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Historical Perspective

Revisiting Clements and Gleason: Insights from Plant Distributions on Pikes Peak, Clements's Life-Long Study Site

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abstract: How do species' distributions respond to their environments? This question was at the heart of the Clements-Gleason controversy, ecology's most famous debate. Do species respond to the environment in concerted ways, leading to distinct and cohesive assemblages (the Clementsian paradigm), or do species respond to the environment independently (the Gleasonian paradigm)? Using plant occurrences along the elevation gradient of Pikes Peak (Colorado) as a lens through which to gain insight into Clements's perspectives on the debate, we formally test for community patterns along this gradient using a modern framework unavailable at the time of Clements and Gleason. The Pikes Peak region was Clements's study area for more than 40 years, where he established a research lab and distributed sites along the elevational gradient. His investigations of plant distributions on this mountain likely influenced his views on communities. We found mixed support for the paradigms, with neither the Gleasonian paradigm nor the Clementsian paradigm fully supported. While distributions along the gradient showed evidence of clustering of species range edges, considered to be consistent with the Clementsian paradigm, the pattern was weak, and neither range edges nor species turnover peaked at ecotone elevations, as expected under the Clementsian paradigm. Our results illuminate the Clements-Gleason debate by allowing us to probe issues that complicate conclusively testing the paradigms, such as deciding on how we quantify environmental gradients and determining the appropriate scales for community patterns and processes that might generate them. Revisiting the debate also revealed that Clements's and Gleason's views had more in common than we realize. The debate may be less neatly resolved than we assume from mythos, and it continues to have relevance to basic and applied ecology today, as its legacy has shaped our (still tenuous) notion of ecological communities and the trajectory of our field.

Keywords: plant community, elevational gradient, Clements, Gleason, gradient analysis, boundary clumping.

Introduction

How species sort themselves along gradients of environmental conditions is a matter of long-standing interest and debate in ecology. Do species respond in concerted ways, leading to distinct, predictable assemblages? Or do species respond to those gradients individualistically and independently? These questions evoke one of ecology's most famous debates nearly a century ago, the Clements-Gleason controversy. Far from an outdated quibble, those questions remain relevant to this day, as the answer gets at the heart of what the concept of a community is (Underwood 1986; Mittelbach 2012): a distinct "organic entity" (Clements 1916) or "merely the fortuitous juxtaposition" of species (Gleason 1952). These views of communities and the legacy of the debate also continue to have significant relevance to areas of modern ecology, such as restoration ecology (Hilderbrand et al. 2005; Pickett et al. 2009; Hallett et al. 2023) and the concept of novel ecosystems (Hobbs et al. 2009), metacommunity ecology (Leibold and Mikkelson 2002; Leibold and Chase 2018), species distribution modeling (Pollock et al. 2014; Ovaskainen and Abrego 2020), niche and neutral theory (Hubbell 2001; Chase and Leibold 2003; Chase 2014), and the role of positive and negative species interactions in community assembly (Callaway 2007; Bimler et al. 2018).

Frederic E. Clements (1874–1945) is considered a founding figure in plant ecology (Egerton 2013; Oberg 2019). Expanding on the works of Cowles and others (e.g., Cowles 1899;

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and see Whittaker 1962), Clements studied the relationship between plants and their environments and became best known for his views on plant communities (later also animals; Clements and Shelford 1939), especially in the context of succession (Clements 1916). He is known for contending that plant communities undergo predictable stages to reach a climax whose identity is determined by climate (Clements 1916, 1936). Clements developed an elaborate system of classification of species assemblages and notably posited that species sort along the environment, especially along climactic gradations, to constitute cohesive, discrete units (Clements 1916, 1936). He described these units as assemblages of characteristic plants that define a community (Clements 1916, 1936) using an analogy to a complex organism, drawing parallels between ontogeny and succession culminating in the maturation of a (mono)climax community (Clements 1916; Whittaker 1962).

Enter Henry Gleason (1882–1975), a plant ecologist best known for his views of plant communities contrasting with those of the Clementsian paradigm. Gleason instead posited an individualistic view of plant associations (Gleason 1926). Under this perspective, species segregate along environmental gradients according to their own "peculiarities of migration and environmental requirements" and assemble under stochastic processes of succession (Gleason 1926, p. 26). Gleason contrasted this view with the leading Clementsian paradigm of the time, criticizing the analogy of plant assemblages as complex organisms (Gleason 1926, 1952). Gleason saw "no reason at all for the segregation of definite communities," instead envisioning communities as "not an organism, scarcely even a vegetation unit, but merely a coincidence" (Gleason 1926, p. 26).

Clements and Gleason's concepts of communities thus presented apparently opposite and incompatible models. On one side, Clements presented species as closely associated with one another within closed communities; species within those communities would be bounded within coinciding ecological limits. On the other side, Gleason presented species distributed independently of others in open communities; species within those communities would be bounded by ecological limits corresponding independently for each species. Figure 1 shows a common depiction of Clementsian and Gleasonian paradigms. While curves like these were never drawn by either Clements or Gleason to illustrate their views, they were later used by Robert Whittaker to illustrate species distributions from his empirical studies using "gradient analysis" (e.g., Whittaker 1956), which played an important role in the Clements-Gleason debate (we expand on this topic below).

The Clementsian concept was dogma in plant ecology in the early decades of the twentieth century (Whittaker 1962; Kingsland 1991). Starting in the 1930s, criticism of the Clementsian concept mounted (e.g., Tansley 1935; references in Whittaker 1962) and support among plant ecologists declined (Nicolson 2016) until an eventual, and perhaps equally dogmatic, paradigm shift to the Gleasonian alternative. Despite this shift, Clements stood firm in his views (Hagen 1993). How did Clements come to have those views and why did he hold them so tightly? Do the vegetation patterns seen by Clements match his views on communities? Can we empirically distinguish between the two paradigms? We explore these questions with a heuristic case study of plant distributions along the 2,500-m elevation gradient of Pikes Peak (Colorado), Clements's life-long study site. We describe the historical context and the influence of Pikes Peak on Clements's ideas in box 1.

