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A Review of Landscape Ecology Approaches for Studying Plant Invasions

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Abstract

Context

Alien plant invasions challenge biodiversity conservation and ecological restoration. The transdisciplinary nature of plant invasion prevention and management requires a holistic and spatially explicit perspective, to which landscape ecology can contribute.

Objectives

We aimed to understand how landscape ecology approaches have been applied to investigate the causes, processes, and impacts of plant invasion. Based on this analysis, we synthesized the current research opportunities and challenges in applying landscape ecology approaches to plant invasion studies.

Methods

We followed Reporting Standards for Systematic Evidence Syntheses (ROSES) to conduct the article search, screening, and analysis. We then synthesized the findings through the lens of landscape ecology-based research approaches, theoretical foundations, and methods.

Results

Research has disproportionately focused on explaining plant invasion patterns in landscapes with landscape structure (patchiness) often used as a proxy for ecological processes, especially disturbance. Fewer studies have directly modeled processes, whether investigating the effects of invasion patterns on ecological processes or the relationship between invasion processes and other landscape patterns/processes. Effects of spatial and temporal scales were rarely studied, with limited integration of hierarchical perspectives. Pattern-based statistical landscape models integrating environmental and landscape structure variables dominated, while gradient surface and process-based models were less applied despite their potential to capture floristic gradients and link patterns and processes.

Conclusions

Comprehensively considering hierarchical pattern-process relationships when deploying models could help in detangling complex invasion mechanisms and provide accurate information for invasion control. We highlighted the opportunities and advancing insights that hierarchy theory and gradient surface models could bring, as well as practical pathways for their application.

Key words: disturbance, gradient surface model, hierarchical framework, landscape ecology approach, plant invasion, scale effect

Introduction

Human-induced environmental change and alien plant invasion interact to cause major ecological and socioeconomic damage, which has challenged biodiversity conservation and ecological restoration (Turbelin and Catford 2021; Weidlich et al. 2020). Alien plant invasion changes the composition of native communities, resulting in native species decline and habitat structure change, which further alters ecosystem functions including nutrient and fire cycles and hydrology, to name a few (Ehrenfeld 2010; Simberloff 2011). These consequences can lead to reductions in ecosystem services related to provisioning, regulating, and cultural aspects (Castro-Díez et al. 2019; Eviner et al. 2012). Thus, plant invasion prevention and management have gained increasing attention over the past decades (Convention on Biological Diversity [CBD] 2010, 2022), with population-based and community-based approaches being common approaches to answer questions related to the establishment and spread of invasive plants (Gallien and Carboni 2017; González et al. 2010; Sakai et al. 2001; Ward et al. 2008). The transdisciplinary nature of plant invasion management, however, also requires a more holistic approach that considers all components and their interactions on landscapes (Hulme 2017; Kumar Rai and Singh 2020).

Landscape ecology emphasizes pattern-process relationships and scale effects when interpreting ecological questions, where pattern refers to the spatial composition and configuration of landscape features (e.g., fragmentation of forests, urbanization gradients), and process refers to biotic, abiotic, or anthropogenic processes (e.g., species competition, fire, nutrient flow) that not only create spatial patterns but also can be affected by spatial patterns (Turner, 1989; Wu and Hobbs, 2007). Thus, landscape ecology offers a spatially explicit perspective into what factors might help or hinder plant invasion and guide comprehensive invasion control (Gillson et al. 2008; Theoharides and Dukes 2007; Vilà and Ibáñez 2011; With 2002). Particularly, the multi-scaled approaches promoted by landscape ecology (Holland and Yang 2016) are essential since the causes and impacts of plant invasion are scale-dependent (Pauchard and Shea 2006). In addition, landscape ecology approaches can help answer questions about the role of disturbances (e.g., fire, development, agriculture, and fragmentation) on plant dynamics (De Blois et al. 2002). This perspective can be extended to plant invasion studies as disturbances are known to increase community invasibility (Hobbs and Huenneke 1992). Lastly, anthropogenic disturbances, which are the main driver of plant invasion and biodiversity loss (Hulme et al. 2023), generate fragmentation and environmental heterogeneity across space, which provides suitable conditions for alien plant establishment, influences propagule availability, and may promote the spread of invasive populations (Saunders et al. 1991; Štajerová et al. 2017; Vilà and Ibáñez 2011; With 2004).

In the past two decades, researchers have adopted various landscape-based approaches to understand pattern-process relationships and disentangle the disturbance mechanisms behind plant invasion.

Simultaneously, a range of landscape-based invasion theories have been offered, such as the role of landscape structure or environmental heterogeneity in promoting invasion, as well as the scale-dependency of determinant invasion factors or effects (Melbourne et al. 2007; O'Reilly-Nugent et al. 2016; Pauchard and Shea 2006; Theoharides and Dukes 2007; Vilà and Ibáñez 2011; With 2002). These theories have been tested through various landscape metrics and models to describe patterns and processes, with careful selection of scales, metrics, models, and analytical tests contributing to successful outcomes (Jones et al. 2010; Thuiller et al. 2010). Advances in data acquisition and analytical technologies have also facilitated the elucidation of invasion mechanisms and effects, thereby improving management efficiency (Fusco et al. 2023; Müllerová et al. 2023; PyšEK and Hulme 2005).

Prior reviews have examined the influence of environmental heterogeneity, landscape structure, and their interactions with other ecological processes on biological invasions, across taxa as well as specifically focused on plant invasions (Melbourne et al. 2007; O'Reilly-Nugent et al. 2016; Vilà and Ibáñez 2011; With 2002). Reviews have also highlighted the role of scale on plant invasion processes (Milbau et al. 2009; Pauchard and Shea 2006). However, a recent and comprehensive understanding of how landscape ecology approaches have been used to study the causes, processes, and impacts of plant invasion is lacking and could offer new insights into how human-induced disturbances can be managed. With the increasing need to effectively manage biological invasions under global change, it is an opportune time to synthesize how landscape ecology approaches have been applied to study invasive plants and explore their potential for biodiversity conservation.

This review synthesizes how landscape ecology approaches have been used to study plant invasions and how these approaches contribute to understanding plant invasion. We define landscape ecology approaches as those exploring the relationship between pattern, process, and scale, with a goal of advancing transdisciplinary practical application (e.g., conservation, planning, decision-making) and sustainable development. We perform a systematic search and review of the literature focused on landscape ecology approaches to plant invasion research, and extract the research themes, theoretical foundations, and methods from each paper. We then synthesize these findings to show how theories and methods have been incorporated to test and advance plant invasion knowledge and discuss the advantages, opportunities, and challenges of using landscape ecology approaches for advancing plant invasion knowledge.

Materials and methods

Article search and screening strategy

We followed the Reporting Standards for Systematic Evidence Syntheses (ROSES) to conduct the article search, screening, analysis, and synthesis of the results. First, we performed an advanced literature search on 7 February 2024 through Web of Science (WoS), the most popular and authoritative source of scientific publications and citations (Birkle et al. 2020). The search considered title, abstract, keyword plus, and author keywords. The query comprised terms to capture key concepts in landscape ecology, including heterogeneity, scale, pattern, and process, as well as common disturbances studied in the discipline. Since the term "invasive" is debated, we included several alternative terms in our keyword combination, such as "alien" and "nonnative." The final query was: TS=(("invasion*" OR "invasive" OR "non-native" OR "nonnative" OR "exotic" OR "non-indigenous" OR "alien ") AND ("plant" OR "vegetation") AND ("landscape" OR "region*" OR "heterogeneity" OR "fragmentation" OR "pattern" OR "gradient*" OR "process" OR "spatial" OR "scale" OR "scaling" OR "hierarch*") AND ("disturbance" OR "fire" OR "land use" OR "land cover" OR "landuse" OR "landcover" OR "agricultur*" OR "anthropogenic" OR "urban*") AND ("dispers*" OR "spread")).

The initial query identified 2,515 studies, which we refined by limiting topics and research areas (Fig. 1), reducing the number to 2,050. We further limited the search to Q1 journals, resulting in 785 articles. We then manually screened the abstracts and excluded articles that did not reflect basic landscape ecology principles, which reduced the pool to 193 articles. We excluded an additional 17 studies that were conceptualized according to a landscape ecology paradigm but did not employ spatial-based analysis (e.g., only had conceptual models or economic analyses). In total, 176 studies were identified for full review.

