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Integrating gradient with scale in ecological and evolutionary studies

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Abstract

Gradient and scale are two key concepts in ecology and evolution that are closely related but inherently distinct. While scale commonly refers to the dimensional space of a specific ecological/evolutionary (eco–evo) issue, gradient measures the range of a given variable. Gradient and scale can jointly and interactively influence eco–evo patterns. Extensive previous research investigated how changing scales may affect the observation and interpretation of eco–evo patterns; however, relatively little attention has been paid to the role of changing gradients. Here, synthesizing recent research progress, we suggest that the role of scale in the emergence of ecological patterns should be evaluated in conjunction with considering the underlying environmental gradients. This is important because, in most studies, the range of the gradient is often part of its full potential range. The difference between sampled (partial) versus potential (full) environmental gradients may profoundly impact observed eco–evo patterns and alter scale–gradient relationships. Based on observations from both field and experimental studies, we illustrate the underlying features of gradients and how they may affect observed patterns, along with the linkages of these features to scales. Since sampled gradients often do not cover their full potential ranges, we discuss how the breadth and the starting and ending positions of key gradients may affect research design and data interpretation. We then outline potential approaches and related perspectives to better integrate gradient with scale in future studies.

KEYWORDS

adaptive sampling, macroecology, outlier analysis, partial versus full gradient, sampled versus true gradient, space, time

INTRODUCTION

In ecological and evolutionary (eco–evo) studies, scale usually denotes the spatial size or temporal duration of observations, while gradient often indicates the range (or breadth) of a variable or a set of variables. A given scale can include different known and unknown (latent) gradients, while a given gradient for a specific variable (e.g., pH) can exist across different scales. Although scale and gradient are often positively correlated, these concepts are fundamentally different and represent very different ecological attributes. Importantly, scale often appears to be associated with many observed eco–evo patterns, but underlying gradients are the root causes that affect how a species or community responds to environmental changes (Box 1).

To date, the role of scale in governing and explaining variations in many observed spatial and temporal eco–evo patterns has been well recognized (Levin, 1992; Wu, 2004). However, the underlying environmental gradients across varying scales have long been underappreciated (Fox et al., 2011), as demonstrated by the much greater proportion of eco–evo studies focusing on scales than on gradients (Figure 1, Appendix S1: Table S1). In fact, even in studies where both scale and gradient appear in the keywords or abstracts, most of them only examine the role of scale but do not examine the role of gradient (Figure 1). One potential reason for the underappreciation of the gradient in eco–evo studies in previous research is the unconscious perception of scale and gradient as interchangeable. Subsequently, much of the research conveniently considered scale as the cause of observed patterns without examining changes in environmental gradients with scale. This interchangeable use of scale and gradient could be problematic because the relationships between the two concepts can vary drastically across different habitats or landscapes and are not

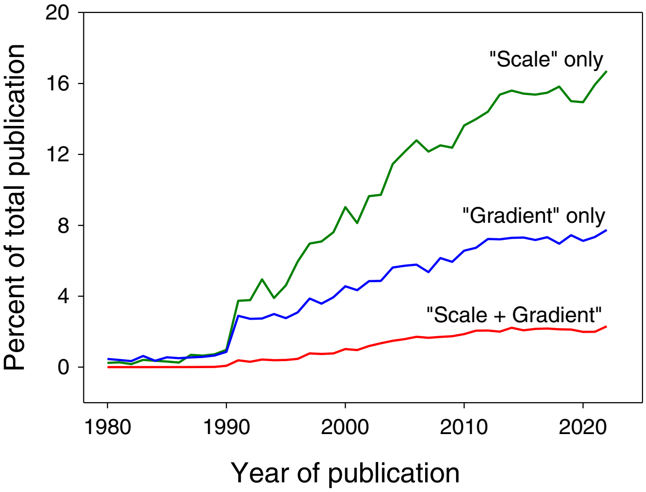

FIGURE 1 Comparison of the proportion of ecological/evolutionary (eco–evo) studies with scale, gradient, or both terms in keywords and topics, respectively, based on Web of Science query of peer-reviewed literature within the topic area of "Ecology" (total number of publications 1980–2022 = 597,369, total number of publications mentioning gradients = 32,455, and total number of publications mentioning both scale and gradient = 3613). The proportion of studies that address both scale and gradient is very low (mean = 1.08%). Curves indicate the appearance of the term scale and gradient in titles, keywords, and abstracts. Most scale-related studies only mention the term gradient but do not actually analyze the underlying gradients (see also Appendix S1: Table S1).

BOX 1 Scale and gradient are fundamentally different concepts that are each composed of different components.

Scale = Extent + Grain size.

Extent refers to the area or the amount of time covered in the study (e.g., a spatial extent of a state/province, a country, or a global analysis; a temporal extent of a month, a year, or a decade). Grain size refers to the resolution at which the data were collected. For example, the spatial resolution (i.e., grain size) may be 1 m^2, 100 m^2, or 100 km^2, while temporal resolution (i.e., grain size or time step) may be 1 min, 1 day, or 1 year. In this paper, we focus primarily on the "extent" aspect of scale. In some cases, a scale can also be organizational (e.g., individual, population, ecosystem) or taxonomical (genus, family, class).

Gradient = Breadth + Start/end points + Steepness.

Breadth indicates the range of the gradient considered (e.g., a temperature gradient from 10°C to 20°C). Steepness indicates the rate of change of a gradient across space or over time (e.g., a change of 1°C/100 m in elevation). Gradient positions (start/end) are also key features to be considered.