Since Pikes Peak's flora was likely important in shaping Clements's views of communities (Clements and Clements 1914; Clements 1916), analyzing the elevational distributions of the plant species in this area could illuminate how they may have shaped his tenacious view of vegetation and represent a lens through which to reexamine the debate. We can now apply modern theoretical and statistical frameworks (Leibold and Mikkelson 2002; Presley et al. 2010; Dallas 2014; McCain and Beck 2016) combined with databases containing thousands of species occurrence records from the area to formally test for community patterns. Perhaps some vindication is in order and there are merits to Clements's paradigm, at least in the context of this steep environmental gradient with sometimes sharp ecotones. Or perhaps Gleason's paradigm is superior even in the context of Pikes Peak, Clements's life-long study area. Or perhaps the approach to testing these paradigms requires a more nuanced evaluation or a reevaluation of the dichotomy of the debate.

Here we ask whether there is evidence of the Clementsian paradigm in plants, as Clements knew them, along the elevational gradient of Pikes Peak and whether range edges cluster around ecotones. To this end, we created a species list for Pikes Peak based on Clements's flora (Clements and Clements 1914) and refined this list against regional species lists for Pikes Peak. We used this refined species list to collect species records from the region to estimate species' elevational distributions. We hypothesize that if Pikes Peak's flora is strongly structured along an elevational gradient into distinct assemblages, as espoused by Clements, then we would expect to find evidence of clustering of range edges ("boundary clumping" sensu Leibold and Mikkelson 2002) and those range edges and species turnover to cluster around ecotones (e.g., Lomolino 2001; fig. 1). Alternatively, if Pikes Peak's flora is more individualistically structured along an environmental gradient, as espoused by Gleason, then we would expect to find no evidence of clustering of range edges and no clustering at ecotones (fig. 1). We discuss whether these analyses fully test

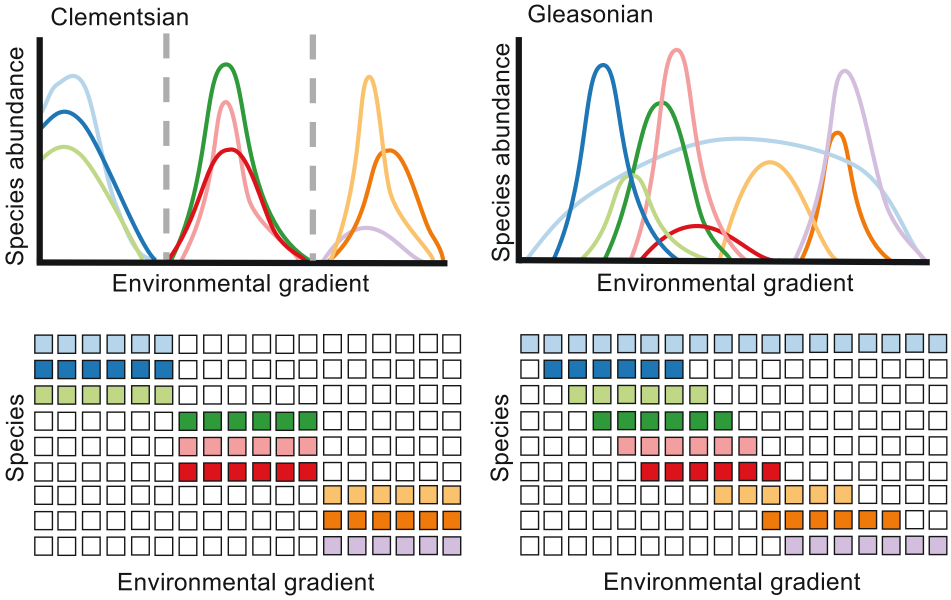

Figure 1: Hypothetical assemblages depicting Clementsian and Gleasonian concepts. The curves on top show a common representation of the Clementsian and Gleasonian concepts of communities (modified from Ricklefs 1990). In the depiction of both conceptualizations, these hypothetical species are distributed along and constrained by an environmental gradient. In the Clementsian concept, species sort into relatively cohesive and closed associations demarcated by ecotones, depicted as vertical dashed lines. In the Gleasonian concept, species respond to the environmental gradient individualistically and independently. In Leibold and Mikkelson's (2002) framework, an incidence matrix, like the one shown below the curves, can be used to test for Clementsian and Gleasonian structures using "boundary clumping," which refers to how the edges of species range boundaries are distributed in relation to each other. Boundary clumping is quantified using Morisita's index (I; Morisita 1971), a measure of the dispersion of species occurrences among sites. A Morisita's I equal to 1 indicates that species boundaries are neither clumped nor hyperdispersed and that the arrangement of species ranges along the gradient is independent and thus in agreement with the Gleasonian structure. A Morisita's I greater than 1 indicates that species boundaries are clumped, thus indicating that the arrangement and replacement of species ranges along the gradient is cohesive and thus in agreement with the Clementsian structure. In the hypothetical assemblages shown, the Clementsian assemblage has Morisita's $I = 4$ (significantly differing from 1; $P < .001$), while the Gleasonian assemblage has Morisita's $I = 0.7$ ($P = .35$).

Clements's and Gleason's views as well as the imprint of this historical debate on modern ecology.