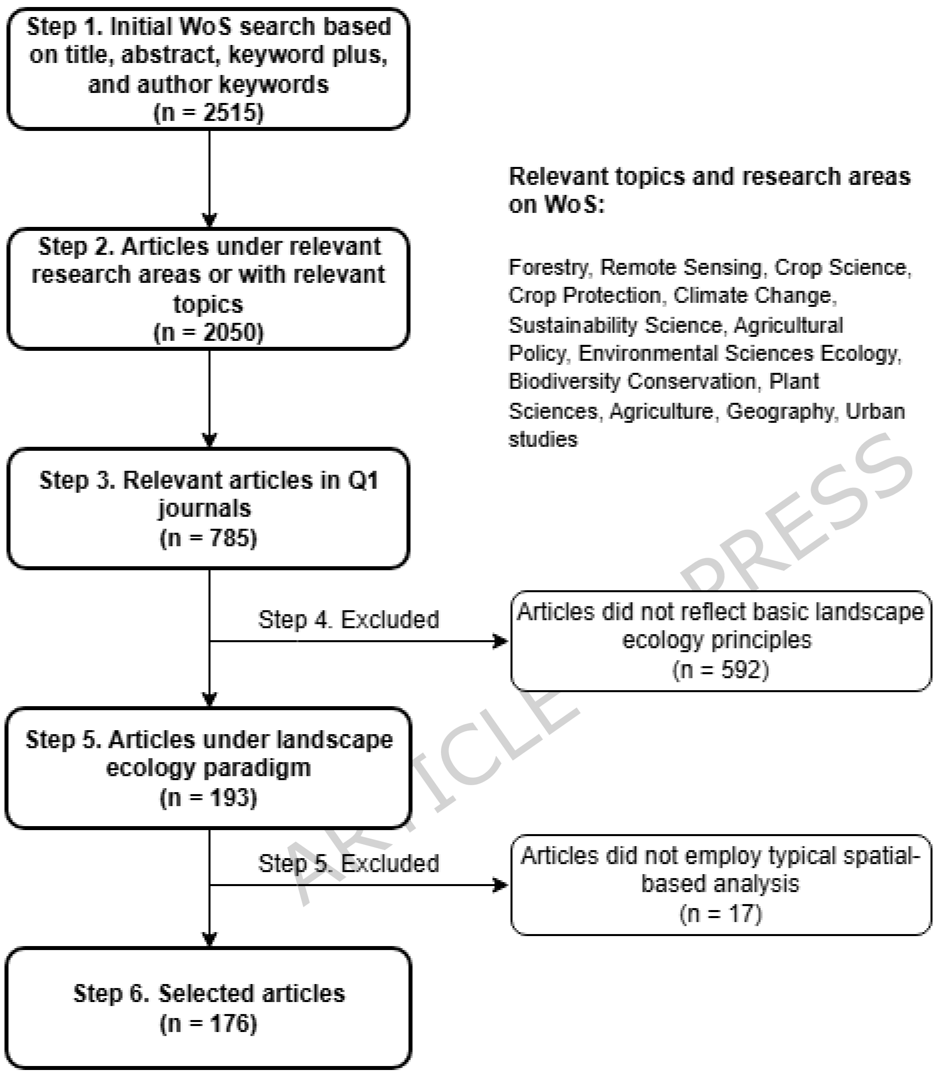

Fig. 1 Process for identifying and screening articles. WoS = Web of Science

Data extraction and content analysis

We developed a set of 16 reporting parameters across seven categories related to study context, plant attributes, theoretical foundations, landscape models, and landscape metrics (see Appendix 1). Each of the 176 articles was read in its entirety and coded against these 16 parameters. We computed descriptive statistics for each parameter and synthesized the current state of landscape ecology-based plant invasion research based on the article text. Based on the syntheses, we discuss the challenges and opportunities of this approach for plant invasions, specifically as it relates to the development of relevant theories and invasion management.

Results

Publication and topical trends

Since the 1990s, the number of landscape ecology-based articles related to plant invasion has increased steadily, peaking in 2021 (Fig. 2a). Studies have been conducted throughout the globe, with the majority in the Global North, mainly North America (31.8%) and Europe (31.3%). Notably, 29.5% of studies were conducted in the United States, followed by China (7.4%), South Africa (6.8%), Australia (4.5%), France (4.5%), and Spain (4.5%). The studies were published in various journals related to ecology and conservation, including *Landscape Ecology*, *Diversity and Distributions*, *Journal of Applied Ecology*, and *Biological Conservation* (Fig. 2b).

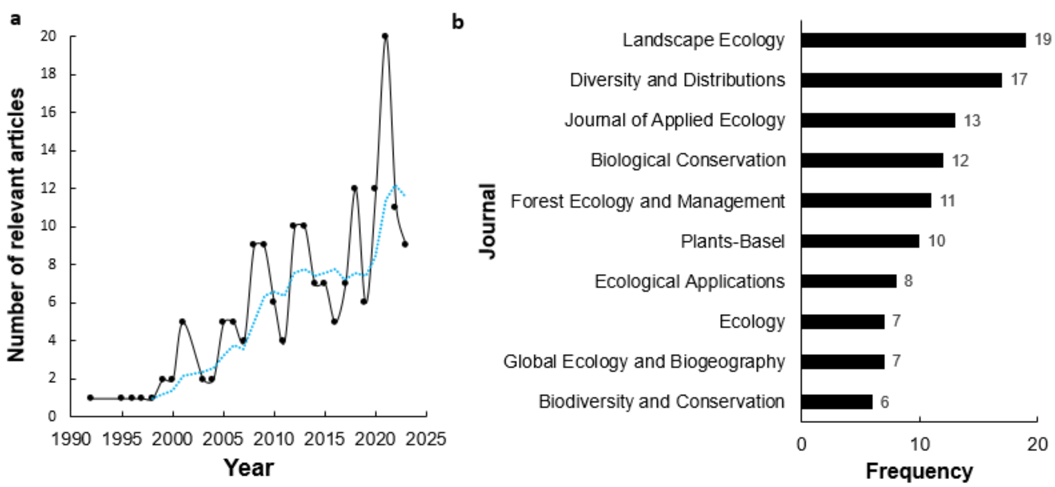

Fig. 2 (a) Publication trends for landscape ecology-based plant invasion articles (1992-2023), with blue dashed line indicating 5-year moving average, and (b) the top ten journals in terms of the frequency with which related articles were published.

Over the past two decades, landscape ecology approaches were employed in plant invasion studies across diverse landscapes and involved various plant types. Most studies (51%) were conducted on heterogeneous landscapes with multiple land use and land cover types (Fig. 3a). For those focusing on a single type, forests garnered the most attention (19%) and were studied nearly 1.6 times more than riparian, coastal, or wetland zones (12%), around three times more than agricultural landscape (6%), and four to five times more than urban (5%) and grassland (4%) landscapes (Fig. 3a). Shrubland (2%) and savanna (1%) landscapes received much less attention, despite their risk of invasion. Grasses were the most commonly studied invasive plants (35%), followed by forbs/herbs (30%), shrubs/subshrubs (14%), and trees (11%) (Fig. 3b). Although at least 3,093 distinct invasive or alien species were identified, studies tended to focus on overall invasion levels by considering all detected invasive plants, rather than focusing on individual species. Only 92 species were explicitly targeted, including 38 trees, 30 forbs/herbs, 20 shrubs/subshrubs, 13 grasses, 5 succulents, 3 vines, and an aquatic plant (Appendix 2).

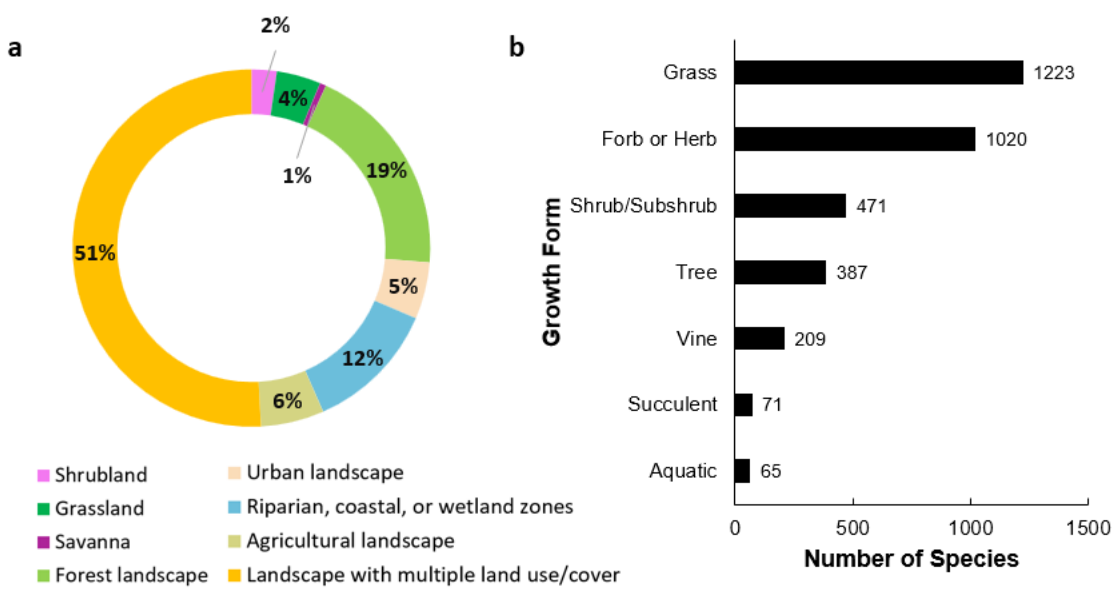

Fig. 3 (a) Target landscape types of the studies reviewed, and (b) growth forms of target invasive species identified in the reviewed papers. Some species may exhibit multiple growth forms, depending on the environment.

