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REVIEW

Computational Methods in Landscape Ecology

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Abstract

Purpose of Review Landscapes can be defined as mosaics of different land covers, habitats, ecosystems, or land-use systems. The link between spatial heterogeneous patterns and ecological processes is the core concept in the research field of landscape ecology. Nowadays, advanced computational methods are essential to the field due to its cross-disciplinary nature, the increasing availability of data, and the complexity of landscape systems.

Recent Findings This review provides an overview of recent developments in computational methods that have advanced the research field of landscape ecology. We focus on key topics such as spatial patterns, connectivity, landscape genetics, sampling, simulations and modeling, and spatial planning.

Summary The review highlights key innovations, challenges, and potential future directions in the field, emphasizing the role of computational methods in addressing complex ecological questions.

Keywords Spatial data · Spatial patterns · Pattern-process link · Open-source · Scientific software

Introduction

Landscapes are typically defined in landscape ecology as mosaics of different ecosystems, habitats, land covers, or land-use systems [1], with emphasis on heterogeneity of at least one factor of interest [2]. Linking spatial heterogeneity and ecological processes, including potential interactions between heterogeneity and processes, is the fundamental concept of landscape ecology [2]. Typical research topics include, but are not limited to, pattern-process links, landscape complexity, ecological flows, scale effects, landscape modeling, conservation, drivers and consequences of land use and land cover (LULC) change, and human activities within landscapes [3].

Computational science analyzes abstracted core mechanisms of research questions using data and algorithms and is one of the most important tools of modern science [4]. Following, computational ecology can be defined as computational science that is used to address ecological research questions with focus on data-driven and model-driven approaches [5]. Computational ecology is crucial for landscape ecology as a research field because data is often context- and scale-dependent, making it challenging to design controllable, reproducible, and replicable experiments [6], but see [7] for a review of experimental studies]. Additionally, because landscape ecology is a cross-disciplinary field [8], the availability of data increases steadily [9], and the complexity of landscape systems [10], there is a need for advanced computational methods.

Here, we provide a perspective on recent developments and advances in computational methods in multiple key topics of landscape ecology (Fig. 1), including software that implements them or is potentially capable of creating novel insights in these topics (Tab. 1). In this context, we are focusing on open-source software and scripting languages such as R, Python, and Julia. However, we do not aim to

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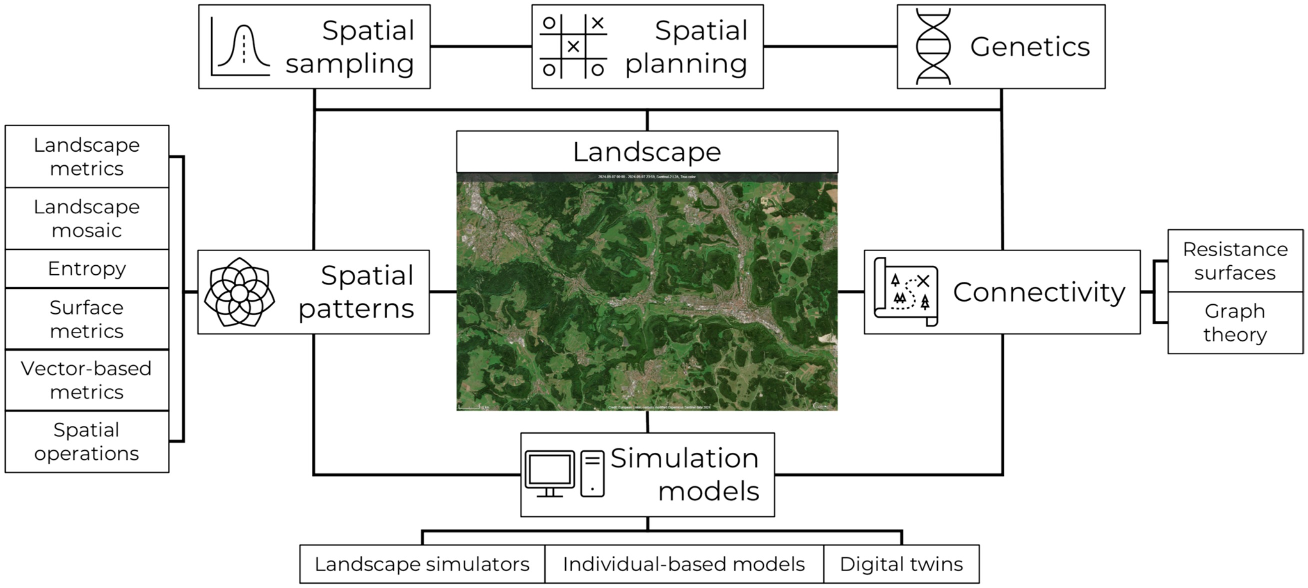

