Small-scale Spatial Structures of Plant Species: Mechanisms, Implications, and Future Directions

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Cấu trúc không gian ở quy mô nhỏ của các loài cây: cơ chế, ý nghĩa và hướng nghiên cứu trong tương lai

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ABSTRACT

Small-scale spatial structures of plant communities represent a critical driver of population dynamics, species interactions, and fundamental ecological processes. At localized scales, plants experience biotic and abiotic conditions that often deviate from broader environmental gradients. These conditions are shaped by conspecific and heterospecific neighborhood interactions, which directly influence individual fitness, survival, and regeneration. Small -scale spatial patterns arise from habitat heterogeneity, dispersal limitations, plant-plant facilitation or competition, interactions with biotic agents (e.g., pollinators, herbivores), and stochastic disturbances. Despite their ecological significance, a comprehensive synthesis of the mechanisms driving these spatial structures remains incomplete, hindering their integration into predictive models of community dynamics. This review synthesizes current knowledge to address critical gaps in understanding, focusing on six key determinants of small-scale spatial organization: (1) habitat heterogeneity, (2) plant dispersal mechanisms, (3) intra- and interspecific interactions, (4) biological environment, (5) disturbance regimes, and (6) multifactorial synergies. Additionally, the functional consequences of these spatial patterns are evaluated, particularly their roles in biodiversity maintenance, intraspecific genetic diversity, and ecosystem recovery trajectories. Methodological limitations are critically examined, including scale mismatches in spatial analyses, overreliance on equilibrium assumptions, and insufficient incorporation of plant functional traits. To address these challenges, several research priorities are proposed: (i) integrating small-scale spatial data into macroecological models using hierarchical frameworks, (ii) adopting plant-centric approaches to quantify individual-level interactions, (iii) identifying ecologically relevant spatial scales through gradient analysis, and (iv) employing spatially explicit models (e.g., point-pattern analysis, agent-based simulations) to disentangle stochastic and deterministic drivers. Finally, the translation of insights from small-scale spatial ecology into restoration practices is emphasized, advocating for leveraging pattern-process feedback loops and incorporating spatial heterogeneity into conservation frameworks. This approach aims to bridge the gap between theoretical understanding and practical applications in ecosystem management.

Từ khóa:
Ảnh hưởng của sự xáo trộn, cơ chế phát tán, duy trì đa dạng sinh học, động thái quần xã, tương tác thực vật.

TÓM TẮT

Cấu trúc không gian của thực vật đóng vai trò trung tâm trong việc định hình động thái quần thể, điều chỉnh sự tương tác loài và thể hiện các quá trình sinh thái cơ bản. Mặc dù có ý nghĩa sinh thái quan trọng, các cơ chế hình thành cấu trúc không gian ở quy mô nhỏ của thực vật vẫn chưa được tổng hợp một cách hệ thống. Bài báo này nhằm giải quyết những lỗ hổng kiến thức hiện tại bằng cách phân tích và thảo luận các nghiên cứu gần đây, tập trung vào sáu yếu tố chính quyết định cấu trúc không gian quy mô nhỏ của thực vật: (1) sự không đồng nhất của môi trường sống, (2) cơ chế phát tán, (3) *sự tương tác lân cận, (4) ảnh hưởng của các yếu tố sinh học, (5) chế độ xáo trộn và (6) sự tương tác đa yếu tố. Ngoài ra, bài báo cũng làm rõ ý nghĩa của hướng nghiên cứu này với việc duy trì đa dạng sinh học trong quần xã và phát triển các chiến lược phục hồi hệ sinh thái. Những hạn chế trong các phương pháp nghiên cứu trước đây cũng được chỉ ra, từ đó đề xuất bốn hướng nghiên cứu ưu tiên nhằm cải thiện sự hiểu biết trong lĩnh vực bao gồm: (i) tích hợp dữ liệu không gian quy mô nhỏ vào mô hình vĩ mô để cải thiện dự đoán động thái quần xã, (ii) áp dụng phương pháp tiếp cận cá thể để hiểu rõ hơn về tương tác giữa các cá thể thực vật, (iii) xác định quy mô không gian phù hợp, giúp tối ưu hóa thiết kế nghiên cứu và diễn giải kết quả, (iv) sử dụng các mô hình không gian như phân tích điểm mẫu để tách biệt các yếu tố ngẫu nhiên và quyết định trong cấu trúc không gian. Bài tổng quan này góp phần thúc đẩy nghiên cứu sinh thái không gian bằng cách kết hợp các quan sát thực nghiệm với các giả thuyết thống kê sinh thái, cung cấp lý thuyết để làm sáng tỏ tính phức tạp của cấu trúc không gian ở quy mô nhỏ của thực vật và dự đoán phản ứng của quần xã rừng trong bối cảnh biến đổi khí hậu toàn cầu.*