Characteristics of landscape ecology approach

Theoretical foundations

We identified eight general theoretical mechanisms that guided investigations of plant invasions via a landscape ecology approach. These mechanisms included (i) the impact of landscape patterns on invasion patterns, (ii) the impact of landscape patterns on invasion processes, (iii) the impact of landscape processes on invasion patterns, (iv) the impact of landscape processes on invasion processes, (v) the impact of invasion patterns on landscape patterns/processes, (vi) the impact of invasion processes on landscape patterns/processes; (vii) the impact of spatial/temporal scale on plant invasion patterns/processes, and (viii) the use of hierarchy theory. However, there was an imbalance in both the directionality and magnitude of these mechanisms (Fig. 4), with the most attention being paid to how key landscape ecology elements (e.g., patterns and processes) impact plant invasion patterns and very few studies focusing on the impact of plant invasion patterns/processes on landscape patterns/processes. Only eight studies focused on how invasion patterns impacted other ecological patterns/processes (Fig.4, red arrows on the right), such as native plant regeneration (Lázaro-Lobo et al. 2021) or landscape fragmentation processes (Coppedge et al. 2001). Three studies investigated the impact of invasion processes on landscape patterns/processes through incorporating the feedback loop between invasion processes and other disturbances in modeling plant invasion (e.g., Higgins et al. 2001; Wang et al. 2019).

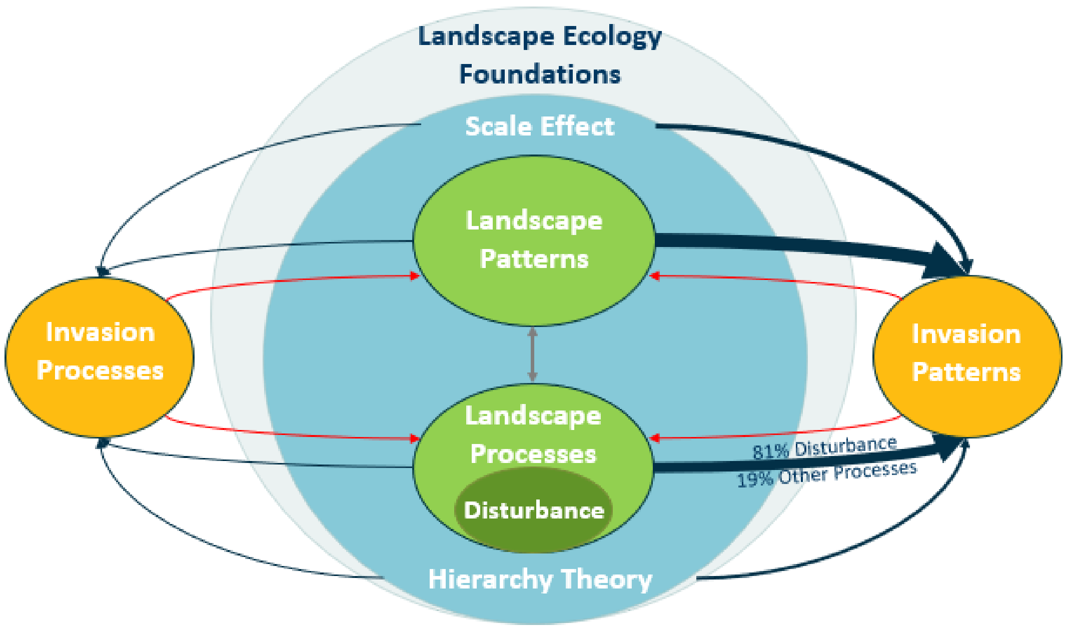

Fig. 4 Landscape ecology theoretical foundations used to study plant invasions. The direction of the arrows indicates the direction of the relationship investigated in the reviewed studies (e.g., the red arrows show the impact of invasion patterns/processes on landscape patterns and landscape processes). Arrow width is proportional to the number of studies that employed each foundation. A total of 176 studies were reviewed, but studies could incorporate multiple theoretical foundations.

The dominant landscape ecological theory investigated was how landscape patterns impacted invasion patterns (165 of 176 studies). Specifically, 149 studies investigated the effects of landscape patchiness, and 44 studies considered the effects of environmental heterogeneity (e.g., spatial gradient in climate factors) on invasion patterns; note that some studies addressed both aspects. For example, the total length of motorways and landscape mean patch area were found to be positively related to the percentage of invaded area (Mouta et al. 2021), while future scenarios of climate and land use/cover change were found to be useful for predicting potential suitable habitat for invasive plants (Manzoor et al. 2021). However, the impact of landscape patterns on invasion processes—another central tenet of landscape ecology

(Kupfer 2011)—received much less attention, such as the impacts of distance from propagule source on dispersal of invasive plants (Egawa 2017; Zhang et al. 2022).

The theoretical foundation receiving the second-most attention (149 studies) was the impact of landscape processes (primarily disturbances) on invasion patterns. This pattern-process coupling was evident in the number of studies that used pattern variables to quantify landscape processes (126 studies). For example, road density (Dark 2004) and distance (Landi et al. 2020) were used to evaluate how transportation development and urbanization impacted invasion patterns. Similarly, the proportion of wildland–urban interface was used as an indicator of housing development to investigate its effect on invasion patterns (Gavier-Pizarro et al. 2010). Additionally, some landscape processes—such as fire and grazing (Wang et al. 2019)—were incorporated into model simulations (16 studies). Conducting comparative analysis across different disturbance regimes (7 studies) was another approach to investigate the impact of landscape processes on invasion patterns. One study investigated the impact of agricultural practices on plant invasion patterns by inferring from the spatial arrangement of 'genetic' population diversity under broad disturbance contexts instead of directly quantifying or simulating processes (Magda and Gonnet 2001). Notably, the impact of landscape processes on invasion processes was less studied (8 studies), with the main focus on the impact of disturbances (e.g., fire) on invasion spread (Higgins et al. 2001; Shackelford et al. 2013).

The scale dependency of landscape composition and configuration is well established in landscape ecology (Turner et al. 1989), with it being widely understood that multiscale information is required to understand landscape structure and function (Wu 2004). Additionally, predicting the impacts of landscape pattern or processes on invasive patterns/processes requires, at minimum, understanding how the scale of invasive species' response aligns with the scale of the driving landscape pattern or processes that were observed (With 2002) and how such cross-scale relationships help explain invasion mechanisms and patterns (Levin 1992). The three key dimensions of scale in landscape ecology (spatial, temporal, and organizational level) (Wu 2007) received relatively balanced attention in the literature. Here, we consider organizational-level effects as being rooted in hierarchy theory, which should be distinguished from spatial and temporal scale effects that include extent, grain, coverage, and spacing as key components. Studies involving multiple scale effects primarily focused on both spatial/temporal scales and cross-organizational dynamics (Fig 5). As mentioned above, studies incorporating multiple organizational levels were framed within the hierarchical paradigm, acknowledging plant invasions are often driven by processes happening at multiple biological levels (Gallien and Carboni 2017; Pauchard and Shea 2006; Sakai et al. 2001; Ward et al. 2008).