Fig. 1 Overview of landscape ecology topics discussed in relation to computational methods. All topics are highly interconnected. For example, the quantification of spatial patterns often relies on sampling approaches and can serve as target values for simulation models. Simulated neutral landscapes may act as null hypotheses for connectivity analyses. Landscape genetic analyses frequently depend on connectivity estimates, which can, in turn, inform spatial planning decisions. The image uses modified Copernicus Sentinel-2 data from 2024–09-07

provide a systematic literature review or a general introduction to (computational) landscape ecology. For such, please see [2, 11], or [8].

Data Models

There are two fundamental data models used to represents landscapes, namely the raster and the vector data model. The raster data model typically uses regularly spaced grid cells, while the vector data model uses points, lines, and polygons to represent landscape features [8]. Often, the choice of the data model is driven by data and software availability or by familiarity with the approach [60]. For example, many LULC maps are provided as gridded raster data as they often relate to underlying remote sensing products.

Similarly, the issue of scale is closely related to the used data model. This includes the extent of the study area and resolution of the data (i.e., the smallest data unit). Additionally, thematic resolution in landscape ecology often refers to the values describing landscape features, e.g., the number of discrete LULC categories or habitats [61]. Various classification systems are relevant at local, regional, and global extent, such as the National Land Cover Database (NLCD), the Coordination of Information on the Environment (CORINE), or the Food and Agriculture Organization (FAO) systems [62]. Lastly, temporal scales are relevant in terms of extent and resolution, but also with regards to the detail of captured ecological processes.

The spatial reference system of the data is less frequently discussed but often critical. Cartesian coordinate reference systems measure distances between two points in Euclidean distances, typically in meters. In contrast, geographic coordinate reference systems are based on degrees and measure distances as great-circle distances. Numerous coordinate reference systems exist and novel projections are constantly being developed to improve spatial cohesion, efficiency and accuracy [63]. However each reference systems comes with distinct properties that may distort areas, distances, angles, and aimed to represent specific regions or countries. Therefore, it is essential to choose the appropriate spatial reference system based on the available data, area of interest, and the specific research question.

Data quality is generally variable, and data products are not flawless, potentially containing errors and biases. For example, global land-cover products typically have an overall accuracy of 70 to 80% [64], indicating that 20 to 30% of the grid cells may be misclassified. Furthermore, these misclassifications are not random, but are often correlated with specific LULC types, regions, and seasonal variations [65]. Rather than relying on global products, however, there are also increasingly voices that advocate for the production and use of regional land-cover products [66]. Nevertheless, many landscape ecology studies tend to accept the data at face value, neglecting its accuracy and inherent uncertainty.

Table 1 Software and models that implement recent methodological advances in landscape ecology

Topic	Programming language	Software	Reference
Spatial patterns	R	sf	[12]
		terra	[13]
		landscapemetrics	[14]
		multilandr	[15]
		bespatial	[16]
		rasterdiv	[17]
		LandComp	[18]
		geodiv	[19]
		glcm	[20]
		vectormetrics	[21]
		motif	[22]
	Python	GeoPandas	[23]
		Rasterio	[24]
		PyLandStats	[25]
		LecoS	[26]
	Julia	GeoStats	[27]
		GeoInterface	[28]
	Stand-alone software	FRAGSTATS	[29]
		GuidosToolbox	[30]
Connectivity	R	ResistanceGA	[31]
		lconnect	[32]
		grainscape	[33]
	Julia	Circuitscape	[34]
		ConScape	[35]
		Omniscape	[36]
	Stand-alone software	Graphab	[37]
		Conefor	[38]
		LSCorridors	[39]
Landscape genetics	R	graph4lg	[40]
		landgenreport	[41]
		adegenet	[42]
		ape	[43]
	Python	Python based scripts	[44]
		SDMtoolbox 2.0	[45]
Sampling	Python	ZonalMetrics	[46]
Simulation models	R	NLMR	[47]
		rflsgen	[48]
	Python	NLMpy	[49]
		Pathwalker	[50]
	Julia	NeutralLandscapes	[51]
	Stand-alone software	GradientLand	[52]
		Landscape Generator	[53]
		HexSim	[54]
		RangeShifter2.0	[55]
Spatial planning	R	prioritizr	[56]
		CoCo	[57]
		restoptr	[58]
	Python	CAPTAIN	[59]

Spatial Patterns

Spatial patterns can be defined as the scale-dependent predictability of the physical arrangement of observations [67] or as clearly identifiable structures in nature itself or data extracted from nature [68]. Importantly, patterns observed in nature contain information about the history of the system, such as demographic processes, dispersal characteristics, or climatic patterns [69]. However, spatial patterns are not only a result of processes but could also be drivers of them. Thus, untangling a landscape's history and linking its spatial patterns to ecological processes is one of the core concepts of landscape ecology [2].

