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Theories in landscape ecology. An overview of theoretical contributions merging spatial, ecological and social logics in the study of cultural landscapes

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Abstract
Context Landscape ecology is endowed with a wealth of accumulated insights into how spatial, ecological and social research can be fruitfully combined and synthesised. This has the potential to contribute significantly to how cultural landscapes are observed, analysed, conceptualised and explained.
Objectives This article provides an overview of theories in landscape ecology relevant to the study of cultural landscapes. Based on a review of selected contributions formulated since the field's first inception, it is outlined how theory was developed within the field and how proven methods of theory generation can inspire further development.
Methods A systematic review covering historical and contemporary theoretical contributions to landscape ecology was conducted. Theories were analysed to uncover by what methods they were formulated. On this basis, an overview of theories in landscape ecology relevant to the study of cultural landscapes was developed.
Results A total of 32 theories were included in the review and described. Four pathways of theory development characteristic for the way knowledge is accumulated in landscape ecology were identified. These pathways exhibit modes of knowledge transfer between observations and actions taking place in concrete empirical contexts, knowledge which is transferable across contexts, as well as generally applicable concepts. An annotated overview of primary and secondary sources is provided. Contemporary literature building on the theories was identified, linking sources of conceptual inspiration to the current state of the art.
Conclusions The review illustrates that a wealth of complementary theories exists in the field, creating a condition of theoretical multiplicity. Key theories and tendencies for theory development are outlined, and it is discussed how theoretical advancement in the study of cultural landscapes may be improved.

Keywords Environment · Land Use · Sustainability · General theory · Theoretical multiplicity · Geography

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Introduction

Landscape ecology is an interdisciplinary field of research and practice dealing with the relationship

between ecological processes and spatial patterns in landscapes, exploring "the biological and societal causes and consequences of landscape heterogeneity" (Miller et al. 2021). It studies the structure, functioning and dynamics of different types of landscapes on a range of spatial and temporal scales and organisational levels and forms a nexus for accumulation of theory and models explaining and describing landscape dynamics (Forman 1995; Wu 2013a).

Since its inception as a field in the mid-20th century (Troll 1939a, 1950b), landscape ecology has encompassed a powerful component of applied research addressing sustainable land use and conservation through "the science and art of studying and improving the relationship between spatial pattern and ecological processes" (Wu 2019). A great variety of approaches from research traditions across the natural, social and human sciences are relevant to pursuing this research agenda, and therefore landscape ecology incorporates "multiple viewpoints about what constitutes the domain of landscape ecology" (Wiens 1992). This is one of the great strengths of the field because it means that the field can sustain integrative research addressing social and ecological facets of cultural landscapes, reflected in the fact that "the vast majority of landscape ecology research has a direct or indirect focus on human impacts on the systems under investigation" (Francis and Antrop 2021). However, the breadth of perspectives included within landscape ecology also constitutes a challenge to the field, since accumulation and synthesis of findings have to take place across a wide range of research traditions, theoretical viewpoints and associated conceptual models.

So far this has been achieved mainly because the field comes together around a shared research interest emphasising "spatially explicit or locational" factors in research on "the structure and dynamics of spatial mosaics and their ecological causes and consequences" (Wiens 2005). This shared spatial, systematic focus has offered researchers a common ground for combining their insights in practice by using common sets of spatial units to organise observations and analysis (Kienast et al. 2021). As such, more than any other common denominator, the field is characterised by a perspective concentrating on accumulation of knowledge about the causes and effects of spatial organisation of landscape phenomena, thereby merging spatial, ecological and social logics in the study of cultural landscapes. This focus has been retained as an identifying characteristic of the field since its formation and early development (Troll 1971). This review article summarises selected elements of this tradition, tracking the pathways of development of theoretical insights addressing aspects of the ecology of cultural landscapes as these have developed historically, accumulated in the field and evolved until today by identifying different trends and future directions in theory development in landscape ecology.

Theories addressing cultural landscapes and their significance

In addition to using spatially explicit units of analysis, many landscape ecologists have tended to share an interest in integrative research perspectives, focusing attention on the ecology of landscapes that include people, societies and their land use practices. As Wiens et al. (2007a) have expressed it, "because most landscapes are modified by human actions, landscape ecology also integrates humans with natural ecosystems". In research dealing with cultural landscapes, i.e. landscapes dominated by people, landscape ecology has championed an inclusive, integrative research agenda where "a cultural landscape consists not only of its natural elements and the infrastructure of the economy, settlement and transport, but also the influence and output of its inhabitants: their traditions, language, nationality, social structure, artistic development and feeling for art, and religion" (Troll 1950a; see also Wu 2010 for a contemporary perspective). Taking into account this broad palette of phenomena makes understanding of landscape processes more complete. This has become increasingly valuable since research tasks, to an increasing extent, deal directly with human land use practices, which are embedded within sociocultural contexts included in landscape analysis frameworks (Farina 2009a; Wu 2010; Antrop 2018). Therefore the relationship between social systems, landscape patterns and processes forms an essential research topic within the field, including within applied research on planning and other interventions addressing political and social aims for sustainable land use and development (Kizos et al. 2018; Hersperger et al. 2021). Because of the long term interdisciplinary history of the field, landscape ecology has accumulated a comprehensive range of theoretical and conceptual insights on these

topics, which are sought after in cognate fields and contexts of application (Diaz et al. 2019; Meyfroidt et al. 2022). As such, the accumulation of theory may be considered one of several valuable contributions of Landscape ecology over the years, through which the field has come to support the conceptualisation of reasoning which underscores how spatial, ecological and social logics of scientific discovery, evidence gathering and explanation can be combined. This observation was the motivation for the review of theoretical contributions to the study of cultural landscapes presented here.

Aims and methodology of the review

We used an adapted version of the methodological framework of systematic theoretical reviews outlined by Campbell et al. (2014) (see also Cooper et al. 2019). The review process included the following steps: (1) A broad preliminary list of materials considered for inclusion in the review was compiled based on a reading of papers and books within the field. This process was conducted over several years from 2017 to 2022 where all potentially relevant contributions were collected in a database, resulting in a comprehensive corpus of texts; (2) Review papers, overview works and books summarising progress in the field were used iteratively as a source for checking if we had achieved sufficient breadth and to make sure that no important contributions were overlooked (works consulted include Troll 1971; Schreiber 1990; Zonneveld 1990; Leser 1991; Naveh 1991; Naveh and Lieberman 1994; Brandt 1995; Zonneveld 1995; Farina 1998; Bastian and Steinhardt 2002; Burel 2003; Haber 2004; Wiens 2005; Wiens et al. 2007a; Cushman 2009; Farina 2009b; Wu 2013a, 2017, 2021; Barrett et al. 2015; Forman 2015; Antrop and Eetvelde 2017; Gergel and Turner 2017; Christensen et al. 2017; With 2019; Milovanović et al. 2020; Francis et al. 2021; Hersperger et al. 2021); (3) All texts in the compiled corpus were read and considered for inclusion based on predefined selection criteria; (4) The selected texts were investigated in further detail, subsequent reference to the texts were assessed and texts were deselected if found not to fit the criteria.