The terms we used to describe the formulated definitions for scale and gradient are by no means inclusive—they only include key features. In general, examining results across different scales can illustrate the patterns of an eco–evo phenomenon, but examining the gradients can help elucidate the processes underlying such patterns.

always linearly related (cf. short environmental gradients across vast Sahara versus longer gradients on a tropical mountain in a small geographic area). Moreover, the indistinction between gradient and scale may have led researchers to miss important underlying mechanisms of many observed eco–evo patterns.

Field and experimental findings often depend strongly on the range and the start/end positions of the surveyed environmental gradients (Figure 2). For various reasons, most gradient- and scale-related studies only sampled parts of the entire potential gradient (Gaston et al., 1998). Yet observed patterns often depend on the position (section) and length of the sampled gradient relative to its full (or global) range (He et al., 2013; Kreyling et al., 2018). As a result, different studies that focus on similar questions can reach diverse or even contradictory conclusions (Figure 2) (Fei et al., 2018; Lyons & Willig, 2002). This problem can be even more complicated if the relationship between the dependent and independent variables is nonlinear, resulting in contradictory conclusions at different scales that are often considered a “paradox.”

Although the role of a gradient’s range has long been recognized, it has rarely been explicitly stressed and discussed. It is even rarer to consider the start/end positions of a sampled gradient range when inconsistent results are found. Predictive modeling or mapping informed by data that do not represent a full gradient can lead to erroneous results. For example, machine learning methods, such as random forest algorithms, are often used to make large-scale (e.g., landscape, global) maps of ecological variables. However, machine learning and other supervised classification methods cannot be extrapolated outside of the region (in physical or variable space) where data are used to train the models, making model assessment a near-impossible task (Meyer & Pebesma, 2022) if data covering a sufficient range or breadth of a target environmental gradient are unavailable. Furthermore, the results and explanations regarding the latitudinal and elevational diversity patterns are frequently influenced by the latitudinal and elevational range and start/end positions (surrogates of underlying gradients), which vary dramatically among mountains around the globe (Guo et al., 2013; Nogues-Bravo et al., 2008). In addition, Udy et al. (2021) recently reported that ecological heterogeneity (a factor strongly related to gradients) can better predict global species richness patterns than area (i.e., a component of spatial scale) (Ricklefs, 2004).

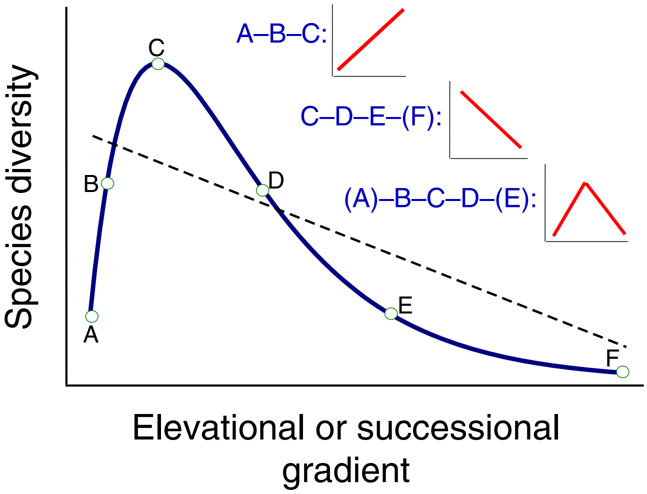

FIGURE 2 Hypothetical example showing how sampling partial gradients, rather than the full gradients, can change the perceived patterns of diversity (e.g., positions A–C vs. C–E). Here, elevation or succession is used as a surrogate of an underlying gradient and the observed patterns of diversity depend on both the position (section) and the length of the sampled gradient. “^” indicates a unimodal (hump-shaped) pattern. The dashed lines indicate relationships when all data points are fitted with linear regression.

Clear distinctions between scale and gradient are underconsidered, and most scale-dependency studies do not specifically stress the underlying importance of environmental gradients associated with scale. Considering the imbalance in the literature regarding scale versus gradient, we believe it is necessary to highlight major features of gradients in both field and experimental settings, that is, range, position, start/end points, and steepness (Sandel & Smith, 2009). In what follows, we unpack the differences between gradient and scale and then discuss the importance of gradient breadth, position, steepness, and their interactive effects. In so doing, we provide an extensive critical review of the relationships between scale and gradient in the contexts of the gradient’s breadth and start/end points. Finally, we outline how ecologists could improve sampling design and more effectively incorporate gradient and scale into their research.

GRADIENT VERSUS SCALE

An environmental gradient represents the continuous change, either smooth or abrupt, in environmental conditions through space or time. A gradient can be physical (e.g., precipitation, nitrogen, disturbance) or biological (e.g., the intensity of competition or grazing). Scale in part refers to the extent of a study across space, over time, or of biological organization (Box 1). Both terms can range from local to global extents. However, as we outline in detail in what follows, the two terms are clearly different and should not be used interchangeably. After all, it is the range of the underlying gradient, not the spatial–temporal scale, that provides an effective space for individual organisms to interact with each other and respond to environmental changes (Luck & Wu, 2002).

First, the extent (spatial or temporal) of a scale and the range of a gradient are not always linearly correlated. Even when correlated, the strength of the correlation between them may vary across latitudes and among different regions (Figure 3) (Schweiger et al., 2016). The same length of gradient (i.e., range) can often be found across small but more heterogeneous scales as across large yet less heterogeneous scales. Many environmental variables, such as nitrogen (N), water, and their changes (gradients), are not always scale-dependent, a fact long recognized by ecologists (He & Bertness, 2014; Sandel & Smith, 2009). Therefore, although certain correlations between scale and gradient are widely observed, the range of a gradient and the spatial–temporal scale (extent) are not always interchangeable.