Methods

Pikes Peak is a prominent mountain in the southern Front Range of the Rocky Mountains, peaking at 4,302 m (14,115 ft). Pikes Peak's ancestral name is Tava (meaning "Sun Mountain"), given by the Tabeguache (meaning "People of Tava") band of the Ute, who resided in the region until the early 1880s (the decade before the Clements's arrival; box 1), when they were forced to relocate to the Uintah Reservation in northeastern Utah (Reynolds Kaelin 2014; Flores 2018; Southern Ute Indian Tribe 2024). Characteristic life zones (Merriam 1895; Marr 1961) are apparent as vegetation changes along the elevational gradient from the plains at the base of the mountain to the alpine at the top of Pikes Peak. Along the elevation gradient of Pikes Peak, the change in vegetation is remarkable and sometimes quite sharp. For example, the tree line at 3,500 m is demarcated by a narrow band of stunted bristlecone pine (*Pinus aristata*) that separates the enclosed subalpine forest, dominated by conifers like Engelmann spruce (*Picea engelmannii*) and limber pine (*Pinus flexilis*), from the exposed alpine tundra that extends to the summit of Pikes Peak. Elevation is often used to classify vegetation units (or life zones) based around dominant species in descriptions of the flora of Pikes Peak (Whitfield 1933; Powell 2011; Kelso 2012) and the Rocky Mountains (Marr 1961; Ackerfield 2015). Elevation is consequently also used to define ecotones between these vegetation units. Kelso (2012) describes Pikes Peak's vegetation zones as plains, foothills scrub/pinyon-juniper woodlands, montane conifer forest, subalpine forest, and alpine tundra. The area along this gradient has a long history of protection and management by the US Department of Agriculture Forest Service as part of Pike National Forests and previously the Pikes Peak Timberland Reserve in the early 1900s, along with management activities prior to the creation of the reserve (Vance and Vance 2011).

Box 1: Historical context of Clements at Pikes Peak

Frederic Clements and his spouse, botanist and illustrator Edith S. Clements, first visited the Pikes Peak area in 1899 (Clements 1960; Brunk 1998). Clements was awestruck by this mountain of uniform granite that forms an impressively steep gradient rising nearly 2,500 m above the Great Plains over 12 km (Clements 1960). Clements considered climate as "paramount" in the formation of climaxes (Clements 1936, p. 253) and mused that along this elevational gradient, there were "as many different climates as there are from the Gulf of Mexico to the Arctic Circle" (Clements 1960, p. 16). Of the area, Clements is reported to have said that "there's no place like it in the world . . . no such opportunities to study the effects of the environment on plants" (Clements 1960, p. 16). Shortly after their first visit, the couple founded the Alpine Laboratory (box fig. 1) in the montane forest below Pikes Peak at Minnehaha, Colorado (2,591 m elevation), which would for more than four decades serve as a biological research station in service of the study of the effects of the environment on plants under the direction of the Clements (Clements 1960). With the Alpine Laboratory as home base, the Clements and their team spent summers studying the plants of Pikes Peak from the late 1890s to the 1940s (Edith S. and Frederic E. Clements Papers 1876–1969). The Alpine Laboratory was on the itinerary for nearly every summer of the Clements's field excursions (Edith S. and Frederic E. Clements Papers 1876–1969) and was a location for experiments and training of field botanists (Oberg 2019; Edith S. and Frederic E. Clements Papers 1876–1969). The Clements established research outposts along the elevational gradient from the grasslands in Colorado Springs to the alpine tundra (Brunk 1998). The Alpine Laboratory closed in 1947 shortly after the death of Frederic Clements (Brunk 1998).

It is apparent that Pikes Peak could have been important for shaping Clements's thinking about plant communities. In *Plant Succession: An Analysis of the Development of Vegetation* (Clements 1916, p. 3), his central monograph describing his concept of plant communities, he begins by stating, "The present book constitutes the general part of a monograph on Rocky Mountain vegetation which has been underway since 1899" (the year that the Clements first visited Pikes Peak). In a historical piece on the Clements, Oberg (2019, p. 1) emphasized the importance of the Pikes Peak region and elevation to their research: "[The Clements] tested and taught their theory of plant succession, known as Clementsian ecology, for nearly four decades at their Alpine laboratory in Colorado . . . conduct[ing] experiments in different climates as influenced by altitude." Clements (1936, p. 266) stated that "the clisere is

Box Figure 1: Frederic Clements on the veranda of Pinecroft, one of the cabins at the Alpine Laboratory at Minnehaha on Pikes Peak. Edith S. and Frederic E. Clements Papers (1876–1969), American Heritage Center, University of Wyoming, Laramie, Wyoming.

Box 1 (*Continued*)

most readily comprehended in the case of high ranges or summits, such as Pikes Peak, where the entire series of climaxes is readily visible." He defined a "clisere" as "the series of climax formations or zones which follow each other in a particular climatic region in consequence of a distinct change of climate" (Clements 1916, p. 347). Clements clearly recognized the utility of elevation variability for studying plant-environment relationships. While Clements also studied ecosystems all over North America and drew upon them for his ideas, the Pikes Peak region was where he conducted research and trained other plant ecologists in the summers for four decades. Place-based research, "research that assigns the idiosyncrasies of place, time, and taxon a central and creative role in its design and interpretation" (Price and Billick 2010, p. 16), has a recognized role for shaping ecological thinking and theory development (Kingsland 2010). It is worth noting that McIntosh (1975, p. 256) speculated that Clements and Gleason's early study systems in the midwestern United States may have been influential in the "imprinting" of the "diametrically opposed views" of the two ecologists, with Clements's early work being in the presumably more stable plant communities of the central Great Plains of Nebraska and Gleason's early work being in the presumably more dynamic plant communities of the forest-prairie ecotone of Illinois.