Qualitative, relational selection criteria were used to focus the review and ensure only contributions of relevance to subsequent research in the field were included (Saini and Shlonsky 2012). We selected texts that contributed with theoretical concepts and/or models to the field, where the conceptual contributions either: (a) were still in use in the literature of landscape ecology, indicating continued relevance for current research or as background concepts; or (b) were referred to as formative reference points in subsequent research publications, indicating continued relevance as seminal examples of reasoning and approaches employed within the field. The result of this review method was a compilation of key theoretical concepts used in landscape ecology to study cultural landscapes. Each of the theoretical contributions included was investigated with an aim to uncover and describe: (1) what empirical material the contribution was originally developed from, (2) the method of theory formulation used, i.e. how knowledge was transferred to a broader context than that within which it was first derived, and (3) the range of applicability of the theory in time and space, i.e. under what conditions the theory is relevant as an explanatory device.

Research questions addressed in the review

Based on the reviewed literature, the following research questions are discussed:

1. Which key theoretical concepts addressing cultural landscapes have significantly contributed to the development of landscape ecology?
2. What are typical steps and characteristics in the development of theory addressing cultural landscapes within landscape ecology?
3. What pathways of development can be identified in the formulation of theories within landscape ecology?

Further details regarding the choice of thematic and temporal focus for the review are outlined below. The paper then introduces a perspective on how theory in landscape ecology may be defined and characterised (Sect. "Some roles of theory in knowledge accumulation within landscape ecology"). On this basis, a comparative framework for describing the development of theory in landscape ecology is presented (Sect. "Comparing and interpreting theory development in landscape ecology"). A review of selected theories is then reported, with contributions grouped according to how theories were developed (Sect. "Review of theories in landscape ecology").

The discussion reflects on the history and practices of the development of theories in landscape ecology (Sect. "Discussion").

Temporal scope: what time period is covered?

As Wiens et al. (2007a) have argued, "new disciplines or fields of study do not spring into life fully formed… instead, they usually begin with glimmerings of new ideas or different perspectives, often developed as part of some seemingly unrelated disciplines". Therefore it can be difficult to establish where a line of thought starts and how long back in time it extends. This is especially the case, i.e. in this review, when the aim is to outline key theoretical concepts within a field, which may have been in use long before the field as such was founded. Therefore this review starts from the writings of Carl Troll and those works that Troll himself referred to as reference points for his development of the field. Troll coined the term landscape ecology in 1939, elaborated on it in his later works and helped establish the field as we know it (Troll 1939a, 1950a). His thinking was "deeply influenced by Alexander Von Humboldt" and the tradition of spatial-ecological thinking Von Humboldt had inspired, which was especially pronounced among European-continental geographers (Holtmeier 2015) and which, through Carl Sauer and others, came to inspire North American research communities (Wiens et al. 2007b). Troll and his contemporaries viewed these figures as their intellectual forebears, considered them with "awe and humility", and used their work as direct conceptual inspiration (Troll 1960; see also Gade 1996). We therefore limit our account of the development of theoretical concepts in landscape ecology to those direct influences on Carl Troll and his contemporaries, which are necessary for a full appreciation of how the first landscape ecological concept and theories were developed (Francis and Antrop 2021; see also Kienast et al. 2021). We outline in the review how contributions predating the field informed later work in landscape ecology. From those early beginnings, conceptual developments in the field are tracked forward in time until today, within the limits imposed by the review focus.

Thematic scope: focus and limitations

The review focuses on conceptual advancements in the field relevant to how cultural landscapes are conceptualised, analysed, observed and explained. Due to this rather conceptual focus, applied, solution-oriented and aesthetic contributions fall outside the scope of the review, despite their considerable impact on the field. These include contributions to biological conservation, land management, wildlife management, planning, design, aesthetics and landscape architecture. Landscape ecology is a broad field of research, so no single review is likely to be able to encompass its full complexity and diversity. The present review has been conducted from a particular thematic position within the field, influencing what contributions have been included. Our view of landscape ecology is one among several established perspectives, representing what has been referred to as "Anglo-European notions of landscape and landscape research" (Kienast et al. 2021). Other perspectives could have been emphasised, likely leading to other selections of theory in the review. By using a consistent and transparent emphasis, we have strived to complement other reviews of theoretical contributions to the field.

Some roles of theory in knowledge accumulation within landscape ecology

Theory in landscape ecology serves several purposes, the most obvious being to collect concepts, models and understandings to work from, both when dealing with well-known phenomena and when confronting new empirical contexts. Having an overview of theoretical vocabularies and alternative models of classification allows researchers to make informed choices, identify knowledge gaps and locate horizons of knowledge. However, these practical procedures involving theory build on a more basic function that theory performs, namely its performance as the primary vehicle for breaking down barriers between individual phenomena through the production of transferable knowledge based on multiple landscapes and landscape types (Francis and Antrop 2021). This is an essential function of theory, given that a field consisting only of observations that cannot be compared with standards is anecdotal and does not

constitute a science (Newig and Rose 2020). Given that each landscape is essentially unique, a field without effective mechanisms to produce theory would have multiple "proto-theories", each belonging to a particular set of observations, which it would not be possible to synthesise and report as aggregate, transferable, decontextualised knowledge, concepts and models. This points to a key characteristic of theory: it should posit knowledge that is (potentially) useful outside its original context (Mills 2000)—i.e. transferable from one landscape to another, between landscapes under comparison, and/or from a sample to a larger field. As such, theory can be defined as knowledge that is at least partly decontextualised from the context where it was generated, meaning that it is described in a transferable to other landscapes, making the degree of transferability (or conversely expressed: the degree of contextual specificity) an important feature of theory. This means that information about under what conditions a theory is or may be applicable plays an important role in assessing its potential usefulness and range of appropriate application, which in landscape ecology may be taken to refer to the range of landscapes and situations in landscapes to which the theory may be expected to apply.

What is theory?

Theory can be defined as the raw material produced through processes of knowledge accumulation. It exists as a library of concepts, terms, understandings, modes of reasoning and accepted facts constituting a research field. It enables researchers to stand on the shoulders of previous investigators. As such, theory exists both as formal, explicit formulations expressed in language and mathematics and as implicit background concepts that researchers use as part of day-to-day reflection and conversation about their research topics (Kuhn 1962).

Theory can be distinguished from presuppositions in that theoretical knowledge affords assessment of correctness and relevance through testing. In contrast, presuppositions can be defined as knowledge that is taken for granted—i.e. which "convey backgrounded, uncontroversial information with respect to the context of utterance" which is "already known to be true and accepted by the conversational participants" (Sudo 2014). As such, using a broad definition, theory can be defined as the subset of knowledge within a research field that either (1) was made subject to rigorous, explicit reflection and testing at the time of its first use or proposition, (2) is currently undergoing such assessments in the field, or (3) is known to have sufficient argumentative depth and/or evidence behind it to make such reflection possible. Within this definition, theory can be understood to displace common sense when confronted with it, reconstructing understandings of phenomena in light of evidence and argument. This is irrespective of whether or not the theory in question is currently taken for granted (through presupposition) or made subject to explicit debate (through proposition). In this way, theory forms part of background thinking that influences decisions, for example, on strategies for further research and has the power to overturn less argued understandings. As such, theory can be considered performative as well as descriptive (Lyotard 1997). In this view, theory is characterised by its ability to influence and co-construct further thinking and practice—for example, through an additional accumulation of knowledge—but also through replication of mistakes and unreflected repetition of biases (Chouliaraki 2002; Newig and Rose 2020). Therefore, formulation and continuous critical debate of theory can be understood as a process through which awareness, diligence, consistency and truthfulness can be furthered.