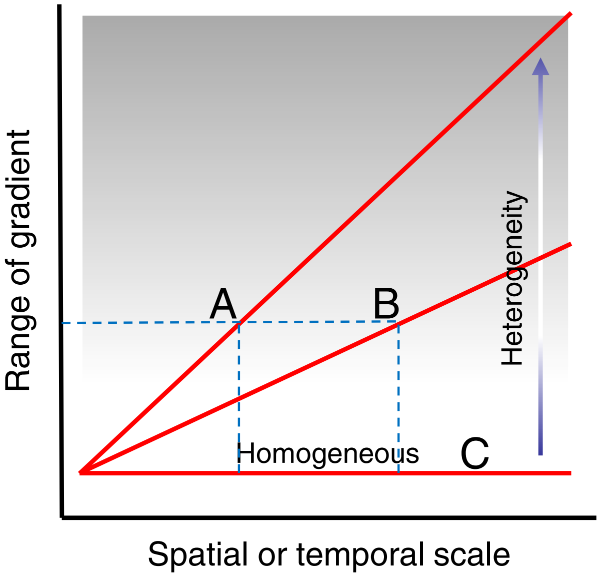

FIGURE 3 The relationships between spatial–temporal scale and environmental gradient within a heterogeneous (A and B) versus homogeneous region or habitat (C). The same length of the gradient can be achieved across smaller but more heterogeneous scales (A) than larger but less heterogeneous scales (B). In natural settings, relationships between gradients and scales are likely to be nonlinear (especially A and B), and the slopes will vary with the steepness of the gradient. For example, the underlying environmental gradients along a 200-m elevational transect on a steep tropical mountain would be much longer than a 200-km transect over a flat region such as the Great Plains in the United States.

In relatively homogeneous habitats, observed patterns may be less scale-dependent than in heterogeneous habitats. For example, many environmental gradients across the entire Sahara may be narrower than those across a small tropical mountain. For this reason, the degree of habitat heterogeneity should be considered for scale-dependent comparisons (Figure 3). Another example is the commonly documented positive species–area relationship, one of the major ecological "laws" (Rosenzweig, 1995) describing how a key ecological variable (i.e., species richness) changes with scale (i.e., area). This species–area relationship is valid only when comparing habitats/areas with more or less similar environmental conditions (e.g., islands with similar climates) and could fail when comparing tropical islands with Arctic islands or rainforest patches with Saharan deserts.

Furthermore, vertical gradients (e.g., temperature) from the bottom to the top of a tropical mountain could well cover that of the full latitude range (0–90°) on Earth; over the same spatial scale or extent, tropical mountains cover a longer, steeper, and more complete temperature gradient than boreal or temperate mountains (Figure 4). This regional difference in the velocity of environmental gradient change raises a question about sampling

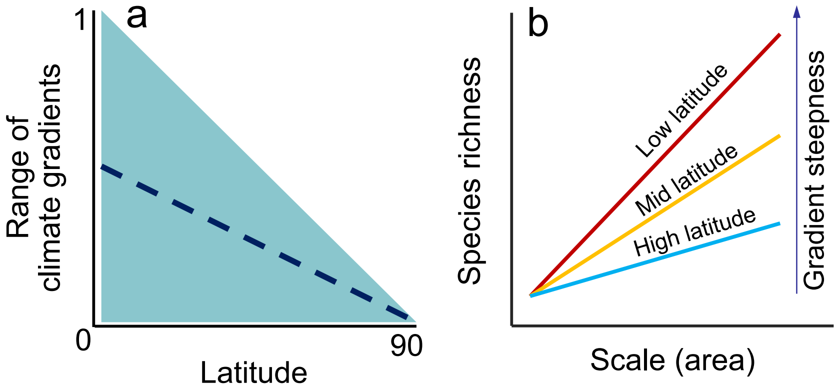

FIGURE 4 (a) Environmental gradients are generally steeper and broader at lower than at higher latitudes (as indicated by the dashed line) mostly due to the greater variation in temperature and precipitation along elevational gradients on tropical mountains than those in polar regions (see also Figure 3). In other words, tropics can have both hot (lowlands) and cold places (high altitudes) while high latitudes only have cold places. (b) Correspondingly, across the same spatial scales, species richness increases faster at low latitudes than at high latitudes.

intensity. Coarse sampling over a large space could miss unexpected species responses across critical portions of the gradient between sampling locations, but intensive sampling over a small space may not catch larger-scale patterns or encompass longer environmental gradients (McGeoch & Gaston, 2002; Schweiger et al., 2016). Therefore, a balanced sampling framework taking into account both spatial–temporal extents and sampling intensity/costs is required (Fortin et al., 2005; Stewart & Frank, 2008).

Second, the relative importance of different gradients may vary with scales. For example, most biotic gradients (e.g., competition, predation) may be relatively more important at local scales than at larger scales, but abiotic gradients (e.g., temperature, precipitation) are important over both small and large scales (King et al., 2021). Earlier research (i.e., before the wide application of remote sensing and other technologies) might have overwhelmingly focused on small-scale patterns and phenomena because of the expensive labor cost associated with data collection over larger areas/scales (Troudet et al., 2017). In population biology, great emphasis has been placed on growth models (e.g., birth vs. death rates in early expansion stages vs. long-term fluctuations) of a population after establishment (Yoshinaga et al., 2001); yet in geology and paleobiology, researchers focus more on examining the history of a given taxon often at the species level or above. After all, more than 99.99% of species that once lived on Earth have gone extinct after going through the rising, mature, and falling phases (Brown, 1995; p. 160).