Landscape Metrics

Traditionally and at present, many prominent approaches that quantify spatial patterns revolve around raster data using categorical values based on the patch mosaic model [60, 70]. The strength of landscape metrics is that they are easy to apply, communicate, and can be calculated straightforwardly from raster data based on remote sensing derived products [71, 72]. However, limitations have also been identified for many landscape metrics. These include shortcomings to quantify the spatial structure, sensitivity to both spatial scale and thematic resolution, and correlation and redundancy between metrics [71, 73, 74].

To address limitations related to correlation and redundancy several approaches have been used to identify core metrics that capture main components of landscape patterns, such as multivariate factor analysis [75], multivariate statistics [76], principal component analysis [77], or the variance inflation factor [78]. More recently, principal component analysis over a set of landscape blocks revealed two main components of landscape configuration, namely complexity and aggregation which together explain about 70% of variance [79]. These results are in line with recent reviews that have similarly suggested that there are two fundamental components of landscape patterns, namely amount and adjacency [80, 81]. These components are connected to complexity and aggregation as suggested by [79] and later formalized in [82].

Landscape Mosaic Method

The landscape mosaic method offers a way to quantify spatial patterns through a tri-polar classification model involving three LULC classes [83]. The approach uses a moving window to determine the proportions of these three classes within each focal grid cell. These proportions are then classified into 19 mosaic classes based on thresholds that describe the presence, dominance, or uniqueness of each class. This allows the assessment of content, context, and interface zones of LULC data in a scale-dependent manner. Recently, the method has been improved by expanding the classification to 103 classes and incorporating heatmap visualizations and summaries [84].

Entropy

Entropy measures in landscape ecology are mainly derived from information theory and thermodynamics. They are mainly used to quantify the complexity of the landscape (spatial heterogeneity), and less often unpredictability (temporal heterogeneity), as well as scale dependence (spatio-temporal heterogeneity) [85]. However, studies show that insights gained from entropy measures depend on the formulation of the selected measure and on the underlining data model, e.g., the composition of categories or the co-occurrence matrix representation [86].

The Shannon diversity index [87] quantifies the richness and evenness of categories in the landscape, omitting the spatial configuration. Shannon's entropy can also be modified to include the landscape's spatial configuration, e.g., by weights calculated from intra- and interclass distances [88]. However, to quantify the spatial configuration and the total complexity of the landscape, other measures from information theory must be adapted. Nowosad and Stepinski [82] proposed to compress information about the landscape's composition and configuration into a co-occurrence matrix which could be used to calculate various entropy measures. This includes conditional entropy (representing configurational complexity), joint entropy (representing overall spatial-thematic complexity), mutual information, and relative mutual information (both representing the degree of spatial autocorrelation).

Based on concepts from thermodynamics initiated by the work of [89] and [85], in the last few years, there has been a surge in the development of entropy-based metrics for landscape ecology. In the late 1800s, Boltzmann formulated a probabilistic interpretation of the second law of thermodynamics using the concepts of "macrostate" (the general state of a system) and "microstate" (the configuration of the system elements) [90]. [91] proposed to relate the edge length (defined as the side lengths of neighboring cells with different LULC classes) to the microstate of the landscape and use the proportion of microstates to compute the relative Boltzmann entropy of a landscape mosaic. This approach was later generalized for calculations based on the raster surface model and point patterns [92]. Subsequently [93], proposed to use the Boltzmann entropy to quantify the complexity of a landscape surface by transforming the input raster into a series of landscape surfaces with different levels of detail (microstate) and calculating the Boltzmann entropy based on the total number of microstates that are able to generate the observed macrostate. Recently [94], extended the original definition of Boltzmann entropy to incorporate information about the adjacency of the same categories in the landscape mosaic by using the number of contiguous patches of the same category. The relationship between Shannon and Boltzmann entropies in landscape ecology remains contentious, with recent studies challenging the thermodynamic interpretation of Boltzmann-inspired measures and advocating for Shannon entropy as a more general form [95, 96], highlighting the need for further research to elucidate their connections to environmental processes.