Quality criteria for theories

Theories may be expected to live up to certain logical quality criteria to be of practical use. They may be expected to be internally consistent, i.e. not encompassing statements that are logically at odds with other parts of the theory. This entails attention to the relationship between statements and underlying assumptions and to the appropriateness of employed categories and distinctions. Similarly, theories may be expected to be externally consistent with or complementary to other theories in the field dealing with the same phenomena. As such, differences in how two or more theories describe the same phenomena should be resolved, or it should be possible to demonstrate complementarity—i.e. that the theories address different dimensions or facets of the same phenomena, e.g. cultural landscapes, expressing several different truths about the same empirical phenomenon. This type of productive coexistence of multiple valid

perspectives on the same subject matter has been referred to as "theoretical multiplicity" (Hansen and Simonsen 2005) and "plurality" (Cadena and Blaser 2018) and may hold transdisciplinary, socio-political potentials that can be relevant for research where different interests, cultures, social groups or polities are part of the same fact-world being described and conceptualised theoretically (Cadena and Blaser 2018; Raffn et al. 2021). For example, in contemporary cultural landscapes where numerous land uses coincide spatially and temporally (Brandt and Vejre 2004; Hölting et al. 2020a), it may be necessary to represent plurality conceptually (Primdahl 2018). In this view, when observations involve humans and the effects of their actions, it may be argued that "a number of theoretical approaches are required in order to capture all of the facets of an object of investigation" (Martin 2021). This entails a view of theory as something less than monolithic and uniform, yet consistent, transferable and suitable for empirical testing within well-defined landscape contexts. We find that this set of quality criteria for theory fits the history and subject matter of conceptual development covered in the review well, wherefore we have used it as a basis for investigating the theories included.

Comparing and interpreting theory development in landscape ecology

A large part of what we can learn from theory is about how it was formulated. Theory exposes brilliant modes of reasoning that are often remembered for their internal logic and method, alongside particular contributions to our understanding of the empirical world. This applies particularly to theories that have become classical or normalised within a research field. Foundational and classical theories within a given field of research "are of interest to subsequent generations not so much for their substantive claims as for their status as (…) paradigms or exemplars which show us how we might wish ourselves to theorise" (Outhwaite 2000). The work of Carl Troll is an example of this (Troll Troll 1939b, 1950b). Few contemporary researchers are likely to be interested in his specific findings about the relationships between land use, land cover and soil patterns. His contribution today is nonetheless monumental, for he is remembered for formulating a spatial logic regarding how to investigate spatial correlations of factors in landscapes, which was illustrated in his empirical work (Christensen et al. 2017). This dual mode of learning from theory, either as an example or as a substantive knowledge contribution, means that it is necessary to provide an outline of how each theory was developed in order to capture the contribution of theories in landscape ecology. We need to know what evidence was used, by what process of reasoning the facts were explained, and how the resulting knowledge was made available and relevant for a wider array of empirical contexts.

To investigate this in a systematic manner, theories included in the review were analysed, grouped and presented below according to the way they were developed. For each theory, it was investigated how transferable knowledge was obtained through the construction of links between three components of knowledge: (1) observations and actions taking place in concrete empirical contexts, (2) knowledge transfer and comparison across empirical contexts, and (3) formulation of generally applicable theoretical constructs. The analysis of the theories shows that four different pathways exist with respect to how theory is derived through transfers of knowledge bridging these three components. This constitutes four methods of knowledge transfer along gradients of spatial and temporal magnitude, from specific to general knowledge of landscape(s). The theoretical contributions included in the review below (Sect. "Review of theories in landscape ecology") are presented according to these groups.

Review of theories in landscape ecology

Based on the analysis of the selected literature, four modes of theory development in landscape ecology and its immediate antecedents can be distinguished. Each of these four pathways has its own way of sequencing components in the process of theory development. Consequently, the theories differ in how they are derived from specific observations or are influenced by other theories. The four sections below include the inventory of the 32 identified theories in this review, which are listed and described in detail according to their mode of development.

Names of the theories and concepts included in the review were defined by balancing a concern

for maintaining the original title if one existed and achieving clarity for contemporary and interdisciplinary readers. In cases where the original theory did not have an explicit title, a descriptive moniker was adopted for clarity. Complete references to the original texts are included alongside references to later publications of the same author(s), as well as literature adding to and debating the theory and contemporary work on the theory linking it to current research agendas in the field.

Group A: theory derived from empirical observation through comparative analysis

The first group of theories comprise contributions that started from a series of local context-specific observations, for example one particular case or a series of local observations of the same type of phenomena that were compared. Transferable knowledge was developed from this outset, which was then further advanced into a generally applicable theory. In total, 13 theories were developed in this way, listed in Table 1.

The oldest theory in this group is the theory of geoecological correlation (A.1) proposed in the work of Alexander von Humboldt. As an intrepid naturalist and explorer, he executed fieldwork in the Andes, Alps, Ural and Altai mountains, where he was inspired to consider the earth as one great living organism, emphasising how land forms, life forms and ecosystems were connected. He made spatially explicit inventories of vegetation, elevation and climatic conditions. On this basis and by comparing correlations between variables at different locations, he formulated a general model of the pattern and conditions of montane vegetation, visualised in cross-section diagrams (von Humboldt and Bonpland 1805). These later became the "most influential diagrams in the history of environmental science" (Moret et al. 2019) in that they express a holistic understanding of nature, emphasising the mutual interplay between life forms and their living conditions. Subsequently, a theoretical vocabulary describing the earth surface as the most basic reference point for correlating observations was formulated. The importance of von Humboldt for the later development of landscape ecology and geography is widely recognised (Troll 1960; see also Marsh and Lowenthal 2003; Martin and Martin 2005; Egerton 2009).

Another example is the theory of cultural landscapes (A.5) proposed by Carl Sauer. Based on fieldwork in North and Latin America, he recognised that cultural and physical factors were complementary to determining the pattern and morphology of landscapes (Bowen 1996). This led to his definition of landscape as a primary unit of geographical analysis arising from the combination of factors present at a given location (Sauer 1925). This inspired Sauer to formulate a general theory of how human societies create spatial patterns where "the cultural landscape is fashioned from a natural landscape by a culture group. Culture is the agent, the natural area is the medium, the cultural landscape is the result" (Sauer 1925).

Another cluster of theories in this group deals with spatial relationships and complexity in cultural landscapes in various ways, emphasising how landscapes form comprehensive systems suited for interdisciplinary investigation. These include the first novel approaches to describing landscape phenomena as relational systems. One of the seminal inspirations for this was the theory of landscape ecological interdisciplinarity (A.9) formulated in the work of Carl Troll. Based on a combination of photogrammetry and field observations in Europe, South America, Africa and the Himalayas, Troll developed a three-dimensional understanding of landscapes and a range of new methods to provide a synoptic, multi-layered view of landscape patterns and functional relationships between patches in landscapes (Troll 1939a). On this basis, an interdisciplinary understanding of landscapes was formulated, emphasising how landscape ecology demands the presence of multiple interacting disciplinary components. Building on this line of research, I.S. Zonneveld contributed with a theory of hierarchical landscape systems (A.10). This approach was rooted in a systematic long term longitudinal field study of an estuarine environment in The Netherlands, aiming to understand the temporal relationship between land use, vegetation and physical landscape characteristics (Zonneveld 1959). Consequently, a conceptual model explaining the dynamic interrelationship in and between physiographic land units was developed, which was applied in land evaluation projects around the world and came to inform a widely used pragmatic holistic approach to landscape analysis (Zonneveld 1995, 2005).