To build a species list representative of the flora of Pikes Peak as Clements knew it, we transcribed the species found in Clements and Clements (1914). We subset this species list using local species lists for Pikes Peak (see the supplemental PDF for details). We downloaded occurrence records for species from this list from the Global Biodiversity Information Facility using the R package rgbif (ver. 3.5.2; Chamberlain et al. 2021) and obtained elevations using elevatr (ver. 0.3.4; Hollister et al. 2021). We removed species with spatial uncertainty and few observations in the study area (see the supplemental PDF for details). We estimated the lower and upper bounds of species' elevational ranges using the minimum and maximum values. For comparison to the minimum and maximum values, we also calculated the 10th and 90th percentiles of elevation values from a fitted Weibull distribution for each species. The minimum and maximum elevation values and the 10th and 90th percentile values of a Weibull distribution were strongly correlated (Pearson's correlation coefficients: 0.81 and 0.89). The former are presented in the main text, and the latter are in the supplemental PDF.

We used a framework developed by Leibold and Mikkelson (2002) and refined by Presley et al. (2010) to test several kinds of metacommunity patterns in the distribution of species among sites along environmental gradients. This framework represents community patterns based on three elements: coherence, turnover, and boundary clumping. These elements are tested from data from a site-by-species incidence matrix (fig. 1). Coherence refers to embedded absences in a species range along the gradient (here assumed as continuous). Turnover refers to how species compositions change across the gradient and is quantified by calculating the number of times one species replaces another between sites. Boundary clumping refers to how the edges of species range boundaries are distributed in relation to each other. If the condition of there being both coherence and turnover is met, boundary clumping can be used to test for evidence of Clementsian or Gleasonian paradigms. Boundary clumping is quantified using Morisita's index (I; Morisita 1971), a measure of the dispersion of species occurrences among sites. A Morisita's I equal to 1 indicates that species boundaries are neither clumped nor hyperdispersed and that the arrangement of species ranges along the gradient is independent and thus in agreement with the Gleasonian paradigm (fig. 1). A Morisita's I greater than 1 indicates that species boundaries are clumped, so that the arrangement and replacement of species ranges along the gradient is cohesive and thus in agreement with the Clementsian paradigm (fig. 1). A Morisita's I lower than 1 indicates that species boundaries are hyperdispersed, indicating evenly spaced species ranges (Presley et al. 2010).

To create a species incidence matrix, we simulated censuses of plant occurrences at intervals along the elevational gradient assuming continuous distributions (i.e., perfect coherence) along the elevational range of each species. In our analysis, a given species from the species pool is counted as present at a site if the elevation of that site falls within the elevational range of that species. We tested the sensitivity of our boundary clumping results to elevation interval spacing (binning) ranging from 50 to 500 m. Selecting an interval that is too small could lead to nonindependence (and possibly a violation of the turnover condition for testing boundary clumping) by introducing high spatial dependence and essentially resampling much of the same assemblage as the adjacent slice. Alternatively, intervals spaced too far apart could fail to sufficiently sample communities along the gradient by being too coarse. Thus, we tested various interval sizes along the gradient from 50 to 500 m in 50-m increments along the elevational gradient from the bottom to the top of Pikes Peak (1,800–4,302 m). We tested for patterns of boundary clumping to determine whether distributions follow the Clementsian or Gleasonian paradigm. We first tested for evidence of significant turnover along the gradient, a condition to test for patterns of boundary clumping. Because we are using unbroken elevational ranges for species, we did not test for coherence, as all species distributions are treated as perfectly coherent along the gradient in our matrices.

We plotted frequencies of range edges with a histogram to determine whether range edges cluster at ecotones (as in McCain and Beck 2016; Beck et al. 2017). Ecotone elevations were defined by Kelso (2012) and Whitfield (1933) for Pikes Peak, by Powell (2011) for Pike and San Isabel National Forests, by Marr (1961) for the Colorado Front Range, and by Ackerfield (2015) for the Colorado Rocky Mountains. Following the methods of McCain and Beck (2016; cf. Baselga 2010), we measured richness-independent elevational turnover within 100-m and 200-m elevational bands as Simpson's dissimilarity of their component neighboring 50-m and 100-m bands, respectively (Simpson 1943; Baselga 2010; for consistency with McCain and Beck 2016). This method allows plotting turnover patterns over elevation, estimating the probability that the peak is higher than randomly expected, and comparing peak locations with ecotone locations. We used VBA software written by C. M. McCain (available at http://spot.colorado.edu/~mccainc/simulation_programs.htm) for computing elevational turnover. For elevational turnover consistent with the Clementsian paradigm, we would predict major peaks in turnover (higher than expected by random) at all ecotone locations (i.e., >95% confidence intervals of range randomizations based on 5,000 randomizations of empirical range sizes).

Results and Discussion

We found at best mixed support for the Clementsian paradigm for plant distributions along the elevational gradient of Pikes Peak with our approach. Analysis of distributions along the gradient showed significant boundary clumping (fig. 2), perhaps indicating some consistency with the Clementsian paradigm. However, the magnitude of the observed pattern was low (Morisita's $I < 1.3$ compared with Morisita's $I = 4$ in the hypothetical example of a strong Clementsian pattern in fig. 1). Moreover, species range edges tended to occur outside ecotone elevations (fig. 3) and the elevational turnover metric did not peak at ecotone (fig. 4), perhaps contradicting expectations under the Clementsian paradigm. These findings are explained in more detail below.