Moreover, many other entropy-based metrics have been proposed for use in landscape ecology. The Renyi [97] and Gibbs entropies, which are both generalizations of the Shannon entropy, have been applied to quantify landscape complexity. The Rao quadratic entropy [98] has also been applied recently [99], as it measures not only the relative abundances of elements but also the pairwise dissimilarities or distances between them. Thus, it can be useful in cases where the dissimilarities between LULC classes are relevant. Another recent development to describe patterns across scales is the use of Kullback–Leibler divergence (also known as relative entropy) which is a measure of differences between two probability distributions [96].

Surface Metric

Surface metrics are based on the gradient surface model using raster data and continuous values [100, 101]. These metrics are mostly adapted from microscopy and molecular physics [100, 102]. The gradient surface model can increase the resemblance of the data to the natural world because it allows for the inclusion of more heterogeneity within each grid cell [101, 102]. Many surface metrics have analogous landscape metrics [101], however, using surface metrics allows for the exploration of different or additional patterns and potentially pattern-process links [100, 103]. The metrics are able to quantify various characteristics, such as roughness, skewness and kurtosis, total and relative amplitudes, curvatures of local peaks, or surface bearing area ratios [101].

Nevertheless, similar to landscape metrics, also surface metrics are scale-dependent because they are used to quantify landscape heterogeneity which is itself scale-dependent [104]. Software to calculate these metrics is still rare and further research is needed into the specific pattern-process links and ecologically meaningful interpretations [102, 105].

Related to surface metrics, another recent approach to quantifying the gradient surface model is based on frequencies and local adjacencies of continuous input pixel values [106].

Vector-based Metrics

As hundreds of metrics have already been developed for gridded raster data, the most straightforward approach may be to reimplement these same metrics for vector data. Although this is possible for many metrics, there are also metrics specifically related to the corresponding data models [107]. For example, in urban planning vector-based metrics are applied to quantify the shapes of urban areas and characterize the complexity of building footprints [108]. Earlier approaches to quantifying shape complexity included four categories of compactness measures: perimeter-area, single parameters of related circles, dispersion of elements of the area around a centroid, and direct comparison to standard shapes [109]. More recently, a unified theoretical foundation for measuring shape compactness was introduced using a set of ten distinct properties of a circle and metrics associated with each of these properties [110].

However, also vector-based metrics have limitations. The most important limitation relates to computational complexity, which makes calculations of vector-based metrics slower than their raster equivalents. Another technical issue is the requirement for topologically correct data (e.g., geometries cannot overlap), which is often problematic, especially for data from different sources. Last, the pattern-process link for vector-based metrics remains underexplored compared to raster-based metrics.

Operations on Spatial Patterns

Spatial patterns can be analyzed through a range of computational operations, e.g., comparing, searching, or grouping. These operations are based on spatial signatures (multi-numerical representations of landscape pattern) and dissimilarity measures (functions that quantify differences between the signatures), and can be calculated for different areas or for the same area at two different moments in time. Comparing spatial signatures is often used to analyze landscape dynamics, e.g., to detect changes in landscape structure over time [111]. Furthermore, signature-based searches can be used to compare the spatial signature of a focal area to the spatial signatures of multiple other areas. This allows for the identification of areas with similar signatures compared to the focal area, e.g., areas with similar environmental conditions [112]. Additionally, it is possible to calculate spatial signatures for multiple areas and group them to similar clusters based on their signatures [113].

Connectivity

Landscape connectivity describes how landscape features facilitate or impede movement, flow, and dispersal of organisms (e.g., active movement of animals, or dispersal of sessile plants by wind or water). It underpins ecosystem functionality, maintains biodiversity and populations, and plays an important role in many conservation actions [114]. Connectivity can be divided into structural and functional connectivity [115].

Structural connectivity describes the physical arrangement of landscape elements, focusing on spatial aspects such as continuity and adjacency. It is solely a landscape feature and independent of species characteristics [114, 116]. Landscape metrics are commonly used to describe structural connectivity in terms of, e.g., total habitat amount, patch size, or patch isolation. Recently, there has been an increasing focus on within-patch connectivity using metrics such as the effective mesh size [117]. However, landscape metrics are frequently criticized for an ambiguous link to functional connectivity [71, 74]. Functional connectivity, in contrast, integrates landscape structure with the perceptual, behavioral, and dispersal characteristics of species, making it both species- and landscape-specific [115, 118].