In the mid-20th century, two other key theories were formulated that fundamentally influenced spatial and functional analysis in landscape ecology. Robert H. MacArthur and Edward O. Wilson (1963, 1967) observed species richness in arthropod populations on islands in Florida, which enabled them to describe how geographical variables affect the isolation and exchange of species between areas. This led to the formulation of the theory of island biogeography (A.11), adding a spatial component to models of evolution that had been largely absent since Darwin (1859) (A.3). The new theory explained rates of migration and extinction of species as a function of area sizes and their isolation, independent of the type of area. This formed the foundation for many new applications and developments in landscape ecology that study the relationship between isolation or fragmentation of habitats in relation to population dynamics (Opdam et al. 1984; Saunders et al. 1991) as well as anthropogenic impacts on evolutionary processes (Helmus and Behm 2020). In the metapopulation theory (A.12) as formulated by Levins (1969), metapopulations were later defined as "spatially structured populations (…) separated by space or barriers, and connected by dispersal movements" (Opdam 1991). This line of research inspired a wide range of novel ecological research emphasising the spatial dimension of evolution processes, dispersal and population dynamics (Chesson 2013; Hanski and Ovaskainen 2019). It illustrates how a set of generally applicable theoretical insights can be developed from regional and local scale studies through incremental revision and testing on datasets of increasing magnitude and variety (Moilanen and Hanski 1998; Hanski 1999; Hanski and Ovaskainen 2000, 2003).

Group B: theory derived from empirical observation designed on the basis of existing general concepts

The theories in this group were developed from collections of local-scale historical and longitudinal studies conducted and analysed in the explicit context of established theoretical vocabularies (see Table 2). As such, the theories are characterised by a method whereby researchers used general concepts to open up analysis of landscape development processes while continuously redefining the concepts used. There has been a long historical and spatially explicit tradition for this type of landscape research, predominantly with a focus on describing histories, cultures and types of socio-ecological interaction. Early work in this tradition aided in founding a theoretical understanding of the geometry of social-ecological processes. Numerous historical case studies of land use development in Western European village landscapes were explored from the 1950s onwards (see references in Table 3). This led to the formulation of a group of models describing essential geometrical relationships in cultural landscapes (inspired by theory A.5), their settlements, and their development in relation to land qualities and territorial models. The three groups of theories included in the review focus on various scale levels in cultural landscapes, emphasising settlements as the primary and holistic building blocks of landscapes (B.1), resulting in different land use patterns associated with a diverse range of land qualities around the initial settlements (B.2), summarised and analysed in the form of different territorial models (B.3) (Antrop and Van Eetvelde 2017).

Later on, more comprehensive and general models of landscape mosaics were developed, leading to (1) a reinvention and redefinition of landscape ecology in the 1980s that coincided with a quantitative revolution in the field (Forman and Godron 1986; Turner 1991) and to (2) new approaches and models in land-use planning and landscape architecture (Dramstad et al. 1996). Consequently, landscape ecology became a science combining spatial datasets from a broader field of disciplines and—equally important—general theories about landscape structure and developments were formulated out of this. A clear example is the development of the theory of landscape mosaics (B.4), which is based on observations regarding the ecological significance of spatial patterns derived from case studies of woodland landscapes such as the Pine Barrens of New Jersey studied by Richard Forman and colleagues. Forman referred explicitly to the theory of island biogeography (MacArthur and Wilson 1967), applied this to "patchy terrestrial landscapes", which have additional factors compared to the island patterns, and introduced the concept of an ecological mosaic or ecomosaic. The mosaic is defined as "an area containing patches of two or more ecosystems or communities, with a structure based on the spatial distributions of, and the dynamics based on the changes in, the patchily-distributed ecosystems and ecosystem components". This concept later developed into the conceptual "patch-corridor-matrix

Table 1 Group A—Theory derived from empirical observation through comparative analysis

Theory [1]	First reference(s) [2*]	Components of theory development Observations and actions → Insights applied across contexts → Generally applicable theory			Additional references [3]
A.1 Theory of geoecological correlation	von Humboldt and Bonpland (1805) Essai sur la géographie des plantes	> Based on fieldwork in the Andes, Alps, Ural and Altai mountains, the relationship between vegetation, elevation and climate was mapped for a number of extensive case areas.	> A general model of montane vegetation patterns was developed. Cross section diagrams (naturgemälde) and isoline maps were used to show the relationship between geographical and biological factors.	> A holistic understanding of nature was developed, emphasising the mutual interplay between life forms and their living conditions. On this basis, a theoretical vocabulary describing the earth surface as the primary reference point for correlating observations was formulated.	(a) Jackson and Romanowski (2009) Essay on the geography of plants (b) von Humboldt (1808, 1845) (c) Jenkins (2007), Egerton (2009), Buttimer (2010), Debarbieux (2012), Doherr and Baron (2012), Moret et al. (2019)
A.2 Theory of agricultural location	von Thünen (1826) Der isolierte Staat	> Empirical work was conducted at the manorial estate of Mecklenburg (Tellow, Germany), uncovering relationships between the location of market centres and patterns and locations of agricultural land use.	> Spatial and mathematical models were developed to account for observed relationships between agricultural production, accessibility to markets and commodity transport costs, indicating how these define agricultural systems.	> A concentric zoning model and an associated hierarchical classification of agricultural crops based on profit-market capacity were developed, explaining patterns of land use in an isotropic space based on economic factors.	(a) Hall (1966) Von Thünen's isolated state: an English edition of der isolierte staat (b) Curtis (1956) (c) Schneider (1934, 1996), Portugali (1984), O'Kelly and Bryan (1996)
A.3 Theory of evolution by natural selection	Darwin (1859) On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life	> Based on fieldwork in South America and the Pacific, alongside exploration of fossil records of species in combination with inspiration from theories of geological evolution, observations regarding historical relationships between species and environments were developed.	> Explanations for observed correlations were formulated and weighed against existing theories and belief systems. These included theories specific to particular empirical domains as well as broader perspectives on explaining correlations between environmental conditions and species across contexts.	> A theory of evolution by means of natural selection was formulated, emphasising the role of environmental factors in the development and selection of successful lifeforms evolving through geological time.	(b) Darwin (1839) (c) Barlow (1958), Egerton (2010, 2011), Tanghe (2019)
A.4 Theory on the location of industries	Weber (1909) Über den Standort der Industrie	> Studies of how locational parameters affected geographical distributions of heavy industries in Germany from the 1850s to 1910 were conducted.	> A theory of optimal placement of industrial production facilities relative to geographies of raw material supply, demand for products and labour was devised, indicating the combined effect of location parameters and characteristics of raw materials on economic development.	> A general theory of how geographical factors affect economic systems was described, stressing how transport costs and resources in markets among other factors influence industrial development. This inspired a spatialisation of economic thinking, development of spatially explicit and regional development theories.	(a) Friedrich (1929), Alfred Weber's theory of the location of industries (c) Ponsard (1983), Jones and O'Neill (1995), Gorter and Nijkamp (2001)

Table 1 (continued)