1. INTRODUCTION

Spatial structure, defined as the arrangement and distribution of discrete patches within ecological systems, plays a pivotal role in shaping ecosystem composition, functionality, and resilience [1] . Each patch is characterized by its size, shape, and functional attributes, collectively influencing ecological processes across multiple hierarchical levels, from individual populations to communities and entire ecosystems [1, 2]. These ecological processes, including disturbance regimes, competitive interactions, and resource availability, operate across varying spatial and temporal scales, fundamentally regulating population dynamics and interspecific interactions [2]. Consequently, understanding spatial structure is indispensable for elucidating ecological mechanisms across organizational levels, from local to landscape scales.

Central to spatial structure are the interrelated notions of spatial patterns and scales [3]. Spatial patterns describe the variability in the distribution of organisms or ecological processes across space, with their interpretation heavily contingent on the observation scale [4]. Within ecological systems, plants interact with their biotic and abiotic environments within spatially defined contexts, often called "neighborhoods." The extent of these neighborhoods can vary significantly, with small-scale interactions occurring over distances of centimeters to meters, profoundly influencing plant growth, survival, and reproduction [5]. This highlights the critical importance of small spatial scales in shaping population dynamics and community structure.

In contrast, larger-scale spatial structures may exert weaker or negligible influences, underscoring the scale-dependent nature of ecological processes [4, 6]. While small-scale spatial structures provide insights into localized interactions among individual plants, larger-scale structures are more relevant for understanding population-level trends and landscape dynamics [7]. Nevertheless, the significance of small-scale spatial structures in plant communities remains paramount, as they directly mediate the immediate ecological interactions that drive individual and population outcomes [8].

The concept of small spatial scales was formally introduced by Stowe and Waller in 1979, who emphasized the importance of interspecific interactions and environmental factors at small spatial scales, particularly within grassland communities [9]. Most interactions occur among neighboring individuals in plant communities, whether conspecific (intraspecific) or heterospecific (interspecific) [10]. These interactions, including aboveground competition for light and space and belowground competition for water and nutrients, significantly influence individual plant growth and development. Conversely, individuals outside the immediate neighborhood typically have minimal or no direct impact on these dynamics. As a result, species density at broader spatial scales, often modeled using the "mean-field assumption," offers limited insights into the processes operating at smaller spatial scales, such as those within a study plot [11].

Although early studies in plant ecology recognized the existence of spatial structure in plant distributions, the "plant's-eye view" of the local landscape, a critical perspective for understanding community dynamics, has only recently gained substantial attention [12]. With the advent of spatial ecology as a distinct field, research on plant spatial structures has advanced significantly [13]. However, integrating emerging findings and identifying future research directions remain imperative. This paper addresses three key questions: (i) what are the origins and ecological implications of small-scale spatial structure in plants? (ii) what factors drive the spatial structure of plants? (iii) what are the key challenges and opportunities for future plant species-level spatial dynamics research?

2. FACTORS INFLUENCING THE SPATIAL STRUCTURE OF PLANTS

A range of ecological factors influences the spatial structure of plant species. Broadly, six primary factors contribute to the formation and dynamics of these spatial patterns.