Although multiple approaches that measure connectivity have been developed [119, 120], the technical and conceptual quantification of connectivity has proven challenging [115, 121]. Generally, movement and dispersal data from individuals is required to infer the elements in the landscape that organisms preferentially move or disperse through [119]. While improving technologies have made tracking animal movement at high tempo-spatial resolution available [122, 123], it is still logistically challenging to track high numbers of individuals. Thus, in practice connectivity is primarily determined by indirect estimations. Calabrese and Fagan [121] distinguished three types of estimates: *i)* structural connectivity determined by the physical attributes of the landscape, *ii)* potential connectivity as a combination of physical landscape attributes and limited information about dispersal characteristics of species, and *iii)* actual connectivity related to observations of individuals moving through a landscape.

Resistance Surfaces

Many modern connectivity approaches rely on resistance surfaces to represent the landscape [124]. A resistance surface is a raster-based representation of a landscape where each cell is assigned a value reflecting the species specific cost for an individual to traverse or disperse that cell based on landscape features such as habitat type, topography, or barriers [125]. Creating resistance surfaces involves obtaining landscape data for the area of interest, quantifying cost values for each cell using movement and dispersal data, and finally analyzing the surfaces [126]. This can include expert opinion (widely used due to low effort, however, difficult to measure accuracy) [127], detection data (single point locations of unknown individuals), relocation data (multiple sequential locations of the same individual but at low frequency), pathway data (high-frequency relocation data allowing for movement track inference), or genetic data (samples used to calculate genetic distances between populations).

Least-cost modeling identifies potential pathways between two points that minimizes the related movement or dispersal costs based on the resistance surface [118]. By calculating pathways between two points it is possible to estimate connectivity between these points based on the accumulated cost along the path. This method can also generate accumulated cost surfaces depicting the minimum cost from a single point to all other locations helping to identify reachable areas within a threshold. The creation of least-cost paths is a well established technique and there are highly optimized and efficient algorithms available for its calculation.

Contrastingly, circuit theory considers all possible pathways between locations simultaneously [128]. In this approach, the landscape is represented as a network of electrical nodes connected by resistors (weighted by the values in the resistance surface), and movement is analogous to electrical current flow. Circuit theory is particularly useful when multiple alternative pathways are available. It can describe isolation by measuring multiple low- or high resistance pathways and identify areas of high movement probability highlighting important corridors and bottlenecks in the landscape [129].

However, resistance surfaces are not free of critique including missing spatio-temporal variability or context dependency [130, 131]. Thus, recent developments have shifted towards a combination of both resistance and processes-based modeling approaches [50, 54, 55], modeling of dynamic landscape connectivity [132], inclusion of stochasticity and spatial context [39], genetic optimization algorithms [31], or general computational improvements [133].

Graph Theory

Following the formative work of [134], graph theory has become a cornerstone approach to studying landscape connectivity by integrating landscape features and species movement and dispersal in landscape graphs [129]. Graph theory and related connectivity metrics can be applied over various geographical contexts and for various species [135], require very little data inputs [136], and can provide key information for conservation planning and management. For example, graph theory based metrics can assist wildlife movement corridor planning [137], assist infrastructure placement while minimizing habitat fragmentation [138], or identify habitat patches that maintain overall landscape connectivity [139].

Within the landscape, discrete habitat patches are modeled as nodes, and the potential movement and dispersal between patches is modeled as edges. The edges can be binary representing whether a connection between two nodes exists or not, weighted by cost values representing movement or dispersal efforts from one patch to another, or undirected or directed allowing movement or dispersal in both or only one direction [134, 140]. Connectivity can be quantified through various graph-theoretical metrics describing different aspects, such as the importance of specific patches in maintaining connectivity. Widely reported connectivity metrics include the probability of connectivity index [141], habitat availability metrics quantifying potential and functional connectivity [138, 142], or the integral index of connectivity which is based on a binary connection model [142, 143].

Recently, a new generation of graph-theoretical metrics, commonly reported in combination [144], have been developed to account for landscape features that are critical for space use and species-specific movement or dispersal [140]. Furthermore, the modeling framework was initially only applied to single species, but is increasingly being used to model multispecies landscapes to account for interspecific movement and dispersal abilities and habitat preferences [145–147]. In addition, modern multiple-layer graph approaches enable the modeling of not only spatial but also spatio-temporal graphs [148, 149]. Modeling the temporal dynamics helps to identify habitat patches that impact connectivity over time and the corresponding effects on biodiversity patterns [149].