Theory [1]	First reference(s) [2*]	Components of theory development Observations and actions → Insights applied across contexts → Generally applicable theory			Additional references [3]
A.5 Theory of cultural landscapes	Sauer (1925) The Morphology of Landscape	> Based on fieldwork in Illinois, Missouri, Kentucky, California and later in Latin America, cultural and physical phenomena were recognised as different but equally important factors of landscape pattern and morphology.	> Landscape was proposed as the primary unit of geographical analysis because its patterns and morphology express the combination of cultural and physical factors present in an area.	> Broadly applicable insights were gained regarding how human societies create spatial patterns, thereby expressing and developing cultural characteristics physically in meetings with nature.	(b) Passarge (1919), Troll (1950b), Sauer and Leighly (1976) (c) Parsons (1976), Kenzer (1985), Speth (1993), Bowen (1996), Jones (2003), Howe (2011)
A.6 Theory of sensing the humanly perceived environment	Granö J.G. (1929) Reine geographie	> Based on fieldwork in Finland, Estonia and the Altai mountains in Russia, it was established that perceptual and sensory observations are an important way to understand landscapes and that observations are relative to location and time.	> A vocabulary of perceptual elements in landscape observation was developed, observing that landscapes are perceived primarily through visual modes at a distance and with the totality of senses within closer proximity.	> A nuanced understanding of human sensory and perceptive relationships with landscape was developed, indicating how temporal, spatial and visual aspects of human perception form different but complementary ways of accessing the landscape.	(a) Granö JG, Granö O and Paasi (1997) Pure geography (c) Granö O (2003)
A.7 Central place theory	Christaller (1933) Die zentralen Orte in Süddeutschland	> Studies of settlement patterns in Southern Germany were conducted, emphasising distances between settlements, their hierarchical organisation, and the shape of their territories. The aim was to explain how spatial patterns of settlement were ordered.	> A model describing geometric patterns of settlement and economic development within isotropic spaces was designed, laying out a logic for the development and sharing of space between hierarchically organised nodes within urban societies.	> Insights into relationships between spatial and social ordering were derived, which later informed planning, management, and regional development strategies.	(c) Berry and Pred (1961), Jones and O'Neill (1995), Gorter and Nijkamp (2001)
A.8 Theory of ethical conservation	Leopold (1933) Game Management	> Experience with hunting and outdoor life on farms in Iowa and range management in combination with conservation experiments in Arizona, New Mexico and Wisconsin formed the basis for insights into ecosystem equilibria.	> Experiences with land conservation and the role of predators in wildlife management were synthesised into a relational model linking landscape and fauna. On this basis a holistic theory of conservation and its application in a spatial and dynamic context was formulated.	> A general understanding of humans as situated in nature was unfolded, leading to the formulation of a new concept of conservation, contributions to theories of wilderness, and an environmental ethic for society emphasising relationships between people and the land.	(b) Leopold (1949) (c) Gutherly and Bingham (1992), Silbernagel (2003), Callicott (2013), Meine (2013), Egerton (2019), Van Dyke and Lamb (2020)
A.9 Theory of landscape ecological interdisciplinarity	Troll (1939c) Luftbildplan und ökologische Bodenforschung	> Based on a combination of photogrammetry and field observations in Europe, South America, Africa and the Himalayas, a three-dimensional understanding of landscapes was achieved. It was observed how pedological, vegetational, topographical and other factors correlate in landscape patterns.	> It was proposed that landscape ecological processes are best understood from a unified perspective emphasising spatial (i.e. topological and ecological) relations between multiple factors codetermining landscape morphology.	> An interdisciplinary outlook for landscape research was developed, emphasising that landscape phenomena demand a perspective overstepping the boundaries between disciplines which can be achieved by making spatial units of analysis primary, using them as a common denominator organizing multiple types of observation.	(b) Troll (1950b, 1971b) (c) Butzer (1976), Zonneveld (1995), Gade (1996), Tress and Tress (2001), Naveh (2005), Holtmeier (2015), Kwa (2018)

Table 1 (continued)

Theory [1]	First reference(s) [2*]	Components of theory development Observations and actions → Insights applied across contexts → Generally applicable theory			Additional references [3]
A.10 Theory of hierarchical landscape systems	Zonneveld (1959) De Brabantse Biesbosch: een studie van bodem en vegetatie van een zoetwatergetijdendelta	> Longitudinal field studies were conducted in the Biesbosch located at the estuaries of the rivers Rhine, Meuse, and Scheldt, aiming to understand the dynamic temporal relationship between land use, vegetation and physical characteristics indicating how the landscape functioned as a system.	> A conceptual model of the structure and dynamic interrelationship between physiographic land units within landscapes was developed, stressing how a landscape is composed of relational elements influencing each other, forming a functional totality.	> A general theory of pragmatic holism in landscapes was developed, describing how landscape holons can be conceptualised when encountered empirically. This later inspired work within land evaluation, land use development and land reforms, a.o. fields.	(b) Zonneveld (1989, 1995, 2005) (c) van Wirdum (1981), Barendregt and Klijn (2006), Kwa (2018)
A.11 Theory of island biogeography	MacArthur and Wilson (1963) An Equilibrium Theory of Insular Zoogeography	> Studies of species richness in arthropod populations on islands in Florida were conducted, uncovering how geographical variables affect isolation and exchange of species between areas. Islands were used as units of analysis because they provided a controlled area for study.	> A theory of island biogeography was developed, modelling relationships between the rate of colonisation (migration), evolution, extinction, species richness, area size and distance between areas, independent of the kind of areas concerned.	> The theory of island biogeography was broadened to encompass landscapes in general, interpreting habitats embedded within human-altered landscapes as islands and modelling the exchange of species between them. This inspired the formulation of theories relevant to a wide range of environments with semipermeable boundaries and/or distance between habitat areas.	(b) MacArthur and Wilson (1967) (c) Opdam (1984), Forman and Godron (1986), Saunders et al. (1991), Helmus and Behm (2020)
A.12 Metapopulation theory	Levins (1969) Some Demographic and Genetic Consequences of Environmental Heterogeneity for Biological Control	> A model of population dynamics of insect pests in agricultural landscapes in the United States was developed, taking into account patterns of spatial and temporal variation in environmental conditions.	> The model was further developed, differentiated, and applied in a variety of terrestrial and later marine environments, making it possible to understand and predict population dynamics as a consequence of migration and extinction across a wide range of heterogeneous environments.	> Knowledge of how landscapes sustain populations through systemic functionality arising from the interaction of habitats distributed heterogeneously across the land was revised and improved.	(c) Opdam (1991), Hanski (1983, 1999), Hanski and Ovaskainen (2000, 2003, 2019), Opdam et al. (2018), Chesson (2013)
A.13 Economic theories of the environment	Holdren and Ehrlich (1974) Human population and the global environment. Westman (1977) How much are nature's services worth?	> Studies of the value of air and water lost due to pollution from energy production in California were conducted, as well as the first studies quantifying ecosystem productivity, creating the basis for testing how services of nature could be valued using monetary units.	> Intercontextual frameworks for observing, indexing, comparing, and assessing the relative value of ecosystem functionality to human societies based on monetary units were developed, making exchange value a primary unit of analysis.	> A perspective on landscape understood in the context of capitalist systems of supply and demand was developed and applied broadly, defining ecosystems and landscapes as economic entities delivering services to society in ways suited for evaluation using monetary units relative to historical capitalist markets.	(b) Ehrlich and Erlich (1981), Ehrlich and Mooney (1983) (c) Costanza and Dale (1992), Costanza et al. (1997, 2017), Gómez-Baggethun et al. (2010), Antrop et al. (2013), Potschin et al. (2016), Price (2018)

[1] Names given to theories are based on a compromise between original titles if indicated by the author(s) and how the theory is understood today.
[2] In some cases, a single author or group of authors introduced the concept in question. In cases where a broader array of researchers contributed, a comprehensive selection of works is referenced.
[3] Additional references include (a) English translations of the original work when relevant, (b) other works related to the theory and later developments including antecedents to the theory, and (c) publications about the theory as well as applications and further development within landscape ecology. See the reference list for full references.
* In some cases, theories were developed in parallel by multiple authors, often over prolonged periods of time. In these cases, the earliest publication that we know of is included.