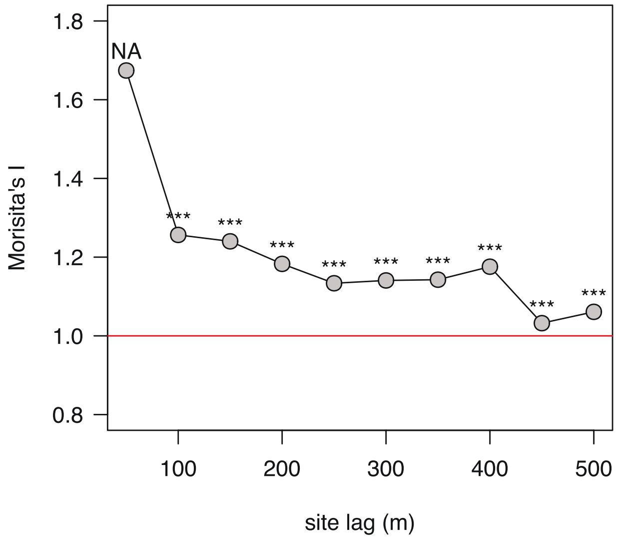

Figure 2: Morisita's index of dispersion (I) for Pikes Peak plant community along an elevational gradient calculated for a range of simulated sampling intervals along the gradient (circles). Here, minimum and maximum elevations were used for species range limits. $I = 1$ indicates a random dispersion indicative of Gleasonian gradients (red line), and $I > 1$ indicates an aggregated dispersion indicative of Clementsan gradients. Asterisks indicate P values at each interval ($^{***}P < .001$). Site lag refers to the spacing between sampling slices along the elevation gradient. The 50-m interval was not included, as the turnover condition for testing boundary clumping was not met.

Across the range of intervals tested (50–500 m), we found evidence for significant Clementsian gradients in boundary clumping (fig. 2). Morisita's I was significantly greater than 1 across intervals tested ($P < .05$ for all). The 50-m interval was not included, as the turnover condition for testing boundary clumping was not met. Positive species turnover was observed along the elevational gradient ($P < .05$ for all) except at 50 m ($P = .53$). We found Morisita's I decreased from 1.7 at 50-m intervals to 1.06 at 500-m intervals, indicating that the interpretation of these patterns may be sensitive to the scale of analysis. Magnitudes of Morisita's I were similar when using the 10th and 90th percentile values of a Weibull distribution for range limits (fig. S3; figs. S1–S7 are available online).

Contrary to expectations for the Clementsian paradigm, we found no clustering of range edges at ecotones (figs. 3, S4), regardless of which ecotone elevations we used to delineate vegetation zones (fig. S5). Similarly, Simpson's dissimilarity as a richness-independent (fig. S6) elevational

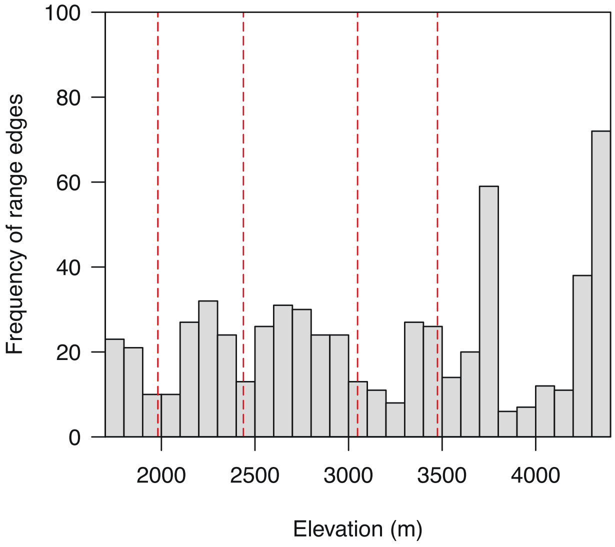

Figure 3: Histogram of range edges (both minimum and maximum) in relation to ecotones between vegetation zones shown in vertical red dashed lines defined by Kelso (2012). From low to high elevation (left to right), the plains to foothills ecotone is at 1,981 m, the foothills to montane ecotone is at 2,438 m, the montane to subalpine ecotone is at 3,048 m, and the subalpine to alpine ecotone is at 3,475 m. The Clementsian paradigm would be supported by peaks at the ecotones (red lines).

turnover metric did not peak at ecotone elevations, and this result was robust to changes in assumptions of the elevations at which ecotones are located (figs. 4, S7). Few turnover values at the two scales were above the 95% confidence intervals of the randomizations (figs. 4, S7). Pikes Peak floral turnover was generally quite low across the gradient (consistently <0.1), whereas values range between 0 (low turnover) and 1 (high turnover). Thus, elevational turnover peaks were neither distinct nor well distinguished from the surrounding low turnover values across the gradient (figs. 4, S7).

Under the Leibold and Mikkelson (2002) framework, Clementsian and Gleasonian patterns of boundary clumping have been found for a variety of organisms and gradients (e.g., Presley et al. 2009; López-González et al. 2012; Heino et al. 2015; He et al. 2020; reviewed in Leibold and Chase 2018). But as noted by Leibold and Chase (2018), statistically significant evidence of "Clementsian gradients" may not reflect community patterns as "tightly as envisioned by Clements." Furthermore, complicating factors such as scale dependence and multiple intersecting gradients can make the interpretation of these patterns difficult. Likewise, in our study several issues could preclude drawing decisive conclusions from the results. These include careful consideration of how we quantify environmental gradients, determining the appropriate scales for Clementsian and Gleasonian patterns and processes that might generate them, and reconciling common misinterpretations of the polarized paradigms. These caveats highlight that Clements's and Gleason's ideas are not set up in a way that is easily testable and falsifiable. Leibold and Mikkelson (2002) admirably set up a framework to test these patterns empirically; however, the interpretation of the results from this framework requires grappling with issues with gradients, scale, and whether these methods