2.1. Habitat heterogeneity

Habitat heterogeneity is a ubiquitous characteristic of ecosystems and a fundamental attribute of biological environments [2]. This heterogeneity manifests across multiple spatial scales, ranging from broad biogeographic regions and landscapes to smaller scales such as individual organisms and specific habitat components like study plots [14]. At smaller spatial scales, the distribution of resources critical for plant establishment, growth, and reproduction often exhibits significant variability [15]. Consequently, the spatial arrangement of plant species is strongly influenced by the spatiotemporal dynamics of habitat resource availability. The patchy distribution of habitat resources governs plant accessibility, shaping how plant species exploit these resources, leading to the observed patchy distribution patterns of vegetation.

Ecological processes, such as disturbances, further modulate the small-scale spatial distribution of plant species by altering resource availability within heterogeneous habitats. For instance, Thiery et al. identified a "tiger bush" vegetation pattern at small scales, driven by terrain features such as slope aspect and gradient [16]. Similarly, Shen investigated vegetation distribution in subtropical mountain forests, emphasizing the role of terrain characteristics, soil properties, and light availability across different spatial scales [17]. These studies revealed strong correlations between terrain-related variables and direct habitat factors, such as soil physicochemical properties and canopy gaps, significantly influencing plant communities' spatial structure. As the observational scale increases, the intensity of small-scale habitat heterogeneity typically diminishes, and the relationships between environmental factors become less pronounced [18]. This highlights the interplay between spatial scale and the strength of ecological processes, with terrain remaining a critical factor in assessing habitat heterogeneity and shaping habitat conditions.

Supporting this perspective, Xie and Deng investigated the spatial distribution of Castanopsis carlesii seedlings in the Wuyun Mountains of Hangzhou, China [19]. They found that habitat heterogeneity contributed to a patchy distribution of seedlings, each adapted to specific microhabitat conditions at small scales. Similarly, Shen and Zhang studied species diversity patterns in the forests of Dalaoling in the Three Gorges area of China, observing pronounced small-scale heterogeneity in tree species distribution [20]. Terrain-related factors such as slope, aspect, and altitude were particularly influential, affecting light availability, temperature, humidity, soil depth, structure, and disturbances associated with canopy gaps.

Under consistent climatic conditions, the spatial heterogeneity of soil physicochemical properties plays a pivotal role in determining small-scale variations in vegetation distribution. For example, in arid regions, soil resources often exhibit significant spatial heterogeneity [21]. Furthermore, in the context of desertification in arid and semi-arid regions, the encroachment of desert shrubs leads to the formation of "fertility islands," which serve as indicators of desertification processes [22]. In tropical forests, heterogeneity in soil conditions has been identified as a common phenomenon [23]. As the heterogeneity of soil resources increases, the degree of vegetation patchiness at small spatial scales also intensifies, underscoring the critical role of resource distribution in shaping plant community dynamics.

2.2. Plant dispersal mechanisms

Plant dispersal plays a pivotal role in enabling species to colonize new ecological niches, thereby shaping the spatial structure of plant communities. This process is fundamental to the survival and expansion of plant populations, as it allows species to escape competition, avoid inbreeding, and adapt to changing environmental conditions. In seed-reproducing plants, seeds typically fall near the parent plant due to gravity, resulting in the aggregation of individuals nearby. However, occasional passive dispersal events can disrupt these aggregated patterns. For example, wind gusts may transport seeds over considerable distances, while animals can extend dispersal ranges by carrying seeds. Silvertown and Law proposed that the spatial limitations of seed dispersal, mainly when seeds are concentrated around the parent plant, can promote species coexistence by fostering aggregated distribution patterns [24]. Empirical studies on the spatial patterns of various plant populations support this hypothesis. For instance, Nguyen Van Quy et al., in their study of the spatial distribution pattern of *Hopea pierrei* on Phu Quoc Island, Vietnam, found that the species' spatial distribution was influenced by wind-mediated dispersal, a common trait among species in the Dipterocarpaceae family [25]. Similarly, investigations of seedling populations of *Castanopsis superba* and *Schima superba* in the natural forests of northern Guangdong, as well as spatial distribution patterns of *Castanopsis fargesii* and *Camellia rosthorniana* in the Jinyun Mountains of China, revealed that dispersal mechanisms, such as gravity-driven seed fall and the clustering of mature seeds around the parent plant, result in small-scale aggregation patterns [19]. Likewise, desert plants often exhibit adaptations, such as large seed sizes or restricted long-distance dispersal, to maintain seed proximity to the parent plant [26]. This ensures the occupation of optimal habitats, as areas near the parent canopy typically have higher moisture levels and more favorable environmental conditions. This localized aggregation of seeds, a phenomenon known as synaptospermy, may also protect against predation and other environmental risks [27].