Third, while there is no single "correct" scale to describe ecological phenomena (Levin, 1992), there can be critical "thresholds" or "tipping points" along environmental gradients at which drastic ecological changes may occur. Such tipping points can occur over both space and time. For example, certain levels of nitrogen and water (both too low and too high) could lead to catastrophic responses of target species (e.g., crops) and even cause the total collapse of an entire system. Considering ecosystem thresholds are especially important under ongoing global change (e.g., nitrogen pollution or eutrophication), nitrogen (and some other elements) must be kept below a certain level (Carpenter et al., 1998). In another example, Stuart-Haëntjens et al. (2015) showed that, in an upper Great Lakes forest ecosystem, productivity declined nonlinearly with disturbance and then remained stable until 60% of the total tree basal area had senesced.

Fourth, defining small versus large scales depends on the type of organisms (e.g., those that have different body sizes or lifespans) and the specific regions (e.g., tropical vs. temperate). For example, studies of the population dynamics of an ant species require drastically less spatial extent than that of an elephant species. For another example, over the same spatial scale, studying the diversity patterns of all plants in a tropical region would require much more effort and time than studying all plants in a temperate region because tropical regions generally have much higher diversity and environmental complexity.

Finally, environmental gradients are different from habitat heterogeneity. The former describes the directional (from low to high) variability of one or multiple variables from one point to the next within the habitat (Grünbaum, 1998), while the latter measures the range of a variable (e.g., competition, temperature, nitrogen) across all possible points within a habitat (Li & Reynolds, 1995).

On a related note, the term "diversity gradient" should only be used in biodiversity experiments when ecosystem properties such as productivity are tested against experimental treatments of different numbers of species (e.g., 0, 2, 4, 8, 16, 32, …). In natural systems where species richness does not vary systematically, field studies could adopt the gradient design where diversity is used as an independent variable (Kreyling et al., 2018).

IMPORTANT CONSIDERATIONS OF GRADIENT

Given the clear distinction between "scale" and "gradient," there is a need to examine closely the key elements of what constitutes a "gradient" that have been largely underdiscussed in the literature (Figure 1, Appendix S1: Table S1). In the following sections, we provide detailed and deepened discussions on the breadth (range, extent), position, and steepness of gradients. We further discuss the interactions between different gradient features and their applications in eco–evo samplings.

Gradient breadth (range)

The interpretation of many observations in eco–evo research depends strongly on the range of underlying gradients (Mackey & Currie, 2001). A classic example of how investigations focused on different parts of a gradient could lead to different conclusions is the contrasting productivity–rodent diversity relationships in the southwestern United States. In two separate studies, both positive (Brown, 1973) and negative relationships (Owen, 1988) between evapotranspiration and rodent diversity were found. However, when plotting rodent diversity along a combined evapotranspiration gradient that spanned both investigations, a unimodal pattern emerged (Rosenzweig, 1992). In a meta-analysis synthesis, He et al. (2013) detected significant shifts in plant interactions toward facilitation or decreased competition with increased length of a stress gradient. Another example is the commonly cited community allometry relationship. Most previous allometry studies did not include very large and/or very old trees in their regression analyses (thereby losing part of the full gradient) (Duncanson et al., 2015), leading to the conclusion that large trees always produced more seeds/fruits. However, a recent study with a large representation of large trees showed that fecundity may plateau at intermediate tree size (Qiu et al., 2021). Young trees or seedlings under different levels of stress may also have quite different allometric relationships (Chen & Li, 2003). Thus, conclusions regarding tree allometries are impacted depending on whether very small or very large trees are included in the analysis.

Similarly, for a given latitudinal range, whether a latitudinal pattern for a specific responding variable such as diversity or body size can be detected (and if so in what shape) may depend on which section of the latitudinal gradient is used. Results may also vary depending on which continent is chosen for investigation given the vast difference among different continents in many aspects (Guo et al., 2022; Rosenzweig, 1992; Stevens, 1989). The range of the gradient under study must be long enough to show detectable biological or ecological responses so that true patterns can be identified. If the range is too short, none or only a portion ("+" or "−") of the true pattern (e.g., unimodal) would be detected, resulting in misleading conclusions. For example, Bergmann's rule that the body sizes of the same species are larger in colder environments and Rapoport's rule that the latitudinal ranges of plants and animals are smaller at lower latitudes (Adams & Church, 2008; Brown, 1995; Lane, 2007), even if they exist, would be difficult to detect if the range of the elevational or latitudinal gradient under observation were too short (Lane, 2007; Willig et al., 2003).

To examine the generality of Rapoport's rule, Gaston et al. (1998) compiled latitudinal distribution data for 37 taxa of varying sizes both on continents and in oceans (for details about the data, see their table. 1). They found evidence that most marine organisms in the dataset did not support Rapoport's rule even with broad latitudinal ranges. We reanalyzed their data on terrestrial organisms and found that, regardless of the taxonomic group and their sizes, studies covering greater latitudes were more likely to support Rapoport's rule than those covering shorter latitudes ($t = 2.392$, $\mathrm{df} = 38$, $p = 0.0218$).

Furthermore, in biodiversity experiments, the range (e.g., 4, 16 vs. 32 species) and start/end points (e.g., 0–8 vs. 6–32 species; see next section) of plant species to be planted play an important role in determining the final observed patterns (e.g., the diversity–productivity relationships) (Gonzalez et al., 2020; Wang et al., 2021). Some of the differences in observed results are due to the nonlinear responses of productivity to planted diversity levels, and productivity could even drop if too many species were planted in small experimental plots, possibly due to inhibitory effects and/or reduced seed abundance per species (e.g., Guo et al., 2006).