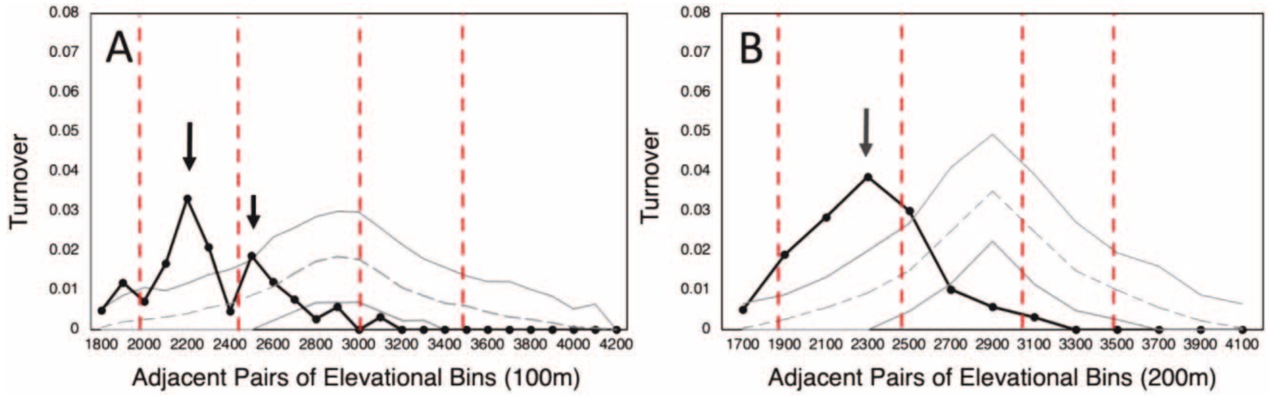

Figure 4: Elevational turnover (using range edges) between adjacent bands between 100 m (*a*) and 200 m (*b*). For elevational turnover consistent with the Clementsian paradigm, we would predict peaks in turnover at ecotone locations (red dashed lines). Turnover estimated using Simpson's dissimilarity, which is independent of species richness, was low (i.e., <0.1). Major peaks in turnover (long arrows) and secondary peaks in turnover (shorter arrows) are shown in relation to ecotone elevations defined by Kelso (2012; red dashed lines). Secondary peaks in turnover are not particularly distinct. Gray 95% confidence intervals and means are expected turnover based on simulations of random overlap of ranges within a bounded domain. Lower and upper bins are excluded for turnover peaks because all remaining species' ranges end within these bins. The Clementsian paradigm would be supported by peaks at the ecotones.

really test what Clements and Gleason had in mind. We expand on these ideas below.

Considering Environmental Gradients and Distributions: Approach and Challenges

Elevational gradients are considered powerful natural experiments for testing ecological and evolutionary responses of species to abiotic influences, such as temperature (von Humboldt and Bonplandt [1807] 2009; Körner 2007; Rahbek et al. 2019), as evidenced by the increasingly common studies of species' range shifts in response to climate change (e.g., Kelly and Goulden 2008). Indeed, elevational gradients played a prominent role in the Clements and Gleason controversy in the work of Whittaker (e.g., Whittaker 1956). Among the criticisms of the Clementsian paradigm was that it was inadequately grounded in rigorous methodology (Nicolson 2016; Oberg 2019; but see Clements 1905). The emergence of "gradient analysis," developed by Whittaker (1956), promised a more rigorous approach by examining species' distributions along gradients (although really this approach consisted of qualitative assessment of patterns of loosely approximated density curves of species along gradients; Bastow Wilson et al. 2004; Nicolson 2016; Malanson and Peet 2020). Whittaker first applied this approach to the vegetation of the Great Smoky Mountains during his dissertation (Whittaker 1956). Based on his findings, he concluded that species distributions along gradients were distributed individualistically (Whittaker 1956). This study proved to be important in changing the general views of ecologists from the Clementsian to the Gleasonian paradigm (Simberloff 1980; Westman and Peet 1982). In addition to elevation, Whittaker also considered gradients in moisture as potentially important in structuring vegetation. Both Clements and Gleason recognized the importance of multiple gradients in determining species distributions (Clements 1916; Gleason 1926).

Geographic gradients are often used as proxies for environmental gradients. Whittaker (1956) recognized that gradients he used in the Smoky Mountains were combined gradients of several correlated factors and that while ecotones may be readily apparent along elevational or other geographic gradients, the same is not necessarily so along environmental gradients (Malanson and Peet 2020). It is thus important to consider whether elevational (and other geographic) gradients are appropriate substitutes for more proximate factors governing species distributions. For example, within a given elevation there are varied microclimates where environmental conditions are influenced by factors such as topography or aspect that are important in determining species distributions. An additional issue is that at any given site environmental conditions will also vary in time.

The issues stated above also complicate identification of the elevation at which ecotones are demarcated. Variations in environmental conditions within elevational gradients can make the identification of elevations at which ecotones occur fuzzy and difficult to define precisely. This idea is articulated for Pikes Peak by Kelso (2012, p. 19): "zones are often difficult to delineate, as plant communities and individual species . . . interfinger and entwine in the upper elevations. . . . 'Treeline' is often irregular . . . Exposure, soil depth, slope stability, and moisture profoundly affect the vegetation patterns of the landscape; vastly different communities can be found at similar elevations but different topography or exposure."

Climate change is shifting the ranges of plant species along elevation gradients (Freeman et al. 2018); therefore, it is conceivable that the plant distributions observed by Clements at Pikes Peak may have undergone significant shifts over time, resulting in changed community patterns. Species range shifts with climate change are marked by variability in responses by organisms due to differences in their ability to disperse and establish in areas with favorable climates and accompanying biotic feedback. This differential response may result in changes in species co-occurrence, driving drastic changes in community composition and eventually creating novel species combinations (no-analog communities; Williams and Jackson 2007; Urban et al. 2012). Ecotone elevations may also shift over time with climate change (Beckage et al. 2008), additionally complicating our ability to link elevation to ecotone.

Variation in recovery from disturbance could affect environmental gradients and mean that plant distributions are not representative of the Clementsian concept of a "climax" community (Clements 1916), which could also blur association patterns. In our case, despite a long history of environmental protection in Pikes Peak, disturbances still occur, and legacies of mining and logging of the nineteenth century (Walcot 1900) on plant communities likely persist in areas. Clements (1916) also recognized that a community is "never in complete equilibrium, nor is it free from disturbed areas in which secondary succession is evident." He recognized that these disturbances could occur at a variety of scales: "An outcrop of rock, a projecting boulder, a change in soil or in exposure, an increase or decrease in the water-content or the light intensity, a rabbit-burrow, an ant-heap, the furrow of a plow, or the tracks worn by wheels, all these and many others initiate successions, often short and minute, but always significant" (Clements 1916, p. 3).