However, despite the robust theoretical underpinnings of graph theory and its powerful application in landscape connectivity research, contradictory results could emerge from different methods used to construct a graph or various data sources. In many cases, data availability limits the representation of the modeled landscape with subsequent implications for the calculated connectivity metrics and inferences of connectivity [135]. For example [136], modelled the same landscape using three different data types which resulted in different distribution of connectivity values.

Landscape Genetics

Genetic data can be applied in complement with ecological data to integrate evolutionary processes and patterns into landscape ecology [150–152]. Landscape genetics unite molecular population genetics, spatial statistics, and landscape ecology and emerged from the goal to study the interaction between landscape features and microevolutionary processes, such as gene flow, genetic drift and selection [151, 152].

Landscape genetic approaches have traditionally been used to inform landscape ecology applications, e.g., through connectivity modeling and spatial conservation planning [150, 151, 153, 154]. Using holistic approaches that consider evolutionary processes and patterns in addition to ecological data can fortify results, e.g., by improving predictive models of species range shifts in response to climate change [155], improving the identification and delineation of landscape connections among populations [156, 157], allowing for the interpretation of spatial structuring in context of socio-cultural connections [158], or understanding local adaptation associated with specific environments [155, 159, 160].

Advances in molecular methodologies and synergistic developments of bioinformatic and computational approaches to analyze large-scale genomic data have recently enabled the integration of genome-wide data with spatial ecological data. This shift towards landscape genomics [161, 162] comes with novel utilities through which researchers can apply genomic data across spatio-temporal scales, including the integration of historic or ancient DNA [163] or simulated present-day and future population genomic data [164, 165]. Analytical frameworks such as the *FOLDS* model (gene flow, genetic offsets, genetic load, dispersal and SDMs) [155], constrained coordination where covarying sets of genotypes are correlated with multivariate environments through redundancy analysis [166], and spatial simulations provide promising potential for future landscape genomic studies. Such studies may explore interactions between complex evolutionary processes, including demography, multidimensional (e.g., strength and direction) gene flow and migration across spatio-temporal scales, genetic differentiation across landscapes, genomic load and adaptive potential, and the interpretation of these evolutionary processes in context of landscape ecology [152, 163–165, 167].

Sampling in Landscape Ecology

Establishing a pattern-process link usually requires fieldwork and data collection. Given the cost of collecting field observations across landscapes, computational sampling tools have been designed to optimize the study designs [168, 169]. To improve the statistical significance of the relationships between landscape features and field observations several aspects need to be considered when selecting sampling sites for data collection. First, selected sites should cover the maximum possible range of landscape heterogeneity to maximize the variance of independent variables. Second, statistical power can be improved by ensuring independence between sites and consequently response variables. Finally, since many landscape features that influence response variables are spatially dependent, it is essential to evaluate spatial autocorrelation.

Furthermore, identifying scales at which the ecological processes of interest operate is a crucial step [170]. However, in practice, the appropriate scales may not be obvious or data at such scales may not be available and landscape-wide and local process interactions can occur across multiple scales [171]. Here analyses at multiple spatial scales can help to identify the scales of interest. For instance, scalograms can be used to reveal scale thresholds that maximize landscape heterogeneity [168] or show the strongest relationships with response variables [15].

Directly related to the location and extent of sampling sites is the issue of overlapping landscapes which can result in a lower range of landscape heterogeneity, lack of statistical independence, or pseudo-replications [169, 172]. Nonetheless, the lack of independence between sites is likely more related to spatial autocorrelation and thus not necessarily prevented by using non-overlapping landscapes [169]. Instead, spatial autocorrelation between sampling sites can be evaluated using comparisons of similarity measures between sampling approaches or spatial scales (e.g., Moran's I) [168]. Furthermore, spatial autocorrelation in model residuals can be diagnosed using the similarity between two sites as a function of the distance between them, i.e., correlograms [173]. If spatial autocorrelation is detected researchers may either consider further data collection or use modeling methods to accommodate for spatial dependencies [169], such as mixed models [173] or apply smoothing kernels that compute distance-weighted averages surrounding the sites [174].