Gradient position sampled (start/end points)

Similar to the breadth, the start/end positions of environmental gradients are also highly pertinent to ecological experiments, in which different levels of species richness, grazers, resources (e.g., nitrogen, water), and disturbances are manipulated to examine ecological responses (Wang et al., 2021). These manipulated variables are often scale-independent. For example, Figure 1 shows that various patterns would be revealed depending on whether the whole (A–F) or part of the entire potential gradient was sampled (e.g., A–C, C–E). For many forest types, sampling the entire successional gradient is rare due to the time required, but ecologists have explored different ways to tackle this challenge, such as by using tree-ring or pollen data.

Another example is biodiversity experiments. Researchers often keep spatial scale constant (e.g., plot size of 5×5 m) while planting or removing different numbers of species (e.g., 1–6 vs. 6–32 species) in each plot, representing different ranges and start/end positions of the artificial "diversity gradients." While the lowest end of diversity is often set at zero (i.e., as "control"), few studies have examined how the highest end (the largest number of species to be planted) should be determined. However, resulting diversity–ecosystem functioning (productivity, stability, or invasibility) relationships could depend on the designated gradient of species richness, that is, the range and start/end number of species seeded across treatments (Table 1) (Isbell et al., 2015). Different conclusions might be reached in the same ecosystem at the same scale if different richness gradients are used. Similar examples can also be found in other field settings or experiments with different biotic gradients such as prescribed burning (e.g., fire intensity, frequency) (Crotteau et al., 2013; Schafer et al., 2015) and grazing (e.g., number of grazers, gazing duration) (Howard et al., 2012). But these biotic gradients usually do not explicitly exploit the concept of scale.

Gradient steepness

The steepness of environmental gradients varies over both space and time. Steep gradients mean rapid change in environmental conditions over space or time and may lead to rapid response or evolutionary turnover (Journe et al., 2022;

TABLE 1 Comparisons among ecological/evolutionary (eco–evo) studies from purely field observations to totally controlled indoor (lab/greenhouse/microcosm) experiments.

	Main types and features of investigation		
Features of study	**Field observation**	**Field experiment**	**Laboratory experiment**
Environment	Heterogeneous	Semi-heterogeneous	Homogeneous
Level of manipulation	Little/no control	Some control	Total control
Scale	Large	Small-intermediate	Small
Length of study	Long	Intermediate-short	Short
No. variables	Large	Medium	Small
Gradient	Continuous	Discrete/categorical	Discrete/categorical
Design	Gradient	Gradient/replicated	Replicated
Organisms	Mostly large	Large-small	Mostly small
Taxonomic group size	Flexible	Mostly small	Small
Data analysis	Correlational	Relationship	Relationship
Mechanisms	Uncertain	Intermediate	More certain

Note: In biodiversity experiments, while the starting point can be set at 0 (i.e., no species is planted in "controls"), the ending point (the highest no. species to be planted) is open (i.e., varies among studies). In latitudinal or elevational studies, the start/end points are also usually different across studies (e.g., the lowest/highest points of a mountain, the start and/or end latitudinal degrees).

Whitney & Gabler, 2008). Steep gradients over a small scale could have the same range as shallow gradients over a large scale. Analogously, the rapid response of a species over a short time period could lead to similar results as that of a slow response over a longer time period. For example, given the same spatial extent (scale), tropical mountains may have longer and steeper environmental gradients that are sufficient for the unimodal diversity pattern to emerge (Janzen, 1967). Such perceptions could be illustrated by the different hypothesized regression lines (e.g., in Figures 2 and 3) representing patterns based on published reports that either support or reject various ecological–evolutionary rules or laws such as the Rapoport's rule (Stevens, 1989), Bergmann's rule, and Cope's rule (Ashton, 2001). Along the temporal scale, species at early successional stages may experience steeper gradients, leading to faster changes in community and ecosystem responses. Also, rapid evolution has been observed in many species, especially among exotic invasive species (Whitney & Gabler, 2008). Thus, the sampling interval needs to be set accordingly to correctly match the rate of changes in species traits.

Interactive effects of different gradient features

Reviews of relevant literature reveal remarkable differences in the elevational range and start/end positions among different mountains across the globe (Nogues-Bravo et al., 2008). Some studies (mostly on islands) examine the elevational patterns beginning at sea level, whereas many other studies begin at mountain bases with varying elevations from several hundred to thousands of meters above sea level. Such variations could have caused some inconsistencies among early studies in the altitude-dependent cloud and moisture distributions that influence many physiological variables. Empirical observations of species diversity change with elevation often follow unimodal curves (hump-shaped but often asymmetrical), which are predominant in tropical and temperate mountains. These frequently observed unimodal curves of elevational patterns in species diversity clearly do not mirror the latitudinal gradient along which diversity usually declines toward the poles (Brown, 1995) in part because the degree of variation in altitude, base/tree-line positions, gradient ranges, and elevational patterns are not universal among mountains of different latitudes or across different continents (Guo et al., 2013).

Furthermore, even if the elevational ranges are similar among selected mountains, their latitudinal locations (geographic zones) would also affect the start/end positions of underlying environmental gradients. For example, the endpoint of a temperature gradient at the tree line of a tropical mountain might be similar to the starting point of a gradient at the base of a cold, temperate mountain. Also, the aspect would have much smaller impacts on tropical mountains than on temperate mountains. Thus, two mountains with the same height and start/end altitudes (but not necessarily the same gradients) located in different latitudinal zones (e.g., tropics vs. cold temperate) may show different elevational diversity patterns (e.g., Guo et al., 2013).