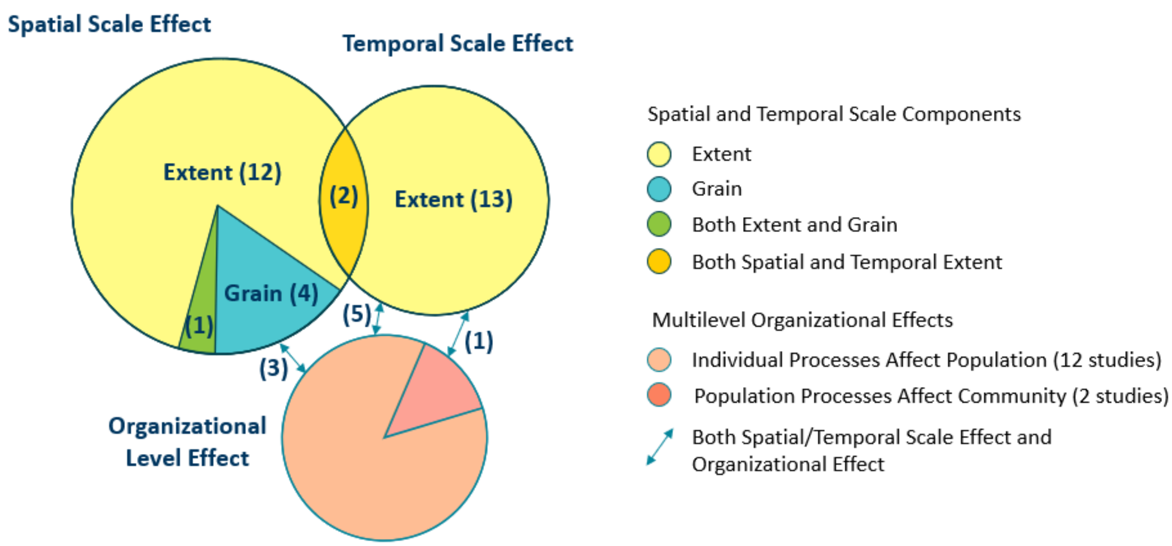

Fig 5 Frequency and types of spatial, temporal, and organizational scale/level effects studied. Circle size represents the number of studies that included each effect, with spatial scale effects being the most prevalent (19 studies), followed by temporal (15 studies) and organizational level effects (14 studies). One study investigated both spatial extent and grain; two investigated both spatial and temporal extent. Arrows indicate studies addressing both spatial/temporal scale effects and organizational level effects. Three studies investigated both spatial grain effect and how individual processes affect population pattern; five studies investigated both temporal extent effect and how individual processes affect population pattern; one study investigated both temporal extent effect and how population processes affect community pattern.

The objective and scope of studies that investigated spatial or temporal scale effects varied. Studies on spatial scale effects tended to focus more on how different scale components impact the relationship between influencing factors and invasion patterns, whereas those addressing temporal scale effects investigated how drivers and temporal scales jointly influence both invasion patterns and processes. The 19 studies that explicitly included spatial scale mainly focused on how the effects of specific drivers on invasion patterns varied across multiple extents. Fewer studies evaluated the impacts of spatial grain on modeling invasion patterns (Higgins et al. 1996, 2001), even though landscape pattern analyses are highly sensitive to grain (Frazier 2016; Hall et al. 2004; Turner 1989; Turner et al. 1989; Wu et al. 2002; Wu 2004). Despite considerable research in landscape ecology on scaling (Frazier 2014; Frazier et al. 2023; Markham et al. 2023). Collingham et al. (2000) remains the only study to focus on this topic and investigate the scaling effectiveness of invasion prediction by cross-applying models independently trained at different spatial scales (fine-scale regional vs. coarse-scale national). That study found that while environmental drivers remained consistent across scales, scaling success is asymmetrical and depends on the interaction between resolution and extent. For example, scaling up a fine-scale regional model is effective for resolution changes within a fixed extent, but the same model fails to maintain predictive power when extrapolated to a national extent using coarser resolution data.

Compared to spatial scale, temporal scale was more widely used to capture how drivers impact invasion processes (spread) over long time periods. The 15 studies that included temporal scale mainly focused on the impact of temporal extent on both invasion patterns and processes. Notably, these temporal extents were related to the impacts of changes in disturbance regimes (e.g., fire, Pausas et al. 2006) or environmental conditions (e.g., urban sprawl and climate warming, Nobis et al. 2009) on invasions. In addition, two studies tested both spatial and temporal scale effects, but in all cases, the studies analyzed the two dimensions of scale effects independently, without exploring the combined impact. Furthermore, our analysis highlights hierarchy theory as a critical yet under-explored framework (19 studies) for linking cross-level landscape processes to invasion dynamics. As mentioned above, studies addressing cross-organizational dynamics often utilized hierarchical frameworks (14 studies) to elucidate how lower-level organizational processes drive larger-scale invasion patterns/processes—most commonly the impact of individual-level dynamics on population-level invasion (12 studies). Unlike the relatively independent treatment of spatial and temporal scale effects, cross-organizational dynamics were more frequently integrated with either spatial (3 studies) or temporal scale effects (6 studies) to investigate how spatial grain or temporal extent influences the modeling of invasion outcomes.

Under the hierarchical framework, lower-level organizational processes are one of the key underlying drivers for the focal-level invasion pattern. Among the three types (20 subtypes) of lower-level organizational processes identified, vital rates and demographic processes were the most widely studied, accounting for 55% of the indicators (e.g., survival, establishment, and recruitment). Dispersal-related processes followed at 30%; notably, the specific indicator of dispersal itself was the most frequently addressed subtype, representing about 25% of the total. Ecological interactions (e.g., competition and plant–soil feedbacks) received relatively less focus, comprising 15% of the identified processes. Except for these biological processes, nine types of disturbances were also incorporated into such hierarchical frameworks and drove the modeling of invasion patterns and processes, among which anthropogenic disturbances (e.g., urbanization, agriculture) and fire were the focus. Unlike lower-level organizational processes, these disturbances function as focal-scale 'trigger' processes—the scale at which invasion patterns are typically observed—while exhibiting significant spatial heterogeneity at finer scales. These disturbances interact with lower-level organizational processes to influence invasion dynamics at focal levels (12 studies). In general, most studies framed under hierarchy theory (17 studies) concurrently consider both lower-scale processes and larger-scale environmental constraints. However, only three studies explicitly addressed the bidirectional interactions (i.e., loop feedback) between small-scale biological processes and disturbance/environmental factors (e.g., local soil characteristics), to determine the final invasion pattern/processes.

Overall, the literature has predominantly focused on how landscape patterns or processes influence invasion patterns or processes, whereas fewer studies have investigated the role of invasion patterns or processes on landscape patterns or processes. This finding highlights a gap in understanding how the patterns and processes of plant invasion, in turn, feed back to shape overall landscape patterns and processes. This dearth may also be hindering a deeper understanding of the invasion process itself and its impacts, resulting in weaker management strategies. Similarly, the limited number of studies investigating invasion across multiple biological levels suggests there is much work to do to understand the hierarchical invasion dynamics in landscapes.

Landscape ecological measurement and metrics

Spread and persistence are key components of successful plant invasion (Santos et al. 2016), so having robust measurements of these two factors is essential to understand invasion dynamics. Studies employed 41 different types of measurements to quantify spread and persistence, which can be grouped into six categories: measurements of (i) composition of invasive plants, (ii) patterns of native species, (iii) composition of species on invaded landscape (both native and non-native plants), (iv) distribution of invasive species, (v) speed of invasion, and (vi) propagule pressure and dispersal (Appendix 3). In addition, some studies used indicators related to plant ecological traits, genetic structure, and invasion potential (Appendix 3) to infer potential spread or persistence. Among these, measurements of plant richness (43), presence (41), and abundance (33) were most commonly employed. Ecological traits of invasive plants (e.g., plant functional traits), propagule pressure and dispersal (e.g., dispersal distance), invasion speed (e.g., rate of population increase and spread rate), and genetic structure (e.g., genetic connectivity) were less measured. Except for focusing on invasive plants themselves, the changes in vegetation composition on the invaded landscape, such as the non-native to native species ratio, were also used as indicators of invasion (Duchesneau et al. 2021). Most of these measurements were acquired or modeled from field observations and were spatially explicit.

Landscape metrics are a fundamental focus of landscape ecology because quantifying structure is central for studying pattern-process relationships (Kupfer 2012). Conventional landscape metrics derived from the patch mosaic model (Frazier and Kedron 2017) were used in 155 studies, primarily as inputs (influencing factors) to a statistical model. Among the commonly used metrics, aggregation metrics were the most widely adopted (106), followed by area and edge metrics (78), diversity metrics (18), and shape metrics (16), reflecting a focus on the impacts of the arrangement of patches and their clumpiness or isolation on invasion. One study used the edge perimeter length of the invasive front to measure invasion (Higgins et al. 1996). Very few studies employed surface metrics (Leimbach-Maus et al. 2020; Pastick et al. 2021), which derive from continuous datasets and mainly focus on 2.5D topographical surfaces (Frazier and Kedron 2017), possibly because their ecological interpretations are not as developed (Kedron and Frazier 2019; McGarigal et al. 2009). However, these metrics may offer a means for scaling pattern-process relationships, particularly as there are tools, including the geodiv R package, to facilitate their computation (Smith et al. 2021).