Scales of Community Pattern and Process

At what scales do patterns of communities arise, and at what scales should these communities be measured? The answers to these questions are not trivial. Plant distributions may vary with environmental variables predictably at large spatial grain; however, they may be unpredictable at small grain (Chase 2014; Damschen 2018). For example, in our study we assumed continuous, unbroken distributions along the elevation gradient. While at broad scales that might be a reasonable assumption (as can be seen in fig. S1), surely these distributions do not accurately reflect what one might observe on the ground at any given site at small scales. Clements's approach for classifying vegetation, characterized as Aristotelian essentialism (Johnson 1979; Pickett et al. 2009), was done by carefully observing which species occurred together and formed representative assemblages (field notes from Edith S. and Frederic E. Clements Papers 1876–1969; Clements 1916). Clements (1916, p. 3) emphasized the importance of detail to mechanistically understand factors controlling vegetation: "Even where the final community seems most homogeneous and its factors uniform, quantitative study by quadrat and instrument reveals a swing of population and a variation in the controlling factors." A small-scale, plot-based approach may be more appropriate, as it would at least ensure species co-occurrence and thus the possibility of interspecific interactions shaping distributions. However, determining the spatial scales at which these plots would correctly capture these interactions and scale up to a community is a difficult challenge (Levin 1992), especially considering species with vastly different sizes, from imposing trees to inconspicuous forbs. A related complication is that in the approach here species are treated as statistically equivalent regardless of their abundance and biomass. Thus, community patterns set by a few dominant species could be masked by hundreds of others. Despite these limitations, the analyses we present are useful if nothing else for their heuristic value in providing a concrete example from which to revisit and probe the Clements and Gleason debate and the challenges for reaching a conclusive resolution.

Reconciling Common Misinterpretations of the Polarized Paradigms

So, was Clements wrong? Was Gleason wrong? Should these paradigms even be viewed as dichotomous, opposing, mutually exclusive stances? In debates, contrary paradigms can polarize and create caricatures of viewpoints, which can lead to misinterpretations (Underwood 1986; Nicolson and McIntosh 2002). As we see above, it can be difficult to empirically make dichotomous conclusions that fully embrace and rule out one or the other. An alternative to the dichotomy proposed is that the "whole and part do not completely determine each other" (Levins and Lewontin 1985, p. 136); in other words, communities could be made up of species that are neither completely dependent nor completely independent of one another. Moreover, much of the controversy exists in the first place because of misrepresentations from the framing of the debate. On one hand, the strict holist (mis)interpretation of the Clementsian organism view may be hard to fathom. Likely few modern ecologists view communities as expressions of a general organizing principle creating a balanced, stable climax community, and it is unclear what mechanisms would make the parts (species) behave according to this abstract principle to create the whole (community; Levins and Lewontin 1985). It has been argued that Clements's view on the organism served as a metaphor and that the interpretation that his view necessitates mutual dependence among species by organizing principle is inaccurate (Kirchhoff 2020). Rather, it is argued that Clements believed that subordinate species in communities are governed by dominant species (Kirchhoff 2020), an idea with older roots in European physiognomic traditions, such as the work of the Finnish ecologist Aimo Kaarlo Cajander (1879–1943; Whittaker 1962; Oksanen 1991). On the other hand, a strict reductionist (mis)interpretation of the Gleasonian view would assume that species occur in isolation and react only to the physical environment. In such a view, there is no reciprocal interaction between species and environment and no clear role for species interactions in affecting species distributions. Likely few modern ecologists view species distributions in this way either. This alludes to critiques of species distribution models entirely based on climate alone (Dormann 2007). Likewise, some have argued that Gleason's view has also been misconstrued and point out that he indeed recognized the role of biotic interactions in shaping species distributions (Nicolson and McIntosh 2002).

Both Gleason and Clements agreed on the importance of dominant species in community patterns. Gleason (1910, p. 35) wrote, "The plant itself is in many cases the controlling agent in the environment; the differentiation of definite associations is mainly due to the interrelation of the component plants; and the physical environment is as often the result as the cause of the vegetation." Clements and Gleason would thus surely agree that the environments experienced by a plant at microsites may themselves be influenced by neighboring plants (as mentioned previously, this makes measuring relevant environmental variables at appropriate scales difficult and can complicate the use of geographic gradients as proxies for environmental conditions experienced by plants). Gleason expressed a healthy skepticism of his own ideas: "I have been an ecological iconoclast in many ways. . . . We have had too many icons set up to be worshipped. Test them out before you become too respectful toward them. Or, in the slang phrase, don't believe anything you hear and only half what you see, and this includes what you hear from me" (Gleason 1952, p. 10). And so the supposed fiercely opposing paradigms may not be so diametrically opposed in some ways and may have had more in common than we often realize. Bastow Wilson et al. (2004, pp. 233–234) went as far as to say that "Clements and Gleason is a useful straw man in introductions to papers. . . . However, their concepts were almost identical, reflecting deep understanding of plant communities that both had, and offer a strong basis for ecology today."

Legacy of the Debate on Ecological Thinking

While ecologists generally hold Gleasonian views, Clementsian influences still permeate the field in ways we may not realize. For example, ecologists often use fixed classifications of vegetation in research and management (e.g., USNVC 2022). Also, there is often little recognition that Eugene P. Odum's (1969) ecosystem concept had strong influences from Clementsian elements, including organismic metaphors (Simberloff 1980). These contradictions suggest that the debate still smolders and we continue to struggle with how to conceptualize ecological communities. It is important to recognize how legacies of the controversy likely affect our perceptions of communities and our approach to ecology.