Regarding the frequently reported unimodal diversity–altitude relationships, the most challenging question is why diversity shows a rapid increase with an initial increase in altitude at low elevations. Note the starting altitude usually consists of a larger area and includes both the relatively flat area (e.g., the bottom of a valley) and the mountain. When the flat area is dominated by agricultural land, low diversity would be expected. However, in natural settings, the starting altitude could also be an ecotone, which should support higher diversity. Here we argue that this unimodal elevational diversity pattern may be associated with the sampling issue (see subsequent discussion in *Sampling issues and applications*), particularly at the starting points (of gradients) in published studies, that is, whether a study has actually sampled the ecotone region.

For elevation-related studies, it is the starting (lower) point that often varies substantially among studies and leads to varying results. But for biodiversity experiments, it is more often the ending points (the maximum number of species to be seeded or planted) that vary substantially among studies and, thus, lead to different conclusions. The same is true in nitrogen (or water) addition experiments in which the results and conclusions depend on the amount of nitrogen added in each treatment and how many treatments are implemented. Nonetheless, the relative importance of gradient range versus position along with background nutrient conditions could also vary substantially among different studies (Vela Díaz et al., 2020).

GRADIENT–SCALE INTEGRATION

Incomplete sampling across the full gradient may lead to inaccurate or biased conclusions. These inaccurate conclusions can arise due to (1) incomplete sampling of a true potential full global gradient as a result of poor sampling design or (2) extrapolation of conclusions and interpretations beyond the investigated area, which often only covers a part of the full gradient. Generally, for species with highly restricted distributions, it is difficult to detect any latitudinal or elevational patterns, even though the species may be very sensitive to temperature variation. Also, the realized distributions of many species may not be primarily limited by climates (cf. the climate niche) but by dispersal, time, and ecological interactions, as demonstrated by the success of exotic invasive species and human-assisted migration. To better integrate gradient and scale into relevant ecological research, we offer eight key recommendations:

1. After a study area is determined, taking gradients into account may drastically change the sampling design and strategy (e.g., scale, sample size, grid/transect size, horizontal and vertical location, spatial and temporal intensity, spatial placement, and timing), as we discuss in the next section on adaptive sampling.
2. For a chosen region or system in which a species, a group of species, or a community will be studied, a suitable scale needs to be determined and then the features of underlying gradients (i.e., the breadth, steepness, and start/end positions) assessed. These decisions will determine the patterns, as possible explanations will depend on the gradients (partial vs. full for a species).
3. For a particular species or community, its full global range of the gradient (nutrient, water) can be estimated (Chown & Gaston, 2016), for example, by referring to the literature. If the target species is an introduced species, related information may be found from its native range (e.g., fundamental vs. realized niches; He & Bertness, 2014; Perret & Sax, 2022).
4. Estimates of key variables that influence ecological processes within the designated study area are encouraged. However, caution should be exercised on any generalization or extrapolation since most studies do not cover the full gradient of certain variables, and results are likely region-specific (e.g., Rapoport's rule may not be supported for a taxon in a specific area of investigation but may be supported over the global scale). Any conclusions drawn from such studies should clearly state that the results are limited to the target species and specific region.
5. When the response of a target species or community to a continuous variable has been chosen for examination, researchers need to make sure the study area encompasses the full gradient of that variable (Schweiger et al., 2016).
6. At any given scale chosen for a study, the "full" ranges of gradients of the concerned variables (e.g., rainfall, temperature) should be assessed and/or evaluated based on available data (prior knowledge) or on new preliminary data collected through pilot surveys (Legendre et al., 2002). This is also helpful for determining whether the chosen scale is appropriate for the study. For certain variables (e.g., vegetation cover), remote sensing may be very helpful for this purpose (i.e., overcoming some of the limitations due to logistics).
7. Consider using mixed sampling designs that include elements of both "gradient design" (i.e., with a maximal number of locations without replication per location; Kreyling et al., 2014, 2018) and "replicated design" (i.e., with at least three true replicates at fewer locations), which may require different methods of analysis (i.e., regression vs. ANOVA) (Cottingham et al., 2005). In either case, sampling intensity should

be positively related to expected spatial and temporal change rates of focused gradients (i.e., more sampling in areas where the gradient changes rapidly). Statistical approaches such as power analyses could be employed to provide a rigorous underpinning to sampling designs—specifically frequency and spacing of sampling.

8. Although scientists sometimes consider extreme conditions/events "outliers," these are part of the full gradients and thus should be included in analysis and interpretation (He & Bertness, 2014). When the full ranges of concerned gradients are sampled, such "outliers" may no longer exist.

In any of the preceding cases, improved sampling design needs to stress the importance of underlying gradients, thereby facilitating the integration of gradients with scales. In other words, future studies should use adaptive sampling design (ASD; see next section) whenever possible to examine the roles of gradient and scale simultaneously. Overall, integrating gradient with scale can significantly improve our understanding of ecological patterns and processes. In Box 2, we outline some specific recommendations for further improving sampling and analysis in future studies.

ADAPTIVE SAMPLING AND APPLICATIONS

"Adaptive sampling" is an approach that concentrates sampling efforts in crucial and/or sensitive eco–evo areas or time periods. Based on our review of gradient versus scale and the discussion on research designs that consider the best knowledge of these important issues, we recommend adaptive sampling (i.e., "response-adaptive designs"), which has slightly different meanings for different fields or researchers (Conroy et al., 2008). Here, we use the term to suggest a sampling design to give more weight to places and time periods with steep gradients such as (1) phase transitions (e.g., ecotones, early succession), (2) highly dense (of abundance) or clustered areas, and (3) places/times with possible breaking points or unusual or rare events/phenomena (e.g., hot spots or hot moments) based on prior knowledge or preliminary observations. This recommendation would thus reduce the use of traditional methods such as systematic and random sampling as research targets are rarely so distributed over space or time. Similarly, niche-based sampling coordinates sampling efforts according to species' climatic niches, not just geographical distribution (Perret & Sax, 2022).