Models and modeling

Models are used to disentangle the mechanisms of plant invasion, such as how landscape heterogeneity impacts the spread and patterns of invasion and how spatial or temporal scale impacts process-pattern relationships. Spatially explicit models were widely used (92%) to study how ecological processes, landscape structure, environmental heterogeneity, and socio-economic factors influence plant invasion, but only 32% of these studies had spatially explicit outputs. Additionally, 8% of studies employed spatially implicit models, which ignore the precise spatial arrangement of landscape elements and rely on landscape-level summary values, evaluating the impacts of landscape composition (e.g., land-cover diversity or proportion of different land covers) on plant invasion. We identified nine typical methods/models (Fig. 6) that include (i) general statistical models that incorporate landscape information, (ii) species distribution models (SDM)/niche models/habitat suitability models, (iii) process-based landscape models, (iv) spatial regression analysis, (v) spatial point pattern analysis, (vi) machine learning models that incorporate landscape information, (vii) spatial dispersal models, (viii) spatial decision models, and (ix) neutral landscape models.

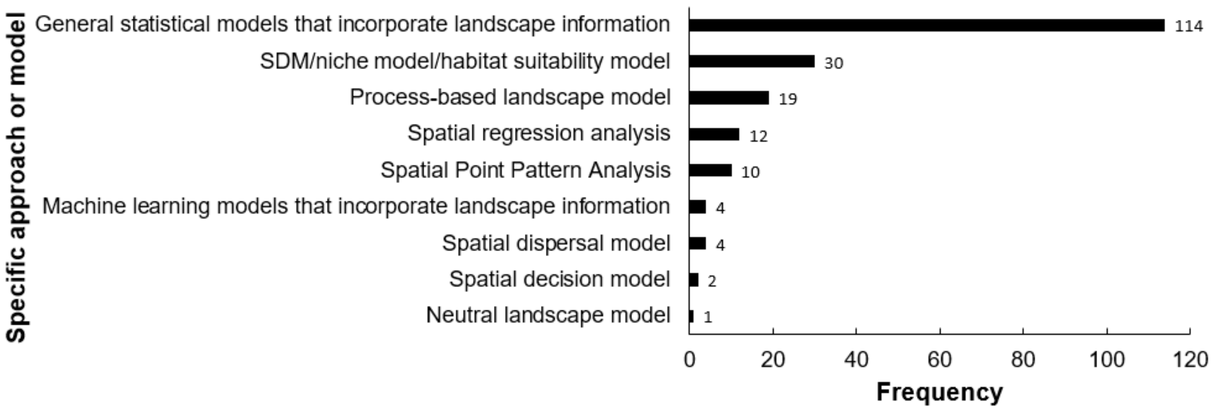

Fig. 6. Usage frequency of landscape models and analyses. Certain studies include multiple categories of landscape models or analyses. SDM = species distribution model.

The most common approach to incorporate landscape information was using landscape pattern variables in general statistical models (i.e., regressions) to investigate how different factors impact invasion patterns or processes (114 studies). The other model types were employed 30 or fewer times each. Species distribution models (SDM)/niche models/habitat suitability models were often used for detecting, predicting, and long-term monitoring of plant invasion patterns. Studies also combined landscape pattern information and other environmental factors with machine-learning tools or spatial regression models to investigate the roles of different influencing factors in determining plant invasion patterns or predicting the distribution of invasive plants (Golivets et al. 2019; Park 2022). Process-based landscape models were employed to embed ecological process information at the pixel level and to simulate the plant invasion dynamics under different forcing regimes and were always used as the approach to test hierarchy theory. For example, cellular automata models were effective in simulating long-term landscape invasion pattern changes under different land management scenarios (e.g., grazing and fire, Wang et al. 2019) and examining temporal dynamics of the plant diversity-invasibility relationship (Clark et al. 2013). Process-based SDMs could comprehensively model invasion patterns under changing environmental scenarios through incorporating population dynamics, biotic interactions, and disturbances within a hierarchical framework (Carboni et al. 2017). Among the fewer applied models, spatially explicit decision-support models have been employed to prioritize invasive plant management by integrating the impacts of invasion drivers, stand characteristics, and management history (Roura-Pascual et al. 2009, 2010). Neutral landscape models were useful in detecting critical thresholds or factors correlated with changes in invasion patterns, but only a single study utilized them (Zurlini et al. 2013).

Factors influencing plant invasion

Disturbances, particularly anthropogenic ones, are the main driver of plant invasion (Hulme et al. 2023). A total of 137 studies analyzed the impacts of anthropogenic disturbances on plant invasion, mainly including the effects of urbanization, transportation development, agriculture, and other anthropogenic activities (Fig. 7a). Anthropogenic disturbances directly impact land use/cover change and can be easily captured through landscape pattern variables (Zurlini et al. 2013) and included in models. For example, building density, a proxy for urbanization, has been found to be positively related to the occupancy and cover of certain invasive plants (Catford et al. 2011). Distance to road can be used to measure the impacts of transportation development, with more invasive plants found closer to roadways (Landi et al. 2020). The impacts of fires—another important disturbance that can be induced by both anthropogenic activity and climate change—were studied using multiple methods, such as landscape experiments (Raynor et al. 2018) or process-based models (Wang et al. 2019).

Abiotic and biotic disturbances, such as storms (Sebert-Cuvillier et al. 2008) and insect defoliation (Huebner et al. 2009), were also identified. However, not all of these kinds of disturbances were represented by landscape patterns, studied by landscape experiments, or incorporated at the pixel-level process simulation. For example, defoliation was represented with a categorical variable for 1, 2, or 3 years of disturbance (Huebner et al. 2009) and incorporated together with other landscape pattern variables in general statistical models. In this case, the disturbance was not explicitly analyzed using landscape ecology approaches, but it still falls within their broader scope. The remaining studies were set against a broader disturbance context, meaning that the predictable factors of invasion include some variables that can indirectly reflect disturbance, such as trade (Chapman et al. 2016), tourism (Carboni et al. 2017), the location and size of river ports (Jehlík et al. 2019), forest harvesting activities (DeGasperis and Motzkin 2007), and other general land use/cover changes (Basnou et al. 2015; Thiele et al. 2009).

Studies also investigated non-disturbance factors to explain invasion (Fig. 7b) including: (i) abiotic conditions, such as climate, topography, geology or soil properties, and hydrology; (ii) biotic components, such as vital rates and demographic processes, vegetation characteristics in the invaded habitat (e.g., canopy cover), dispersal traits of invasive plants, and invasion history (e.g., residence time); (iii) mixed non-disturbance factors, including propagule source availability, ecological interactions (e.g., plant-soil feedback), and habitat availability. Most of these environmental factors are spatially explicit and easy to include in models with spatially explicit outputs, such as the habitat suitability surfaces from SDMs. As mentioned above, the effects of biotic factors were often studied under a hierarchical framework; for example, dispersal traits were usually indicated by the probability of dispersal and incorporated into process-based simulation models (Wadsworth et al. 2000; Williams et al. 2008), although they could also be studied by trait-based methods such as RLQ analysis, which linked species traits to environmental conditions and allowed their spatial patterns to be visualized (Thuiller et al. 2006).