In clonal plants, vegetative reproductive structures, such as rhizomes and stolons, produce genetically identical offspring, leading to patchy distribution patterns at smaller scales. Huang et al. investigated the population dynamics and spatial distribution of four dominant wetland plants in the Qinghai Lake region in China [28]. Their findings demonstrated that clonal plants transition from random to aggregated distribution patterns through offshoot production from basal stems as they spread spatially. This clonal growth significantly influences these species' population structure and spatial organization, underscoring the importance of dispersal mechanisms in shaping plant community dynamics.

2.3. Intra- and interspecific interactions

Intra- and interspecific interactions among individual plants, including competition and facilitation, are critical determinants of the small-scale spatial structure of plant communities, particularly under specific environmental conditions [29]. Neighboring plants can enhance the growth conditions of a target plant through various mechanisms, such as mitigating extreme environmental stressors. For example, in arid ecosystems, neighboring plants can reduce exposure to intense solar radiation, while in subarctic tundra regions, they can provide thermal insulation against extreme cold [30]. These facilitative interactions highlight the importance of plant-plant dynamics in modulating microhabitat conditions.

Recent advancements in spatial ecology have facilitated the development of quantitative models, such as neighbor and local influence models, to analyze plant interactions rigorously [13, 23]. These models incorporate data on a plant's immediate environment and the structural characteristics of its neighbors to elucidate the dynamics of plant populations. The neighbor model posits that the size, similarity, and spatial configuration of neighboring plants can explain variations in plant size [31]. Conversely, the local influence model correlates a plant's size with the spatial extent of its influence [32]. As plants grow, their zones of influence increasingly overlap, resulting in competitive interactions within these overlapping areas. While competition can be symmetric, it often becomes asymmetric as larger plants monopolize a disproportionate share of available resources [33]. These models provide critical insights into how intra- and interspecific interactions shape species' spatial distribution and coexistence within forest communities, offering a robust framework for understanding plant community assembly and dynamics.

2.4. The role of the biological environment

The biological environment, comprising animals and microorganisms, plays a pivotal role in shaping the small-scale spatial structure of plant communities. In contrast to abiotic factors, which tend to remain relatively stable over time, the biological environment is characterized by dynamic spatial variability. A prominent example of this dynamic influence is observed in host-pathogen interactions [34]. Pathogens can induce seedling mortality near parent plants, thereby inhibiting the formation of dense host species aggregations and restricting their potential to dominate the community.

Furthermore, animals and microorganisms significantly influence plant spatial patterns through diverse biotic interactions, including herbivory, seed predation, and mutualistic relationships such as pollination and seed dispersal [35]. These interactions create a dynamic ecological framework wherein abiotic factors do not solely govern plant spatial distribution but are also intricately modulated by the interplay between plants and other organisms. As a result, the biological environment introduces an additional layer of complexity to the mechanisms driving species distribution and community composition, underscoring its critical role in ecosystem dynamics.

2.5. The role of external disturbances

External disturbances encompassing anthropogenic and non-anthropogenic factors alter resource availability, disrupt ecological processes, and reshape habitats. These disturbances vary significantly in scale and impact. For example, Kellner and Bosch demonstrated that the selective grazing behavior of herbivores predominantly influences the spatial distribution of vegetation in semi-arid grasslands [35]. Similarly, Bromley et al. highlighted that grazing pressure and fire regimes are critical determinants of plant patch formation [36]. In a study conducted in the transition zone between oasis and desert landscapes in the Tianshan Mountains of China, Chen et al. analyzed the spatial heterogeneity of vegetation and soil conditions [37]. Their findings underscored that localized human activities, such as overgrazing, land reclamation, and wood harvesting, were the primary drivers of small-scale vegetation variability. These disturbances resulted in increased soil exposure, which impeded plant community development and disrupted their spatial structure. In a related study, Liu and Li investigated the small-scale spatial structure of *Artemisia frigida* and *Cleistogenes squarrosa* populations under varying grazing intensities. Their results revealed that grazing intensity significantly influenced the spatial distribution of these species, thereby affecting tree distributions across different plant communities [38].