Table 2 Group B—Theory derived from empirical observation designed on the basis of existing general concepts

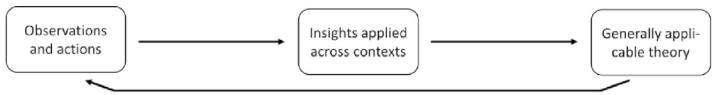
Theory [1]	First reference(s) [2*]	Components of theory development			Additional references [3]
					
B.1 Theories of settlements as primary building blocks of landscapes	Among others von Humboldt (1808), Sauer, (1925), Troll (1939c, 1950b), Lebeau (1979), Chisholm (1962), Roberts (1987), Aston (1997)	> Based on studies of the historical development of settlements within rural landscapes in Western Europe, concepts describing the relationships between different types of sites in the landscapes were developed. This was inspired by previous theoretical work on cultural landscapes and holism.	> Patterns of spatial ordering within traditional European landscapes were described, indicating how the substrate of the land while carrying human life co-determines territorial logics of spatial differentiation within landscapes understood to form geometrical and functional wholes.	> General theories of spatial ordering within traditional landscapes were formulated, emphasising how settlements and their territories in unison form modular primary building blocks that must be analysed in combination. This constituted an early spatial language for landscape models, which later came to inspire contemporary categorial-geometrical models.	(c) Antrop and Van Eetvelde (2017), Forman (2019)
B.2 Theories of land qualities and associated land use patterns	Among others von Thünen (1826), Hoskins (1954), Curtis (1956), Uhlig and Lienau (1972), Aston and Rowley (1974), Haggett et al. (1977), Lebeau (1979), Dodgshon (1980), Antrop (1987), Roberts (1987), Unwin and Nash (1992)	> Historical studies of village landscapes in Western Europe were conducted. On this basis systematic relationships between land qualities and land use patterns were identified. This was inspired by previous theoretical work on geoecological correlation and cultural landscapes.	> Patterns of spatial organisation indicating how the layout and land use of agrarian villages is organised according to land qualities and natural resources were described and mapped. Concepts of spatial ordering emphasising land qualities were developed.	> General theories describing land use geometries, patterns and intensities as expressions of the adaptation of human life forms to the conditions and qualities of the earth surface were formulated.	(c) Sevenant and Antrop (2007), Antrop and Van Eetvelde (2017), Forman (2019)
B.3 Territorial models	Among others Sauer (1925), Christaller (1933), Baker (1971), Antrop (1987), Roberts (1987), Aston (1997)	> Studies of the territorial characteristics and associated spatial differentiation of village landscapes in Western Europe were conducted, focusing on variations in shape, size, complexity and distribution of landscape elements. This was inspired by previous theoretical work on cultural landscapes and location theories.	> A variety of territorial models applicable in specific landscape contexts was developed, indicating patterns of rural settlement, adaptation to land qualities, hierarchies of spatial organisation and spatial properties of territories.	> Theories of territorial organisation were formulated, emphasising compactness as a measure of optimisation. It was proposed that the shape of territories approach maximum compactness under isotropic conditions, with deviations from this indicating land qualities and locational conditions. This formed the basis of studies of forms linking geoecology and human settlement structures.	(c) Roberts and Wrathmell (2003), Sevenant and Antrop (2007), Antrop and Van Eetvelde (2017)

Table 2 (continued)

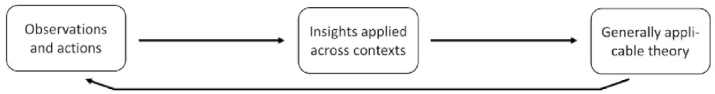
Theory [1]	First reference(s) [2*]	Components of theory development			Additional references [3]
					
B.4 Theory of landscape mosaics	Forman (1979) The Pine Barrens of New Jersey: An Ecological Mosaic	> Based on studies of woodland landscapes in the United States, concepts of ecological mosaics were developed to map and measure ecologically significant aspects of spatial patterns in heterogeneous landscapes. This was inspired by previous theoretical work in island biogeography.	> Categories of land units were formulated, dividing the landscape into types of spaces, making it possible to analyse and compare different landscapes using a common, decontextualised conceptual model emphasising spatial characteristics of ecosystems.	> A categorical spatial language designed to model landscapes in terms of exchange between land units through corridor functionality and contrasts between dominant (matrix) and subdominant (patch) land unit types was proposed. This later formed part of the inspiration for a quantitative revolution in landscape ecology, leading to the development of patch, class, and landscape metrics.	(b) Forman and Godron (1986), Forman (1995, 2015) (c) Hansson et al. (1995), With (2019), Antrop (2021)
B.5 Theory of pattern and process	Forman (1979) The Pine Barrens of New Jersey: An Ecological Mosaic	> Based on studies of woodland landscapes in the United States, the concept of ecomosaics was developed and visualised. Experimental analysis strategies linking spatial structure (i.e. amount and distributions of phenomena) with functions (i.e. flow and change of characters over time) were formulated. This synthesised previous geographical and ecological theories.	> It was observed and modelled how spatial structures and ecological functions in landscapes of various types and under various conditions are related. A preliminary theoretical vocabulary was formulated, emphasising structural and functional traits of ecological mosaics as a framework for further empirical and theoretical work.	> A universal theory of spatially distributed ecological systems was formulated, stating that spatial patterns and ecological processes co-constitute each other and hence cannot be modelled individually. In line with this, an integrative perspective for further research combining spatial and temporal models and methods was laid out.	(b) Forman and Godron (1986), Forman (1995, 2015) (c) Turner (1989), Turner and Gardner (2001), Cassar (2019), Tappeiner et al. (2021)
B.6 Theory of driving forces	Wirth (1969) Zum Problem einer allgemeinen Kulturgeographie Rapport and Friend (1979) Towards a comprehensive framework for environmental statistics: A stress-response approach	> Case studies of variation in land use intensities across Western Europe formed the basis for formulating a force concept, building on distinctions between economic, social and public forces understood to co-constitute geographical spheres of action. A concept of force was defined simultaneously as part of the Stress-Response approach introduced in Canada. Both contributions were inspired by earlier theoretical work formulated within geography and environmental management research.	> Through various stages of development, model frameworks emphasising driving forces, pressures, states, impacts and responses were developed. This included the DPSIR model, describing the interdependent nature of components in environmental systems. Drivers and forces gradually became key concepts used when analysing landscape change and persistence across spatial contexts and scales.	> A general understanding of drivers, forces and associated processes was formulated and applied to landscape change processes and related feedback loops. This later grew to become an important theoretical framework for formulating and evaluating environmental policy in more general terms.	(b) Auclair (1976), OECD (1993), Stanners and Bourdeau (1995), Kates et al. (1997), Brandt et al. (1999), Bürgi (1999) (c) Marcucci (2000), Bürgi et al. ((2004, 2017, 2022), Wood and Handley (2001), Gari et al. (2015), Fayet et al. (2022)