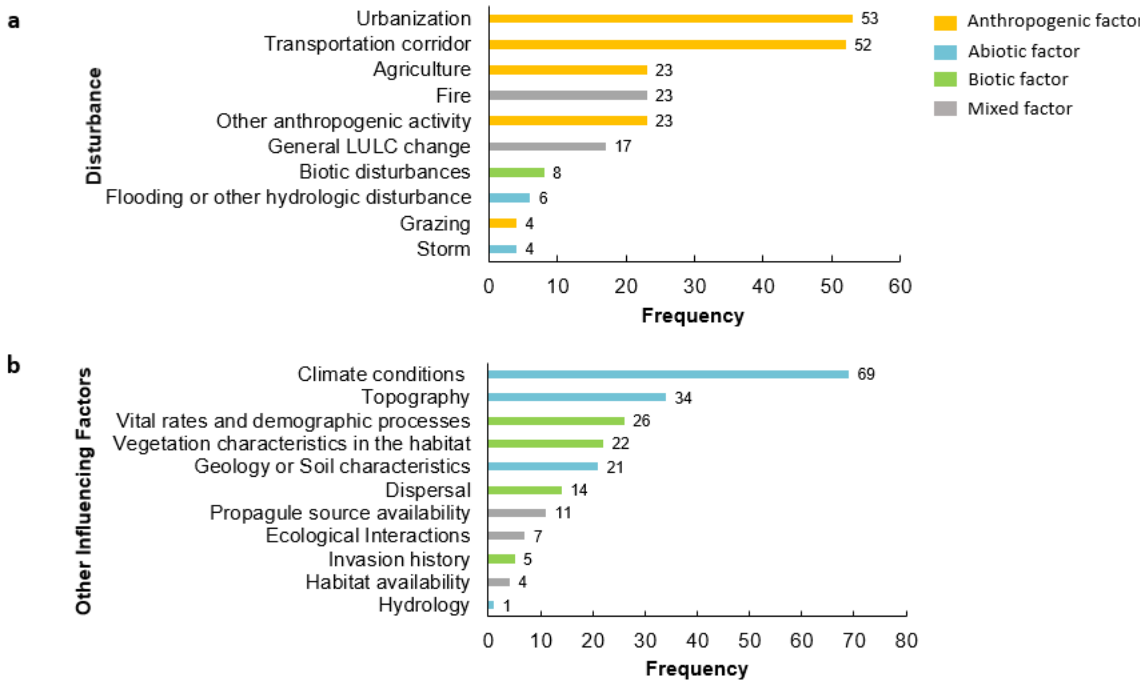

Fig. 7. (a) Frequency of various disturbance types captured in the literature related to landscape ecology approaches to plant invasions, and (b) frequency of other influencing factors on plant invasion. In cases where studies focused on multiple factors, they are included multiple times in the counts.

Discussion

This study reviewed how landscape ecology approaches have been applied to study the mechanisms and effects of plant invasion. We highlight two main findings that have implications for invasive plant research. First, we found that pattern-process relationships have been limited investigated, with disproportionately fewer studies focusing on how landscape patterns affect invasion processes or how invasion patterns/processes feed back to other ecological and landscape processes. These aspects deserve more attention, as spatial patterns influence many important ecological processes (Turner 1989). For example, disturbance-induced changes in landscape connectivity and fragmentation affect resource fluxes, which in turn shape invasion processes (e.g., plant competition, dispersal, and spread) (Alofs and Fowler 2010; Saunders et al. 1991; Vilà and Ibáñez 2011; With 2002). Likewise, invasion patterns can alter ecological processes or change native ecological equilibrium (Foster et al 2022). However, these aspects have remained inadequately addressed in the literature. Second, we found that scale effects have also been understudied in the invasive plant literature. This dearth might hinder a comprehensive understanding and management of plant invasion, as multiple dimensions of scale interact to shape invasion patterns (Melbourne et al. 2007), with variable responses (e.g., competitiveness, abundance) across hierarchical levels (Moraga et al. 2019; Suárez-Castro et al. 2018). These complex, scale-dependent interactions call for a holistic explanation of cross-scale pattern–process relationships, which could contribute to invasion control and ecosystem conservation. To address these two main issues, we first propose a more concerted framing of invasive plant research through hierarchy theory, and second, we propose that shifting from the patch mosaic model (PMM) to the gradient surface model (GSM) could lead to not only earlier identification of the invasion but also better data feeding into monitoring and modeling pattern-process relationships. These two suggestions are discussed in detail below.

An opportunity to bridge pattern and process through hierarchy theory

From the theoretical perspective, landscape ecology theories were widely studied alongside several prominent invasion hypotheses where spatial-based landscape ecological approaches are more readily applied, namely disturbance, empty niche, environmental heterogeneity, island susceptibility hypothesis, and opportunity windows (Catford et al. 2012a; Jeschke and Heger, 2018). Beyond these invasion hypotheses that overlap with landscape ecology theoretical foundations (e.g., the impact of landscape patterns/processes on invasion patterns), landscape ecology approaches could further integrate non-spatial invasion hypotheses, such as the evolution of increased competitive ability, new relationships between non-native and native species, and invasional meltdown (Jeschke and Heger, 2018), Particularly, hierarchy theory provides a robust framework to spatially represent the ecological mechanisms underlying invasion hypotheses within a landscape framework, enabling the spatial mapping of their potential implication. This incorporation of hierarchy theory and invasion hypotheses assists in refining landscape-based invasion models and deepening our understanding of the causes and effects of plant invasion, ultimately guiding effective invasion management.

Applying hierarchy theory to model multi-scale interactions can link local ecological patterns/processes to focal level investigations while emphasizing the constraining feedbacks from higher hierarchical levels (Pacala and Deutschman 1995; Seidl et al. 2012). Such a hierarchical approach could add to our understanding of the role of landscape patterns and processes in driving invasion processes, which is lacking in the literature (Fig. 4). To promote hierarchy theory in plant invasion studies, researchers should, first, carefully select the focal scale for target landscape patterns and processes (Wu and David 2002), which depends on the landscape boundaries, the invasion stage of interest, and the balance between measurability and ecological relevance of landscape patterns, with the spatial resolution aligned to biology and ecological organization level of interest (e.g., individual, population, or community) (Catford et al. 2012b; Pyšek et al. 2009; Wiens 1989). Second, researchers should allow invasion dynamics from different hierarchical levels to be expressed within a common framework. This requires either establishing a theoretical linkage to translate variables across scales (Seidl et al. 2012) or adopting empirical approaches that can reveal hierarchical coordination of invasion processes across organizational levels (Zheng and Lv 2023). Third, researchers should maintain consistency across levels in the hierarchy by applying constraints from higher levels to regulate processes at lower levels when necessary. For example, regional climate conditions often determine the final ranges of plant invasion (Merow et al. 2017), and these conditions can be used to constrain the spatial extent of an investigation. Fourth, researchers should consider bidirectional interactions between plant invasion dynamics and disturbance or environmental factors when modeling, acknowledging that plant invasion itself also actively changes environmental conditions (e.g., soil characteristics, fire regimes) as invasion progresses (Pyšek et al. 2012). Such changes then feed back to the invaded landscape and alter future invasion dynamics, such as dispersal and competition (Higgins et al., 2001). This complexity could be captured by process-based models that couple invasion dynamics with iterative, state-dependent feedback loops, thereby simulating the co-evolution of invasion pattern and environmental heterogeneity (Higgins et al. 2001; Suding et al. 2013).

In addition, researchers should promote data acquisition from both diverse remote sensing approaches and field measurements (Donovan et al. 2023; Müllerová et al. 2023; Safaei et al. 2023), particularly cross-scale measurements of environmental variables, plant functional traits, life history traits, dispersal, ecological interactions (e.g., competition and plant–soil feedbacks), and vital rates and demographic processes, which were lacking in the studies we reviewed. Among these, the acquisition of plant functional traits across organizational levels is key to linking invasion mechanisms and ecological effects. The integration of plant trait data in plant invasion studies is because, first, spatial habitat patterns impact competitiveness and invasion speed by changing the flows of energy, materials, and biological entities (Alofs and Fowler 2010; Saunders et al. 1991; Vilà and Ibáñez 2011; With 2002). These ecological processes and their impacts can be reflected by plant functional traits influencing fitness indirectly through their effects on life history, such as growth, reproduction, and survival (Violle et al., 2007). The combination of different life history characteristics determines different plant ecological strategies to deal with environmental conditions, including competition, stress tolerance, and mechanical tolerance (Grime, 1977). Second, differences in functional group composition could impact the ecological interactions between invasive plants and native habitats and determine the impacts of invasive plants (Catford et al. 2012b; Hooper and Dukes, 2010; Pastick et al. 2021), particularly when studying multiple invasive species. The development of proximal field spectroscopy, multiscale hyperspectral remote sensing, and LiDAR provides reliable approaches to measure such traits, from leaf and individual level to canopy and to landscape levels (Van Cleemput et al. 2020; Schneider et al. 2017). There have also been advances in data integration from citizen science, vegetation survey, and Earth observation to generate continuous, high-resolution plant traits data on global scale (Lusk et al. 2026), and these could be used for capturing traits at different hierarchical levels. At the same time, trait scaling methods, such as community-weighted mean traits (Schellenberger Costa et al. 2017) and the trait-based response–effect framework that guides effective scaling from trait to ecosystem functioning (Chacón-Labella et al. 2023), have also been developed. The integration of such multiscale data and trait scaling methods could facilitate the translation of functional information across scales (Abelleira Martínez et al. 2016; Schneider et al. 2017).