In natural forest ecosystems, disturbances such as tree senescence, pest outbreaks, diseases, and abiotic factors like wind, lightning, and snow accumulation create spatial gaps in the forest canopy. These gaps, referred to as forest gaps, exhibit distinct microclimatic conditions, such as higher light availability and elevated soil and air temperatures, compared to the surrounding forest. Research by Abe et al. and Batik et al. emphasized that the formation and recovery of forest gaps are critical for generating habitat heterogeneity and driving community dynamics [39, 40]. Furthermore, forest gaps are key mechanisms for forest regeneration and succession. Light-demanding pioneer species often colonize these gaps through seed dispersal, facilitating the establishment of new vegetation.

In natural grazing grasslands, micro-patches, small-scale spatial patterns, emerge due to grazing pressures and the activities of grassland rodents. Zhang et al. explored the mechanisms of patch formation and the changes in patch characteristics under varying grazing intensities in alpine meadows [41]. Their findings indicated that as grazing intensity increased, the number and diversity of micro-patches initially expanded. However, beyond a moderate level of degradation, both the number and diversity of patches began to decline. Additionally, individual patches' total area and size increased as degradation intensified. Vegetation attributes, including species composition, cover, height, and aboveground biomass, generally decreased with increasing degradation, although the timing, extent, and patterns of decline varied among patch types. Notably, patch diversity and evenness indices positively correlated with grazing intensity, while fragmentation and dominance indices negatively correlated.

2.6. Multifactorial interactions

A single factor does not govern the small-scale spatial structure of species within plant communities [42]. However, it arises from the complex interplay of multiple influences, often with one factor exerting a dominant effect. Specifically, the spatial arrangement of species at small scales is shaped by a combination of species-specific biological traits, environmental conditions, and their dynamic interactions. The integrated effect of population characteristics, interspecies relationships, and environmental factors ultimately determine this spatial configuration. Jeltsch et al. emphasized that plant distribution patterns result from various interacting factors, including competition, clonal growth, and alterations in vegetation life forms caused by disturbances such as grazing or fire [43].

Supporting this, Xin et al. investigated the patch distribution patterns of *Leymus chinensis* in alkaline grasslands under grazing and enclosure conditions [44]. Their findings revealed that soil processes were the primary drivers of patch distribution in the absence of grazing. However, at smaller spatial scales, the growth and dispersal capabilities of Leymus chinensis also significantly shaped spatial patterns. Under grazing disturbances, small-scale patches often emerged due to severe disturbances, with soil conditions, such as sudden degradation and extreme damage, becoming the primary limiting ecological factors. In these scenarios, grazing disturbance played a secondary role, while its influence became more pronounced in shaping large-scale spatial patterns.

3. IMPLICATIONS OF SMALL-SCALE SPATIAL STRUCTURE IN SPECIES DISTRIBUTIONS

3.1. Implications for biodiversity research

The mechanisms underlying the maintenance of species diversity within ecological communities represent a central question in biodiversity research. Species diversity in any given community reflects a dynamic equilibrium shaped by opposing ecological forces. On one hand, non-biological factors, interspecific interactions, and stochastic events at small spatial scales tend to reduce diversity. On the other hand, species migration from neighboring communities can counteract these effects by enhancing diversity. Although the precise mechanisms remain incompletely understood, substantial evidence suggests that local ecological processes, operating at smaller spatial scales, play a critical role in determining the number of coexisting species. For instance, Yang et al.investigated species distribution patterns in a highly diverse Leymus chinensis and mixed grassland community in the Songnen Plain of China [45]. Their study revealed that 72% of species exhibited aggregated distributions at scales smaller than 0.04 meters. They argued that such aggregation is pivotal in maintaining biodiversity within these communities. Based on these distribution patterns, ecological niches, and interspecific relationships, they proposed a hypothesis regarding the maintenance of grassland community diversity, emphasizing the importance of small-scale competitive dynamics.

