shaped pattern characterized by an upper boundary (solid line) whose slope differs from the mean (dashed line). B) Line-shaped pattern characterized by a homoscedastic distribution of data around the average trend.



Figure 2 : Design and results of the literature review on the generality of polygon-shaped patterns and their analysis and interpretation. A) Processing steps in the literature review. B) Number of articles that fulfil each step. Percentages are relative to the previous category, as shown by dashed lines.



Figure 3: At the upper panel, description of the framework used to calculate plot's filling index es. Logic behind the *filling index* procedure, which tests whether the observed plot show a polygon-shaped pattern when compared to simulated line-shaped plots. A) Calculation of the observed plot filling index. First, the abundance-environment plot is rasterized, indicating whether there is one or more data points within the range of each cell (purple cells). Then, the upper boundary of the point cloud (purple line) is defined by connecting the upper cells of each raster column (dark purple cells). Finally, the rate of occupation is calculated below the upper boundary (i.e., sum of purple cells/sum of all cells below the purple line). Values of 1 indicate that the area below the ceiling is fully filled by data points. B) Generation of a null model based on 999 simulated line-shaped point clouds. The line-shaped simulations use the same environmental data and sample size as the observed data, and resemble the general trend of the observed plot. The *filling index* is calculated for each simulated distribution as described in A. C) Statistical significance of the observed filling index is different to the distribution of the simulated line-shaped patters. The probability of the observed *filling index* (purple line) is greater than the simulated ones (blue distribution) and is calculated at a statistical significance of p < 0.05. At the lower panel, exemplification of the performance of the *filling* index to identify polygon-shaped patterns in two simulated plots: polygon-shaped plot (D), and line-shaped plot (E). For more details on evaluation methods and results see Appendix S6.



Figure 4 : Examples of polygon-shaped plots found in USA trees. Black lines represent the maximum potential abundance of the species estimated across GDD (A-D) and water balance (E-H) gradients, using quantile regression models defined at upper percentiles. The plots in which each species was sampled are represented on the US map.



Figure 5 : Examples of polygon-shaped plots found in USA birds. Black lines represent the maximum potential abundance of the species estimated across GDD (A-D) and water balance (E-H) gradients, using quantile regression models defined at upper percentiles. The plots in which each species was sampled are represented on the USA map.