BOX 2 Summary recommendations for more complete gradient sampling.

Incorrect, biased, or misleading conclusions often result from incomplete sampling: (1) incomplete sampling of true potential full gradients due to poor sampling design and (2) incomplete coverage of gradients' ranges in target study area. Assessing the full extent of potential gradients (e.g., rainfall, temperature) within a study area is critical for sampling design and result interpretation.

1. If the study target is a particular region or landscape, the full ranges of key biotic and environmental gradients in the target region should be estimated through literature searches and preliminary observations.
2. If the study focuses on a target species (or community) in a particular region, the full ranges of key gradients should be estimated. However, in such cases, the results are region specific (not global), and the conclusion must reflect this fact so that readers will not accept it as a general conclusion (e.g., it could be true that a specific eco–evo rule is not supported for certain taxa in a certain region, although the rule may be well supported in other regions or at the global scale). If the target species is an introduced species, related information may be found from its native range (realized vs. fundamental niches).
3. When initiating a new study, researchers need to evaluate and balance the use of "gradient design" versus "replicate design" versus "mixed design" as part of the adaptive sampling strategy.
4. Use adaptive sampling design (ASD) as much as possible to target sensitive places and times (e.g., ecotones/transitional phases, species borders/range limits, community/ecosystem boundaries).
5. Outliers should be included in gradient- and scale-related analyses and data interpretation because they might represent extreme/rare events that are important in leading to catastrophic changes or ecosystem collapse or loss of human life. In certain cases, the "outliers" may fall into the full ranges of concerned gradients if sampling is more complete. If not, a separate analysis may be needed (Aggarwal, 2017).

On the other hand, many traditional studies adopting dichotomic or categorical comparisons and/or large sampling intervals are likely to miss crucial patterns or even tipping points (thresholds or breakpoints like point C in Figure 2) in detecting eco–evo patterns (Scheffer et al., 2001). A response variable may experience multiple paths and transitional trajectories under different conditions along a gradient that could not be revealed with conventional dichotomic comparisons (e.g., low vs. high temperature) (Bonser et al., 2010; Guo, 2005). Therefore, adopting ASDs and developing/choosing the appropriate analytical techniques are critically needed to address this issue (Box 2) (Abbott, 2017; Cottingham et al., 2005; Fei et al., 2016; McGeoch & Gaston, 2002; Scheiner et al., 2011; Schweiger et al., 2016).

Previous studies also revealed a wide variety of sampling/survey methods (especially between field sampling and the use of herbarium records), which have certainly contributed to the inconsistencies in observed spatial and/or temporal diversity patterns (Gonzalez et al., 2020; Kreyling et al., 2018; Scheiner et al., 2011; Schweiger et al., 2016). There is often a mismatch between sampling intensity (especially for systematic sampling) and the spatial or temporal variation in underlying environmental gradients. For example, lower elevations and ecotones are often the areas where peaks in species diversity may occur and thus require high sampling intensity to capture species' responses to strong/fast environmental changes (Figure 2) (Fei et al., 2018; Kreyling et al., 2014; Stewart & Frank, 2008).

Among the most recognized environmental gradients are those involving population dynamics (cycles) and succession. Most observed ecological patterns show the steepest curves at the initial parts of gradients (e.g., initial population growth/expansion, early succession; Figure 2). For example, in succession, the initial stronger responses (steeper curves) in diversity and productivity often occur in early stages after major disturbances (Figure 2). Thus, although systematic sampling (i.e., with same intervals and even spacing for transects and plots) has certain merits, more intensive sampling at the initial parts of temporal gradients would ensure the full or more complete coverage of the focused gradients and responses. Nontraditional sampling methods, such as cyclical (Burrows et al., 2002), fractal (Simpson & Pearse, 2021), and gradient designs (Kreyling et al., 2018), may also provide better gradient coverage.

Traditionally, it is intuitive to design plot size or length of study in line with a target organism's body size/mass. That is, the plot/quadrat size or time needed in field observations or lab experiments generally increases with the body size or lifespan (or generation times) of the target species. However, there are no commonly accepted statistical methods to determine how big the plot/quadrat/tube size should be. Also, the statistical significance of relationships increases with sample size even when the coefficient of determination may remain very low. Thus, more careful considerations incorporating factors such as statistical explanation powers are needed for improving sampling techniques and design.

Current knowledge on gradients and scales is biased toward many short-term and small-scale studies, while long-term and large-scale studies remain rare. This imbalance is mostly due to sampling constraints. Sampling can be labor-intensive and expensive, with greater sampling frequency or extent restricted by multiple factors. Additionally, sampling may be time restricted as funding cycles are often determined by external entities (e.g., National Science Foundation) limiting sampling to those cycles, typically 3–5 years in duration. The lengths of many eco–evo studies are determined by the time it takes to secure a graduate degree (mostly 2–7 years in the United States), imposing an additional external time restriction on studies. For gradient analysis, although most studies do not explore the full spectrum for many taxa, the issue of (in)completeness in sampling is especially important for invasion biology and global change biology. For scale-related studies, studies across large regions and continents or over entire life cycles and long-term succession are scarce, especially for species with long lifespans (i.e., trees). Filling such gaps requires improved sampling logistics with long-term commitments and sustainable funding (Box 2).