3.2. Implications for plant population genetics

The small-scale spatial structure of plant populations plays a pivotal role in shaping their genetic dynamics. Its significance is primarily determined by how population genetics deviate from mean-field assumptions, which presume random distribution and homogeneous interactions within a population. The spatial arrangement of individuals within populations influences genetic outcomes in three primary ways:

3.2.1. Facilitating the success of mutant strains

In spatially structured ecosystems, mainly where seed dispersal is limited, mutant individuals carrying genetic variations often exhibit clumped distribution patterns [46]. The local frequency of these mutants among neighboring individuals is significantly higher than their overall frequency within the population. Consequently, the initial success of a mutant is not solely determined by its population-wide frequency but is also influenced by local spatial interactions between native and mutant individuals. Spatial invasion models have demonstrated that small-scale spatial structure can profoundly alter genetic outcomes, such as the persistence of polymorphisms or the evolutionary stability of strategies [47].

3.2.2. Supporting the maintenance of genetic polymorphism

The spatial heterogeneity of abiotic environments, combined with the immobility of plants, plays a critical role in maintaining genetic polymorphisms within populations. For example, in Pseudomonas fluorescens, non-motile strains rapidly develop polymorphisms within three days, exhibiting spatial segregation from more mobile strains [48]. Similarly, small-scale spatial structures arising from biotic interactions can enhance genetic diversity within plant populations [31]. In aggregated spatial patterns, intense competition among closely spaced individuals may lead to genetic exclusion, favoring specific genotypes' dominance [43].

3.2.3. Driving evolution of dispersal abilities

Phenotypic traits such as growth form, inflorescence size, and dispersal mechanisms (for pollen and seeds) significantly influence reproductive success and the spread of plant populations. These traits have been extensively studied in evolutionary biology. Depending on the local spatial configuration, rare genotypes may experience increased reproductive success in spatially structured populations. For instance, low dispersal ability can result in individuals clustering more tightly, increasing the likelihood of interactions with neighbors sharing similar dispersal traits. Hamilton and May proposed a model highlighting the potential advantages of limited dispersal in patchy environments [49]. Such environments may favor localized dispersal strategies, consistent with ecological predictions that dispersal traits evolve in response to local conditions. Evolutionary models that neglect small-scale spatial structure risk yielding incomplete or misleading conclusions.

On the whole, small-scale spatial structure profoundly influences plant population genetics by shaping the success of mutant strains, maintaining genetic polymorphism, and driving the evolution of dispersal abilities. These insights underscore the importance of incorporating spatial dynamics into genetic and evolutionary models to understand plant population processes comprehensively.

3.3. Implications for restoration ecology

Small-scale spatial heterogeneity is a critical ecological feature, prominently manifested through micro-patches' prevalence within plant communities [1]. These micro-patches are integral to natural grazing systems in grasslands, playing a pivotal role in shaping ecosystem dynamics. Moreover, their presence and spatial configuration are reliable indicators of grassland degradation. Zhang et al. underscored the importance of micro-patch composition, structure, functionality, and diversity in alpine meadows, highlighting their utility as diagnostic tools for assessing and restoring degraded grasslands [41]. Their findings emphasize the necessity of understanding micro-patch dynamics to guide effective grassland management practices, ensuring the sustainable utilization of both productivity and ecological functions. Similarly, Chen et al. demonstrated that analyzing spatial variability in vegetation cover within desertified grasslands enhances our comprehension of desertification processes and facilitates the development of targeted restoration strategies [37]. Preserving micro-patches, particularly at smaller scales, is essential for mitigating desertification and fostering long-term ecological sustainability in grassland ecosystems.

In forest ecosystems, small-scale spatial heterogeneity provides critical insights into species-specific ecological traits, particularly for endangered species at risk of extinction [13]. This information is invaluable for conservation managers, enabling the development of informed strategies to protect and restore vulnerable populations. Furthermore, small-scale spatial structures elucidate interspecies relationships, offering essential data for determining optimal species compositions and planting distances [25]. Such insights are crucial for reforestation, enrichment planting, and restoring degraded forest ecosystems, ensuring the successful rehabilitation of ecological functions and biodiversity.