Callaway (2007) contends that the narrative of the Gleasonian paradigm over the Clementsian paradigm has deeply permeated into many conceptual arenas of ecology, including neutral theory, species distribution modeling, and species interactions, leading to a strong emphasis on competition and an underestimation of facilitation. Furthermore, Callaway argues that the Gleasonian paradigm is not justifiable given large amounts of evidence on the importance of facilitation and evidence of evolutionary relationships driven by interactions among plants and that, moreover, gradient analyses are usually not appropriate to quantify spatial relationships at a scale appropriate to detect positive interactions (i.e., facilitation). Indeed, the role of positive interactions in shaping communities may be underappreciated (Callaway 2007; Holt 2008; Simha et al. 2022). For example, Moore (2020) found far fewer mentions of the word "mutualism" than "predator-prey" or "competition" in theoretical ecology texts. It would be interesting to rigorously link this bias in types of interactions studied and its shifts over time to the legacies of scientific paradigms as well as sociocultural changes. Holt (2008, p. 7) noted that "emphasizing the importance of such positive interactions in natural communities and ecosystems need not at all imply the world view of Gaia (with strains of 'Kumbaya' humming softly in the background), but rather reflects the subtle interplay of positive and negative interactions in weaving the current fabric of life emerging from the Darwinian struggle."

The influence of Clements and Gleason can also be seen in restoration ecology. For example, restoration approaches that aim to re-create an ecosystem as a copy of its previous or ideal state may implicitly subscribe to Clementsian ideas that communities follow predictable successional trajectories toward stable climax communities (the carbon copy myth in Hildebrand et al. 2005). In contrast, restoration approaches that recognize a dynamic, nonequilibrial view of ecosystems may implicitly follow Gleasonian ideas. For example, the concept of novel ecosystems departs from the Clementsian idea of predictable successional trajectories and stable climax communities (Hobbs et al. 2009). Pickett et al. (2009) proposed a framework for vegetation dynamics that integrates the views of both Clements and Gleason. This integrated framework acknowledges both the predictable patterns and the inherent variability and dynamism of ecosystems, providing a more nuanced approach to restoration goals and end points.

Classic studies and ideas have more to offer and relevance to ecology today than we may realize (Oksanen 1991). Both Clements and Gleason were keen naturalists and broad thinkers with ideas that still have value and are worthwhile to revisit and probe. It is important to realize how we may be affected by the historical narrative of the debate and the legacy it has had on the trajectory of our field. Here, revisiting the debate illuminates the difficulty in empirically, conclusively, and fully ruling out either paradigm. Our results illuminate the Clements-Gleason debate by allowing us to identify outstanding issues, such as how we quantify environmental gradients, the mechanisms that might generate Clementsian and Gleasonian patterns, and the scales at which they could be observed. Moreover, the dichotomous framing of the debate has obscured the fact that the two ecologists' views actually had common ground, especially in the recognition of the interplay between species and their environment. Clearly, Clements and Gleason continue to be interesting and have relevance in ecology today as we continue, as they had, to wrestle with conceptualizing ecological communities.

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Statement of Authorship

J.R. led the conceptualization, data analyses, and writing presented here with input from all authors, especially D.P.V. and C.M.M. C.M.M. additionally led species turnover analyses. S.D.O. compiled the species list and provided expertise on Pikes Peak and its flora.

Data and Code Availability

Data and code are available on Figshare (https://doi.org/10.6084/m9.figshare.25097240.v1; Resasco 2024).

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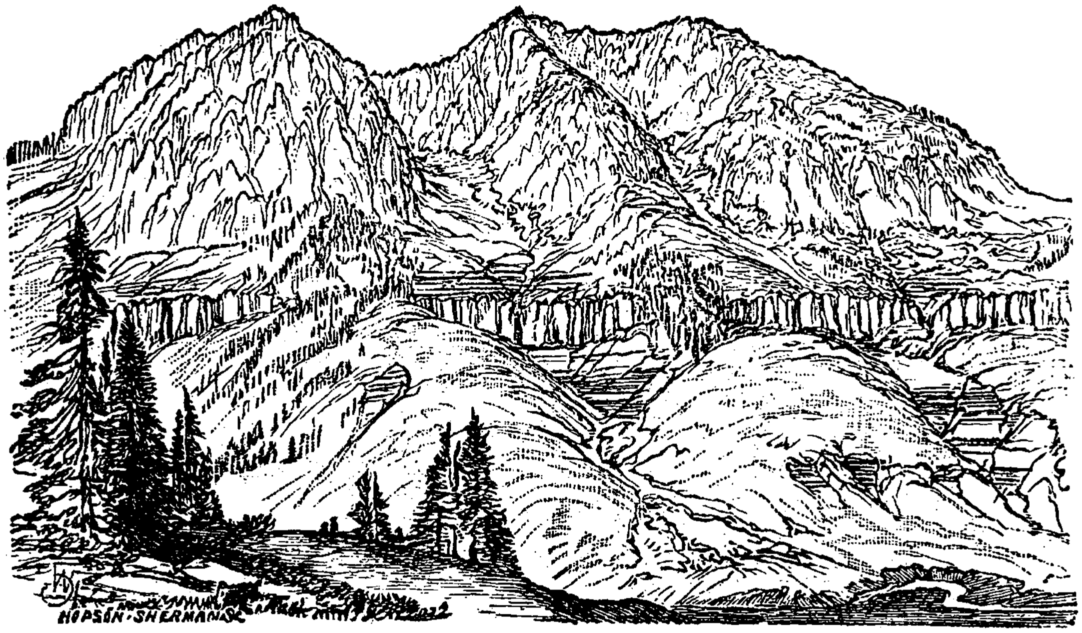

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