Simulation Models

Simulation models are a powerful tool to study complex adaptive socio-ecological systems in controllable, reproducible, and replicable settings [6]. Thus, simulations can be seen as experimental systems that allow all imaginable manipulations which would be impossible in natural systems in order to advance theoretical developments or test hypotheses [175]. Due to the spatio-temporal scales, complex interactions and feedbacks, or scale mismatches between patterns and processes, simulation models are one of the major approaches in landscape ecology [176, 177]. In general, simulation models can be classified using two major divisions, namely *i)* predictive or exploratory models, and *ii)* pattern- or process-based models [175, 177]. Here, we focus mainly on exploratory models, but include both pattern- and process-based models.

Landscapes Simulators

Landscape simulators are typically used to generate null hypotheses, baselines, or scenarios that allow to control certain aspects of the landscape using the raster data model [178, 179] and are generally simpler than ecological simulation models [180]. Landscape simulators can be classified into two major categories, namely pattern-based and process-based approaches [181, 182].

Pattern-based approaches simulate landscapes without assuming any underlying abiotic or biotic processes (i.e., neutral landscape model) [183]. The earliest neutral models are based on percolation theory and assign LULC classes randomly to cells in the landscape [183] or hierarchical models that consider different spatial scales while assigning cell values [184]. Landscapes characterized by continuous values can be simulated by fractal models, such as Brownian motion [185]. Borrowing from computer graphics, more recent neutral landscape models make use of spectral synthesis (e.g., Perlin noise) [186] or binary space partitioning [187]. Neutral landscape models are also able to simulate landscapes dominated by anthropogenic activities based on least-cost networks [188]. In order to ensure realistic neutral landscapes several approaches exist that use comparisons with real landscapes [189], target values optimization (target values are optimized as close as possible) [53], or target value satisfaction (target values are strictly satisfied, or cannot be satisfied) [48].

Contrastingly, processes-based approaches explicitly include abiotic or biotic pattern-forming processes (i.e., landscape generators) [182, 190]. Several earlier landscape generators are based on cellular automata models and are able to simulate urban growth [191] or deforestation [192]. More recent, landscape generators have allowed to simulate patchy landscapes based on Gibbs processes [193], deforestation based on road and agricultural fields access [181], loss of wetlands, expansion of mining and croplands using the Ising model [194], agricultural areas dominated by smallholders [190], or vegetation surrounding watering points in semi-arid savanna rangelands (combining pattern- and process-bases approaches) [180].

Individual-based Models

Individual-based models (or agent-based models) simulate discrete entities that are described by attributes and behavior. Patterns emerge from bottom-up interactions of individuals with each other and their environment [195]. In landscape ecology individual-based models are increasingly used to model social-ecological systems [196–198], but also disturbances [199–201], or connectivity [202]. They can also incorporate a range of socio-economic, political, and governance information to influence how individuals, such as farmers, interact within a landscape [203].

In order to facilitate future model developments recent progress includes adaptable modeling frameworks [54] or reusable building blocks [204]. Furthermore, hybrid approaches, coupling or integrating different model types with individual-based models, could benefit from rich development histories or facilitate corresponding strengths [205], e.g., linking an individual-based and ecosystem model [206].

Digital Twins

The digital twins concept include three connected elements, namely *i)* a physical object or system, *ii)* its digital representation, *iii)* and a data exchange between the former two [207, 208]. The need for timely and evidence-based decision making in combination with increasing data availability make digital twins a powerful tool for landscape ecology. The use of general data processing, statistical and mechanistic models, or artificial intelligence allows digital twins to constantly update the digital representation and analyze, visualize, or predict the physical counterpart. This is further facilitated by the increasing rate of novel sources of data generation in ecology, e.g., due to sensors deployed on airplane, satellites, or unmanned aerial vehicle [209]. Digital twins are particular useful for real-time workflows that allow now- and forecasting of complex dynamics in a landscape.

Digital twins aim to provide real-time state of nature measurements, early detection of conservation trends, relationships of ecosystem trends and environmental conditions, impact assessments of interventions, or to identify uncertainties and information gaps [208]. Thus, there is increasing interest and use of digital twins in both the industry and academia [207]. They are increasingly applied in agricultural landscapes research, e.g., for livestock farming, controlled environment farming, or fertilization management [210, 211]. Further applications include planning of rural ecological landscapes [212] or exploration of relationships between urban expansion and vegetation coverage [213].