Table 2 (continued)

Theory[1]	First reference(s)[2*]	Components of theory development: Observations and actions →	Insights applied across contexts →	Generally applicable theory	Additional references[3]
B.7 Theory of landscape multifunctionality	Vos and Meekes (1999) Trends in European cultural landscape development: perspectives for a sustainable future.	> Based on studies of agricultural landscapes in Europe, concepts of landscape multifunctionality were formulated to encompass ecological, social and economic functions of landscapes within a unified analysis framework. This was inspired by previous theories of functionality derived from ecology and agricultural policy frameworks.	> Typologies and models of functionality and multifunctionality applicable across a wide range of landscape types were developed, creating a basis for comparative research and development of quantitative methods to assess multifunctionality using standardised indexing and assessment approaches.	> Building on ideas of functional integration and spatiotemporal alignment between land use interests, pathways towards sustainable land use through multifunctionality were developed.	(b) Odum (1953), European Community (1988), Leser (1991), UN (1992), Bohman et al. (1999) (c) Vos and Meekes (1999), Naveh (2001), Wiggering et al. (2003), Brandt and Vejre (2004), Pérez-Soba et al. (2008), Huang et al. (2015), Mander and Uumaa (2015), Hölting et al. (2020b)

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[2] In some cases, a single author or group of authors introduced the concept in question. In cases where a broader array of researchers contributed, a comprehensive selection of works is referenced.
[3] Additional references include (a) English translations of the original work when relevant, (b) other works related to the theory and later developments including antecedents to the theory, and (c) publications about the theory as well as applications and further development within landscape ecology. See the reference list for full references.
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model" that has been widely used to model the spatial characteristics of landscapes and formed the inspiration for the development of different landscape ecological metrics (McGarigal and McComb 1995; Cushman et al. 2008). Based on the same case studies and the concept of ecomosaics, the now universally applied theory known as "pattern and process" (B.5) was formulated to capture how spatial pattern and ecological processes co-constitute each other and hence cannot be modelled individually (Forman 1979) nor without including their historical pathways and temporal dimension (Tappeiner et al. 2021).

Since around the year 2000, the field broadened to encompass a great variety of relationships between societies, land use practices and land resources within landscapes. An example is the theory of multifunctional landscapes (B.7) developed from studies of European agricultural land use systems. The first notion of functionality, which inspired later work on landscape multifunctionality, was derived from ecology (Odum 1953) in combination with various agricultural policies at the global and European levels (European Communities Commission 1988; United Nations 1992). This enabled the inclusion of ecological, social and economic functions in analyses of agricultural landscapes, which was later applied to different landscape types using standardised assessment approaches (Wiggering et al. 2003; Brandt and Vejre 2004). The concept of multifunctionality is now considered one of the pathways towards sustainable land use (Pérez-Soba et al. 2008; Hölting et al. 2020b).

Group C: theory derived from comparative analysis organising further empirical observation

Another way of generating theory within landscape ecology has been to synthesise and compare evidence across research contexts (samples, landscapes, regions, etc.) based on or inspired by theoretical constructs loaned from cognate fields. Based on such synthesis work, the field of landscape ecology has contributed to formulating general theories which have later been employed in widespread case study research and used in practical applications. Examples are described in Table 3. An example is how research within the field incorporated and further advanced ideas adopted from holism and systems theory, leading to an increasing focus on relational and systemic

Table 3 Group C—Theory derived from comparative analysis organising further empirical observation

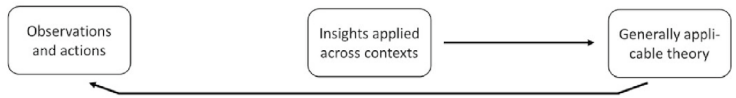
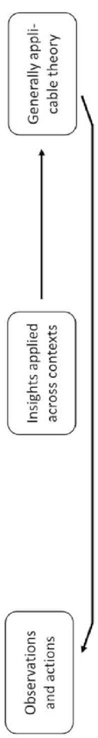
Theory [1]	First reference(s) [2*]	Components of theory development: 			Additional references [3]
C.1 Models of sustainability	von Carlowitz (1713) Sylvicultura oeconomica: Anweisung zur wilden Baum-Zucht.	> Spatially explicit, multi-scale approaches to sustainability in the context of landscapes were developed and applied, forming a normative concept guiding solution-oriented research into landscape management, policy, planning, design and associated practices.	> Based on extensive experience of forestry management in England, France and Saxon Germany, previous notions of sustainable yields in the context of timber production were generalised into a notion of sustainability applied to forest management.	> Informed by existing notions of sustainability and a growing environmental awareness in the global community, a political ideal of sustainable development was defined. This grew to become a primary policy agenda in the 20th century, forming the basis of contemporary policies including the UN sustainable development goals.	(b) Evelyn (1664), Colbert (1669), Meadows et al. (1972), UN (1987), Kidd (1992), Rodiek and Delguidice (1994), Backhouse et al. (2002), Marsh and Lowenthal (2008), UN (2012) (c) Viney (1969), Barret (1992), Forman (1995), Potschin and Haines-Young (2006), Grober (2007), Selman (2012), Spindler (2013), Wu (2013c, 2021), Opdam (2018)
C.2 Theory of holism	Smuts (1926) Holism and evolution	> Holism was applied in empirical work within landscape research from its earlier pioneers in two complementary ways: (1) as an epistemology emphasising interacting particulars rather than individual elements, (2) as an ontology indicating how landscapes are constituted and ordered through interaction of constituent parts forming functional wholes.	> It was recognised as a common denominator in a range of newly founded scientific fields during the 19th century, that reasoning relying on atomism, particularism and various reductionisms did not fully encompass the phenomena encountered. A perspective emphasising interactions between objects or elements in larger wholes were formulated.	> A general theory of holism was formulated by Smuts, inspired by previous work by Goethe, emphasising how nature forms wholes that are greater than the sum of constituent parts through creative evolution, making it relevant and necessary to combine general and individual types of observation and analysis within in a unified conceptual framework.	(b) Goethe and Bell (2018) (c) Troll (1939c), Zonneveld (Zonneveld 1995), Antrop and Van Eetvelde (2000), Li (2000a), Naveh (2000b)
C.3 General Systems Theory	von Bertalanffy (1950) An Outline of General System Theory	> Research into landscape systems and ecosystems co-evolved with, and was continuously stimulated by general systems theory, inspiring the formulation of increasingly nuanced conceptual vocabularies describing aspects of system functionality and organisation relevant to spatially explicit models of ecosystems, landscapes and the total human ecosystem.	> Various approaches to analysis of gestalt- and aggregate phenomena within mathematics, physics, neurophysiology and ecology, among other fields, were brought into contact, leading to the formulation of interdisciplinary system theories emphasising organismic, hierarchical and holistic ontologies.	> A generalised system concept was formulated, based on work to theorise the organism as a hierarchical, organised open system, emphasising the interaction of elements within systems. This formed the basis for further theoretical work on ordered wholeness, ecosystem functionality and complexity, as systems thinking and integrated approaches further evolved.	(b) von Bertalanffy (1951, 1972), (c) Tansely (1935), Lindeman (1942), Odum (1942), Naveh and Lieberman (1994), Forman and Godron (1986), Naveh (2000a), Voigt (2011)