PERSPECTIVES

Our analysis of the distinctions between scale and gradient and our review of past research suggest that the similarities and differences in eco–evo patterns among many different studies may be better explained by a thorough examination of the breadth and start/end positions of the underlying gradients. Because local gradients (e.g., precipitation, temperature) often represent only a fraction of an entire gradient spectrum that could be found in a broader geographical range, we argue that findings from local and individual experimental studies, though likely solid, may not be extrapolated to a broader region. Unless the previously raised gradient breadth and position issues are resolved, researchers should resist the temptation to generalize and instead consider results to be taxa, location, and timeframe specific. In the future, it will be helpful to specify the breadth and position of examined underlying gradients (i.e., along a possible full gradient) when reporting new findings (He & Bertness, 2014). This is urgent especially when results based on incomplete gradients are used, often incorrectly, to reject theories or hypotheses (e.g., Rapoport's rule, Cope's rule; see Ashton, 2001). This is also critical when applying ecological principles to practical applications, such as developing policies for biodiversity management and conservation. Partly because of the constraints of factors related to the uneven distribution of landmasses over the latitudinal zones and continental sizes (e.g., Eurasia vs. Australia), most studies cover only a portion of the entire global latitudes. The differences in locations (e.g., tropics vs. temperate regions) and latitudinal ranges sampled have at least partly been responsible for observed inconsistencies in reported patterns. Some critical questions remain to be addressed. For example, is Rapoport's rule, Bergmann's rule, or Cope's rule more likely to be rejected with a narrower latitudinal range (i.e., 10° rather than 60°) or a shorter time period (i.e., 10 thousand years rather than 10 million years) than a wider range or longer time period (Adams & Church, 2008)?

Ultimately it would be more meaningful if the aforementioned comparative approaches were conducted jointly. The poleward shifts of many species could be easily verified if upward shifts also occurred along the elevational gradient. Also, it is possible that the peak of the hump-shaped diversity curve along the elevational gradient may shift higher, although the magnitudes of the species range and diversity shifts would be different among different aspects and across latitudes. Since nonlinear ecological relationships have been increasingly recognized, "threshold" (and sometimes "asymptote") may become a more commonly used key concept (Clark et al., 2021). Where possible, gradients should be long enough to allow the emergence of more general patterns and associated thresholds or critical points (e.g., diversity or productivity peaks or asymptote for restoration purposes). Otherwise, the results and conclusions should be specified and interpreted for just the particular study and not be generalized (Sanders et al., 2003).

Knowing the full range of the potential gradients (e.g., in the study area, ecosystem, or region for the target species or assemblage) is a key first step for research planning and for interstudy comparisons. Discussion of underlying mechanisms becomes meaningful only when the complete pattern along a certain gradient is revealed. Fortunately, a review of historical literature shows a positive sign that sampling intensity has increased over time and sampling design and techniques continue to improve and are now more sophisticated than ever. Long-term data, particularly those on succession, are also becoming increasingly available. With the rapid developments of (1) new technology such as remote sensing, (2) investments in publicly accessible data repositories such as TRY, EDI, and Dryad, (3) data from community science initiatives such as *i*Naturalist, and (4) software, artificial intelligence (AI), and statistical tools to handle such data through machine learning, patterns associated with full gradients may become clearer and more complete, enabling us to better understand underlying mechanisms.

At the same time, one must also be aware that human activities are profoundly affecting natural patterns (Rickart, 2001). In recent history, climate change and land use change have constantly altered natural gradients over both space and time. For example, global warming is increasing the upper limit of the temperature gradient in many regions (i.e., forming new "extremes") (Askeyev et al., 2021). Also, carbon emissions have drastically increased the CO_2 level in the atmosphere, and nitrogen deposition due to agricultural fertilizer and pollution is leading to eutrophication and increasing the upper limit of the nitrogen gradient across the globe. As a result, the global mean of multiple environmental variables has been changed. Continued changes could result in abrupt transitions or even collapses in many ecosystems because human activities are extending the environmental gradients over critical thresholds (Askeyev et al., 2021; Stuart-Haëntjens et al., 2015). Under extreme conditions, the nature of species interactions, both direct and indirect, is likely to change drastically (He & Bertness, 2014; Isbell et al., 2015), and nonlinear responses of species to environmental gradients could be more frequently observed because of complex interspecific and species–environment interactions in new environments (Clark et al., 2020). As human activities increasingly alter the features of environmental gradients such as atmospheric CO_2 and nutrient (e.g., nitrogen and phosphorus) concentrations in soil and water, such changes may bring irreversible consequences. Thus, close monitoring of possible thresholds and tipping points in these key gradients over space and time is critically needed.

In short, underlying gradients may be the main cause of most if not all scale dependency in eco–evo patterns, highlighting the need for jointly considering scale and gradient in both experimental design and field observations. Explanations of both field and experimental research heavily depend on whether the sampled environmental gradients cover the entire potential gradients. The chance of reporting the actual patterns within and across certain scales increases as sampling along the gradient approaches its full range and could influence the validation results of important hypotheses. For practical reasons, most observational studies to date have only sampled part of the entire potential gradients. Observed temporal ecological patterns often change over space, spatial patterns change over time, and both spatial and temporal patterns change with the breadth and position (start/end points) of the underlying gradients. These important gradient-related features are critical considerations for resolving possible disagreements or inconsistencies among studies and may offer additional insights into the causal mechanisms. Research to date suggests that observed patterns could better follow many proposed ecological laws/rules/principles if the sampled gradients were more complete (e.g., all plants vs. conifers, entire life cycle or successional cycle vs. early stages, and 0–90° vs. 0–10° in latitude) (Guo et al., 2013; Nogues-Bravo et al., 2008). The description and documentation of how observed patterns are scale-dependent and how well those observed patterns approximate the actual patterns along entire gradients may be more precisely described using the proportion of the potential gradient examined in each study. This approach with a shift to a greater emphasis on gradient will help uncover mechanisms underlying patterns across scales in ecology and evolution.

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The authors declare that there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

No data were collected for this study.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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