Spatial Planning

Spatial planning uses decision theory to identify and allocate areas to specific purposes, such as reserve selection through spatial conservation prioritization [214–217]. In the context of landscape ecology, it provides a pattern-process link and outcomes related to decision making by distinguishing between structure, function, and scales [218]. As an integrative approach most spatial planning approaches can benefit from various computational advances in landscape ecology. For example, there have been several recent advances in considering landscape patterns directly in spatial planning or through using simulation model outputs as input features [219]. Generally, spatial patterns influence planning outcomes because of their compactness, contiguity, and connectedness. Furthermore, aggregation can be important because of ecological or practical reasons, for example, by ensuring that selected areas satisfy minimum patch size constraints [220, 221]. Novel computational approaches make use of graph theory to identify valuable landscape areas in terms of compact core habitat and reducing boundary exposure [222]. Similarly, contiguity and connectivity are generally considered important to ensure that landscapes or habitat patches are connected, such as river networks [223]. In particular, recently the direct consideration of connectivity has received increasing attention in spatial planning and new computational methods are developed [219, 224–226].

Particularly noteworthy are two advances that incorporate landscape metrics in spatial planning. One is the use of graph theory to guide conservation and restoration efforts in linear [227] or constraint programming [221]. These spatial networks approaches have the potential to provide more cost-effective and precise solutions to design reserve networks [227]. For example [221], used landscape ecology theory and metrics to spatially optimize restoration efforts aiming to maximize broader landscape connectivity in New Caledonia.

A second development is the increasing use of deep reinforcement learning, a machine learning approach based not on patterns but agents and pathways. Reinforcement learning can be used to identify cost-efficient solutions to area-based conservation planning [59]. Additionally, it can be applied to identify the best possible solutions to improve landscape connectivity indices [228], such as the integral index of connectivity [143]. Advantages of reinforcement learning include the ease of incorporating both linear and non-linear functions as well as the scalability of spatio-temporal processes to larger spatial extents [228]. However, this comes with the drawbacks of reduced interpretability, and similar to traditional spatial planning approaches such as Marxan, it relies on heuristics that can not guarantee that a best possible solution can been found [229].

Multiple open-source software solutions have been developed to support integration of landscape ecology theory and indicators into spatial planning. Most software are based on linear or constrained programming approaches and require a solver to create any outputs. Unfortunately, there are differences between open-source and proprietary solvers in terms of computational efficiency [229] and the performance of any individual solvers can depend on the specific problem, data and computational resources. Nevertheless, existing comparisons often show that proprietary solvers can be used to obtain solutions to complex problems in reasonable time periods [217], however, due to software licenses and related cost certain solvers might not always be openly accessible.

Conclusion

Since its emergence in the 1980s [8], landscape ecology research has constantly evolved and is now highly dependent on computational methods. Thus, future progress within the field will largely depend on integration of novel data sources and available software and computational tools [60]. Here, we present and summarize some recent developments of computational methods related to spatial patterns, connectivity, simulations and modeling, landscape genetics and spatial planning. In this context, we highlight open-source software as a cornerstone of "Open Science" offering key advantages like shareability, reproducibility, and transparency, which provide great benefits to the research community [230, 231].

Alongside the previously introduced methodological advances specific to landscape ecology, the research field will also benefit from technological innovations from related disciplines. This includes advances in remote sensing technology with increasing data availability and diversity from a range of sources, including satellites, unmanned aerial vehicles, and ground-based sensor systems [232, 233]. These systems provide both passive sensors, such as multispectral, hyperspectral, and thermal sensors and active optical sensors, such as LiDAR and SAR [233]. Related to this, there is a growing number of up- and downscaling approaches for remote sensing data which makes a wider range of products accessible [234]. In combination with other increasingly available data sources, e.g., citizen science data, ecology has entered the era of big data, requiring methods that can handle heterogeneous data and high-throughput computing resources [209]. Due to its high flexibility and performance artificial intelligence has become popular in ecology, and deep learning and machine learning algorithms can be used for, e.g., mapping, classifying and extracting features, modeling, or predicting [235–238]. Furthermore, quantum computing may additionally offer a potential pathway to surpass the limits of current computational technologies [239]. Last, landscape ecology will, as many other research fields, benefit from a general paradigm shift related to data sharing, management, and documentation [240].

Climate change, as well as the biodiversity crisis, are two intervening and complex issues that need integrative, multi-disciplinary, and scale-dependent solutions to face them [241, 242]. Landscape ecology is well equipped to provide answers because it connects several research fields at multiple scales, such as social sciences, geography, and ecology and evolution [8]. Up-to-date and constantly evolving computational methods are required to meet the increasing complexity of research questions. Nevertheless, the review provided here that showcases current computational methods in landscape ecology will only be a snapshot in time because of the development and emergence of future analytical approaches.

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  The paper assesses where and how spatial conservation planning have been applied across Europe.

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