Except for plant functional traits, the acquisition of key environmental constraints and underlying ecological processes (e.g., dispersal, vital rates, and demographic processes) used for parameterizing models also relies heavily on an abundance of high-quality field experiments or meta-analyses.

As highlighted above, the development of reasonable scaling methods—key means of predicting variables at unmeasured scales (Frazier et al. 2023a)—is essential for translating invasion characteristics across landscapes, regions, and political units, ultimately supporting more effective invasion control. Various scaling methods have been widely investigated, such as statistical versions of entropy (Huckeba et al. 2023), comparison between field-based measures and broader scale remote sensing data (Safaei et al. 2023), the use of coarse graining and scaling function (Frazier et al. 2023b), and the concept of scope—the ratio of extent to grain (Frazier 2023). However, the scaling from traits to ecosystem processes and the integration of scaling methods within hierarchical frameworks are still nascent and need further investigation (Chacón-Labella et al. 2023; Donovan et al. 2023).

Overall, connecting disturbance regimes and the components of spatial and temporal scales (e.g., grain, extent, coverage, and spacing), and including observations from multiple organizational levels in plant invasion studies, could advance the application of hierarchy theory in plant invasion studies. These aspects can also further promote a comprehensive understanding of how plant invasion and related ecological processes interact across multiple ecological and geographical hierarchies, which in turn guide effective ecological management on target invasion stages (Fig. 8). For example, interactions between invasive and native species at individual or population levels (e.g., resource competition) are key local filters influencing establishment success, which may subsequently affect invasion patterns at larger scales (Theoharides and Dukes 2007). Although challenging, incorporating such competition processes into models while considering abiotic constraints and dispersal is crucial for translating local-scale species interactions to landscape-scale invasion patterns under changing environmental and disturbance regimes (Isabelle et al. 2014).

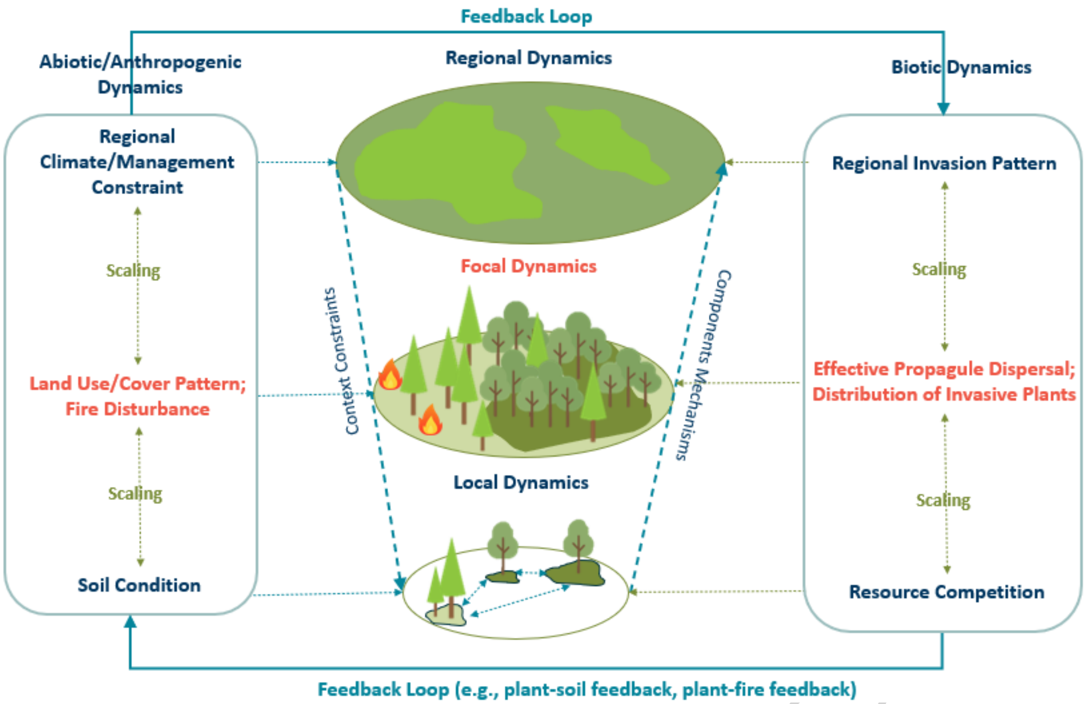

Fig. 8 A conceptual framework for incorporating hierarchy theory in plant invasion studies toward ecological management, focusing on the interaction between disturbances (land use/land cover (LULC) change and fire), and invasion dynamics (effective propagule dispersal and plant invasion distribution) (labeled with red text). The middle funnel illustrates three hierarchical levels, where larger-scale environments or landscapes serve as context constraints for smaller-scale processes, while processes occurring at smaller scales determine emergent larger-scale ecological patterns. The interactions between changes in disturbances, environmental factors and invasion dynamics are scale-dependent. All of these factors need to be considered when addressing cross-scale pattern–process relationships. The left side highlights how abiotic and anthropogenic driving factors operate hierarchically across scales, where climate or management affects the focal scale LULC and fire spread patterns and further shapes the local microenvironment (e.g., soil conditions). The right side highlights biological invasion dynamics across scales. It provides an example of how effective propagule dispersal and spatially distributed abundance of invasive plants can be explained through resource competition at the lower level. At the regional level, effective propagule dispersal and high abundance mean spread and dominance of the invasive plant. Overall, these pattern-process relationships between driving factors and invasion dynamics are bidirectional in nature and generate feedback loops as invasion progresses, such as plant-soil or plant-fire feedback. Incorporating these multiscale and bidirectional interactions into a hierarchical framework requires theoretical linkages that translate local pattern-process relationships into

focal-level invasion patterns under regional constraints. Overall, investigation of multiscale pattern–process interactions can effectively guide multiscale ecological management.

Advancing Insights through Gradient Surface Models of Plant Invasion

Most studies continue to rely on the patch mosaic model (PMM) to compute spatial metrics, but this reliance may eliminate insights that could be gained from using spatially continuous information. The gradient surface model (GSM) provides a valuable alternative by retaining such continuity, thereby broadening the scope of data acquisition and improving our ability to characterize invasion patterns and the factors shaping them throughout different stages. Particularly, it can greatly enhance the detection and mapping of sparsely distributed invasive plants at early stages, and improve modeling of pattern–process relationships at the spread stage.

The first advantage of applying GSM lies in its compatibility with the recent development in remote sensing, which contributes to capturing spatially continuous, high-resolution invasion patterns data. The transition from hard classification to fuzzy classification and gradient mapping allows for a more accurate representation of spatial heterogeneity (Feilhauer et al. 2021). For example, advances in spatial spectral unmixing (Shi and Wang 2014) enable the extraction of subpixel information from coarse-resolution imagery. Data fusion techniques, including super-resolution techniques (Wang et al. 2022; Wang et al. 2023; Zhang et al. 2025), integrate information across spatial, temporal, and spectral domains, facilitating fine-grained representation of spatial and spectral patterns along temporal gradients. Moreover, hyperspectral remote sensing and LiDAR can promote the acquisition of plant functional traits—such as Leaf Area Index (LAI), aboveground biomass, nitrogen content—from canopy spectra and support spatially continuous trait mapping across multiple spatial scales. Such canopy spectra features are critical for not only mapping invasive plants (Gholizadeh et al. 2022), but also assessing ecosystem functioning (Cherif et al. 2023) and assisting in interpreting the mechanisms and effects of invasion, particularly the drivers of invasion spread and the ecological processes altered by invasion. For example, these remotely captured spectral features can be used to evaluate functional diversity across different spatial windows

(Rocchini et al. 2022), which assists in understanding how ecological patterns or processes change across multiple spatial scales due to invasion (Große-Stoltenberg et al. 2025; Khare et al. 2019). These changes can then be linked to alterations in ecosystem services and used to guide ecological restoration.

Second, GSM also facilitates the construction of more realistic spatial surfaces of influencing factors of plant invasion. Evidence shows that complex topography and continuous landscape gradients, such as elevation, can influence ecological dynamics, including seed dispersal and community composition (Katul and Poggi, 2012; McNichol et al. 2024), thereby supporting the idea that the spatial gradient of surface characteristics can affect plant invasion in multiple ways. Such spatially continuous drivers can be better characterized by gradient surface rather than patch-based metrics. The development of surface metrics—conceptual counterparts to landscape metrics in surface metrology (e.g., percent of landscape could correspond to surface volume)—is advancing. While their ecological interpretability remains limited, ongoing efforts to apply surface metrics in ecological contexts and link them with patch-based metrics (Kedron et al. 2018) are expected to enhance their utility for analyzing invasion mechanisms. Another alternative is to calculate traditional patch-based landscape metrics within a moving window, generating continuous surfaces that represent how organisms with perceptual abilities corresponding to the window size might experience or respond to the spatial structure of the landscape (Cushman et al. 2010). This approach is particularly useful when evaluating the invasion consequence under disturbance-driven changes in landscape pattern.