4. ISSUES AND PROSPECTS

Several critical challenges persist despite significant advancements in studying small-scale spatial structures within plant communities. Here, we outline key unresolved issues and propose future research directions to address these gaps.

4.1. Integrating small-scale spatial structure into large-scale vegetation dynamics

While technological innovations such as remote sensing and Geographic Information Systems (GIS) have revolutionized large-scale vegetation studies, they frequently overlook the intricate details of small-scale spatial structures. This omission limits their capacity to fully capture vegetation dynamics in the context of global environmental change. Integrating small-scale spatial patterns into large-scale analyses could bridge this gap, enhancing the precision of vegetation models and fostering a more holistic understanding of plant community processes. Such integration would enable researchers to predict better and mitigate the impacts of global change on ecosystems.

4.2. Plant-centered approach to small-scale spatial structure

From biological and ecological perspectives, research on small-scale spatial structure must prioritize the plant as the fundamental unit of study [50]. This approach requires the identification of ecologically relevant spatial scales and the application of advanced statistical methodologies. With their relatively simple structural organization compared to forests, Grassland communities have served as a model system for investigating spatial patterns and processes. However, to advance this field, future research should adopt plant-centered frameworks, carefully delineate scales that reflect ecological interactions, and refine spatial statistical techniques to capture small-scale vegetation dynamics accurately. Such efforts will ensure that studies of small-scale spatial structure remain biologically meaningful and ecologically relevant.

4.3. Application in ecosystem restoration

Small-scale spatial structure, particularly the composition and spatial arrangement of micro-patches, offers critical insights into ecosystem succession, degradation, and restoration [51]. Current sampling methodologies often fail to adequately capture the variability and complexity of plant patches, leading to incomplete or inaccurate assessments of ecosystem health. Incorporating micro-patch patterns into sampling frameworks could improve ecosystem condition assessment accuracy and predictive capacity. This approach would provide a more robust foundation for designing and implementing effective restoration strategies.

4.4. Integrating local patch patterns to understand community-level characteristics

Ecosystems are characterized by hierarchical patch structures, where small-scale, high-frequency processes drive local variability and resilience. To fully understand community-level dynamics, examining patch dynamics at smaller scales and integrating these findings to infer broader community characteristics is essential. This approach transcends the mere aggregation of local processes, instead exploring how small-scale studies can elucidate the mechanisms underlying community organization and function. Researchers can develop a more comprehensive understanding of ecosystem dynamics by linking small-scale patterns to larger-scale processes.

4.5. Integrating small-scale spatial structure with the mean-field hypothesis

The mean field hypothesis, which assumes random spatial distributions and large-scale interactions, often fails to account for the localized nature of plant interactions [11]. In reality, competition and facilitation predominantly occur at small spatial scales, making small-scale spatial structure a critical factor in shaping population and community dynamics. Integrating small-scale spatial patterns with the mean-field hypothesis can address this limitation, enhancing theoretical and empirical plant community behavior models. This synthesis will provide a more nuanced understanding of the mechanisms driving community dynamics and improve predictions of ecosystem responses to environmental change.

5. CONCLUSION

Studying small-scale spatial structures in plant communities provides critical insights into the mechanisms driving ecological processes and ecosystem functioning. Small-scale spatial patterns, shaped by habitat heterogeneity, dispersal mechanisms, species interactions, and external disturbances, play a pivotal role in regulating population dynamics and species coexistence. These patterns have profound implications for biodiversity conservation, plant population genetics, and restoration ecology, offering a framework for understanding species distributions and community assembly. However, significant challenges remain, particularly in integrating small-scale spatial structures into large-scale vegetation dynamics and refining methodologies to capture small-scale interactions. Future research should adopt plant-centered approaches, develop advanced spatial statistical techniques, and integrate small-scale spatial structures with broader ecological theories such as the mean field hypothesis. By addressing these challenges, we can enhance our understanding of plant community dynamics, improve ecosystem management strategies, and contribute to the conservation and restoration of biodiversity in a rapidly changing world.

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