The shift from patch-based to surface-based landscape data representation will then create opportunities to better understand pattern-process relationships behind plant invasion through modeling. Modeling environmental variation as individually varying gradients can better preserve the complete gradient of spatial heterogeneity and reduce the inaccuracies in boundary placement and class divisions that are caused by the PMM (Cushman et al. 2010). For example, extending wavelet analysis to spatial surfaces can effectively capture multiscale information and assist in analyzing the variation of spatial relationships continuously across space and scales (Cushman et al. 2010; Peng et al. 2020). The application of this method enables revealing the key scales at which disturbances induced environmental changes (e.g., topographic moisture, soil nutrients, and landscape fragmentation) significantly affect ecological functional traits of invasive plants.

A gradient surface approach can also be realized through spatially explicit prediction and simulation models, which can further support the application of hierarchy theory. Studies have shown that linking land-use and ecological models improves our understanding of landscape ecological systems and supports management decisions (Synes et al. 2016). Building on this, advancing process-based models to explicitly incorporate both landscape gradients and ecological processes can further enhance predictions of invasion dynamics and guide effective management (Lázaro-Lobo et al. 2025). For example, gradient data can be incorporated into process-based SDM (e.g., FATE-HD, Carboni et al. 2017) to analyze the combined effects of climate change-induced spatial heterogeneity and biotic interactions on plant invasion dynamics. Beyond such applications, extending the gradient surface framework to neutral landscape models has potential in detecting the existence of critical disturbance thresholds across spatial scales. The implications of these thresholds (Turner and Gardner 2015) for relating various stages of plant invasion dynamics to ecological patterns/processes that induce invasion on landscapes (With 2002) would need more attention. It should be noted that although GSMs have advantages in capturing spatial heterogeneity, using data with suitable spatial resolutions that holistically consider how species interact with landscapes in different invasion stages (Milbau et al. 2009; Pauchard and Shea, 2006) can assist in better invasion mapping and decision-making for control.

Methodological Considerations and Limitations of the Study

To promote the future applications of landscape ecology approaches in the field, it is necessary to consider three aspects: methodological insights from process-based spatially explicit models, limitations inherent in both the scope of the literature reviewed and the discussion on the application of 3D spatial metrics. As discussed above, process-based spatially explicit models provide an important approach to linking ecological processes and patterns across scales, particularly when incorporating hierarchy theory and GSMs into the research framework. However, their practical use also presents challenges.

First, most process-based models need to be properly designed, parameterized, and calibrated for the target processes (e.g., levels of adult fecundity; recruitment and dispersal potential; fire spread), as well as validated against observed pattern-process relationships. These aspects heavily rely on accurate field measurements (Pilowsky et al. 2022) or reliable hypotheses for how ecological processes happen on landscapes (e.g., dispersion path, Osawa et al. 2016). Even though empirical data from previous research or meta-analysis could be alternatives for guiding model structure design, acquiring key parameters, or conducting model validation (Higgins et al. 1996; Higgins et al. 2001; Suding et al. 2013; Wang et al. 2019), challenges remain. The association between invasion dynamics and influencing factors exhibits spatial heterogeneity for different study areas (González-Moreno et al. 2014), which could cause failure in cross-region modelling and validation. Moreover, the calibration of process-based models often relies on fitting to observed data, which does not necessarily ensure the correctness of model structure or parameter identification (Dormann et al. 2012). Thus, it is still essential to fully consider model assumptions and parameter uncertainties, while integrating the strengths of both process-based models and high-quality field-manipulative experiments (Dormann et al. 2012; Wu and Hobb 2007 p.54).

Second, while process-based models can range from simple to complex, their design must be guided by the specific invasion hypothesis being tested, the availability of data, and the scalar alignment between the data and the target ecological processes (DeAngelis and Yurek, 2017). With this context, a complex model could be computationally expensive, such as individual-level modelling complex eco-evolutionary processes for many populations of individuals (Pilowsky et al. 2022), though the computational power increased rapidly in recent years (e.g., high-performance computing). Therefore, it is also important, but challenging, to design models that balance simplicity with mechanistic depth, which means models should be effective in capturing the focused causal pattern-process relationships while excluding those unrelated (DeAngelis and Yurek, 2017; Levin, 1992).

Although concern exists in data acquisition, model design, model assumptions, and parameter uncertainties, their applications bridge the gap between ecological theory and conservation practice through improved mechanistic forecasting (Pilowsky et al. 2022). For example, dynamic global vegetation models can simulate plant functional diversity through underlying biophysical and biochemical processes (Pavlick et al. 2013). Spatially explicit genetic models enable tracking propagule migration rates and genetic diversity patterns (Brown et al. 2016; Chybicki and Robledo-Arnuncio, 2025), which could allow accurate evaluation of potential invasion trends. Process-based SDMs have potential in modeling invasion patterns under changing environmental scenarios by incorporating biotic dynamics and disturbance (Carboni et al. 2017). Except for these advantages, process-based models are also valuable, particularly when experiments fail to capture the change and mechanism of landscape (e.g., dispersal) at the ideal spatial or temporal scale (Turner 1989).

Beyond these methodological considerations, there are four main limitations regarding the search scope used in this study and the discussion on the application of 3D spatial metrics. First, our keyword combination specifies certain disturbances (e.g., fire, urbanization, agriculture), but might omit other processes. Second, non-native plant invasion processes have a multiscale nature with different invasion patterns and mechanisms underlying these patterns at different stages (Theoharides and Dukes 2007), such as transport, introduction, establishment, and spread (expansion and dominance) (Blackburn et al. 2011; Müllerová et al. 2023). Assessing the invasion phase at which a study is conducted is crucial to understanding the effectiveness of landscape ecology approaches in different phases of plant invasion studies and guiding effective invasive plant control. However, the literature captured by the search mainly focused on the expansion and dominance phases, as these are the two stages in which the alien species are easiest to detect at landscape scales. This is likely because most research using a landscape ecology approach relies on remote sensing data. Third, we did not explicitly include studies that assess how landscape ecology approaches were used to study the environmental, ecological, and social impact of plant invasion patterns or processes. The incorporation of this information in decision-making models is also important for invasion control, native ecosystem restoration, and sustainable ecosystem management. Fourth, in the articles we reviewed, we found that no study considered 3D spatial metrics. Since the application of 3D metrics in plant invasion studies is still at an early stage, we did not discuss them here. Although this is certainly an area for future investigation. For instance, 3D metrics can provide an accurate measurement of habitat structure (Davies and Asner, 2014), which could affect invasion (Lemke et al., 2012). It is also possible to use 3D spatial metrics to improve the estimate of functional connectivity from the perspective of landscape genetic analyses (Milanesi et al. 2017), given that genetic patterns of invasive plants can assist in demonstrating evolutionary relationships among populations and in explaining invasion processes (Lu et al. 2022). Despite these limitations, the review still provides useful information on how landscape ecology theories and models are being applied to investigate plant invasion mechanisms. The findings of the current research opportunities can also guide future theory and model development, ultimately guiding ecological restoration and management.

Conclusion

The application of landscape ecology-based approaches to plant invasion studies dates back to the early 1990s and has steadily increased over the past decades, paralleling the growing attention on plant invasion prevention and management. Although widely applied, study frequencies have skewed toward the Global North. Under global change, more attention should be given to the Global South, especially those having high biodiversity and intensive ecosystem disturbance.

Incorporating hierarchy theory into the framework of plant invasion studies could help understand the mechanisms and effects of plant invasion on different scales toward specific requirements of ecosystem management. This requires reliable selection and representation of target landscape patterns and processes, integration of invasion dynamics across hierarchical levels, as well as the development of suitable scaling methods and the acquisition of multiscale, multi-source data. Applying the gradient surface paradigm to plant invasion studies could complement the patch mosaic model by providing more accurate invasion pattern representation and better explanation of pattern-process relationships. Moreover, advancing process-based, spatially explicit models that integrate ecological processes with continuous landscape patterns can strengthen the application of hierarchy theory in invasion research. Building on these approaches, we can enhance current understanding of how invasion patterns/processes interact with other environmental, ecological, and social patterns/processes, as well as guide effective disturbance management across different invasion phases.

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