Table 3 (continued)



Theory [1]	First reference(s) [2*]	Components of theory development:			Additional references [3]
C.4 Theory of landscapes as complex adaptive systems	Levin (1998) Ecosystems and the Biosphere as Complex Adaptive Systems	> Insights gained from theories of complex adaptive systems enabled landscape ecologists to strengthen analysis of cross-scalar interaction and interdependence, outlining how processes at lower levels of organisation produce patterns at higher levels of organisations. This supported an improved understanding of how patterns and processes emerge and interact across scales and system types.	> Studies of weather systems and nonlinear causal pathways of dissipative structures in non-equilibrium thermodynamics, combined with insights previously unfolded within chaos theory led to the formulation of a theory of complexity, emphasising emergence, connectivity, instability, uncomputability and unpredictability within systems.	> A general theory of complex adaptive systems (CAS) was developed, describing the behaviour of systems across the social and natural sciences in terms of interaction, rules, complexity, adaptiveness, agency, emergence, aggregation, nonlinearity, diversity and flows among other key concepts.	(b) Lorenz (1963), Prigogone and Nicolis (1967), Buckley (1968), Kauffman (1989), Holland (1992), Lansing (2003) (c) Hartvigsen et al. (1998), Salvati et al. (2015), Fischer (2018), Rescia et al. (2012), Petrosillo et al. (2015, 2021)

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[3] Additional references include (a) English translations of the original work when relevant, (b) other works related to the theory and later developments including antecedents to the theory, and (c) publications about the theory as well as applications and further development within landscape ecology. See the reference list for full references.

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aspects of landscape ecology during the mid-20th century. A theory of holism (C.2) already existed within the field of ecology, with holism having been defined by Smuts as "The tendency in nature to form wholes that are greater than the sum of the parts through creative evolution" (Smuts 1926). Based on this inspiration, studies of 'wholes' were applied in landscape ecology in two complementary ways: (1) as a way to perceive the world as consisting of connected, interdependent and interacting objects instead of collections of individual elements, and (2) as a way to interpret landscape patterns as wholes with systemic functionality and characteristics. This formed the basis for the analytical strategies promoted by Troll (1939a), the approach to landscape as an open system developed by Zonneveld (1985) and the conceptual model of total human ecosystems proposed byNaveh and Lieberman (1994); Naveh (2000a).

From the 1940s onwards, various approaches were developed and united in systems theory, sharing an interest in the scientific description of "gestalts" (Voigt 2011) and rooted in mathematics, physics, early computer sciences as well as biology, economy and neurophysiology. Von Bertalanffy (1950) formulated the general theory of the organism as a hierarchically organised open system, which was later defined as general systems theory (C.3). This was quickly adopted in landscape ecology and used in coalition with the ecosystem concept introduced by Lindeman (1942) to support the formulation of transdisciplinary research strategies investigating the complexity of landscape systems (Naveh 2000a). In the mid-20th century, the general theory of complex adaptive systems was formulated (Buckley 1968; Holland 1992), building on observations of emergent behaviour in systems stemming from adaptive interactive behaviour of system components. Hartvigsen et al. (1998) were the first of many to apply the theory of complex adaptive systems in ecology, which enabled landscape ecologists to analyse how processes at lower levels of organisation produce patterns and emergent behaviour at higher levels of organisations (Levin 1998; Steffen et al. 2020). The incorporation of variability and adaptation in research on landscapes as complex adaptive systems (C.4) allowed researchers a "greater understanding of how patterns and processes emerge and interact across levels of

Table 4 Group D—Theory derived from application of existing general concepts in new empirical contexts

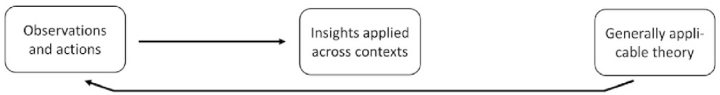
Theory [1]	First reference(s) [2*]	Components of theory development			Additional references [3]
					
D.1 Gestalt theory	von Ehrenfels (1890) Über 'Gestaltqualitäten'	> Based on the Gestalt theory, a vocabulary of concepts applicable to the description of empirical phenomena forming wholes and patterns as well as processes of pattern recognition was developed. This allowed landscape researchers to analyse and model complex spatial associations and understand the perception of landscapes.	> Collections of Gestalt-principles indicating and differentiating types of spatial and visual perception, pattern recognition and meaning attribution to spatial patterns were developed. In this way, insights into how wholes are structured and organised into meaningful entities were advanced and formalised, forming a basis for the formulation of theories of holistic landscape interpretation and design.	> A general theory of Gestalts was formulated, indicating how sensible structures or wholes manifest before and with primacy to their constituent parts. Building on previous work going back to Goethe, the theory of gestalts formed a basis for overcoming forms of ontological dualism within the sciences and for formulating models of how humans perceive, interpret and relate to complex patterns.	(a) von Ehrenfels (1937) On Gestalt-qualities (b) Goethe [1817] (1996), Wertheimer (1923), Köhler (1929), Koffka (1965), Wagemans (2015) (c) Troll (1950b), Blunden (2011), Antrop and Van Eetvelde (2017)
D.2 Theory of landscape character	Bourke et al (1929) The Thames Valley from Cricklade to Staines: A Survey of Its Existing State and Some Suggestions for Its Future Preservation	> The concept of landscape character was developed for use in spatially explicit landscape surveys conducted in the Anglo-Saxon world since the early 20th century. Work to further develop concepts and methods of landscape character assessment led to the formulation of integrated approaches to describe and assess landscapes, linking places to people and histories to spatial forms.	> Methods and concepts for observing and recording landscape character were developed. These came into wide use as an interdisciplinary tool to study, define and assess the distinctiveness of landscapes. Character-based approaches were further developed as a framework for sustainable and integrated landscape planning and policy.	> The concept of character came into use as a way to describe landscapes in the early 19th century, building on previous theoretical development that can be traced back to antiquity. Character was used to denote the identifying or particular qualities of an object or person, later also a landscape, geography or ecology.	(b) Macculloch (1824), Maughan (1934), Thompson et al. (1934, 1935), Waugh (1937), Garber (2020) (c) Swanwick et al. (2002), Wascher et al. (2005), Jessel (2006), Fairclough et al. (2018b), Simensen et al. (2018), Garber (2020)
D.3 Information theory	Shannon (1948) A mathematical theory of communication	> Concepts of information entropy were applied in landscape ecology to assess biological (species) diversity as the relationship between the number of species and their relative abundance, to model the spatial heterogeneity of landscapes using categorical data and to quantify the information content of maps.	> Based on information theory, an array of metrics including the widely used Shannon diversity index were developed to measure the diversity and heterogeneity of spatial phenomena and assess spatial patterns and species richness.	> A mathematical theory of communication using the entropy of a set of possible events as a measure for the information content of a message was formulated, explaining how information is transmitted, forming the basis for further development of communication and information theory.	(b) Brillouin (1962), Kilchenmann (1971, 1972, 1973), Stöcker and Bergmann (1978), Kwakernaak (1984, 1986), Gallager (2001), Schroeder (2004) (c) MacArthur (1955), Margalef (1958), Phipps (1981a, b), Baudry and Burel (1985), Forman and Godron (1986), Farina (1998), Antrop and Van Eetvelde (2000), Jost (2006), Vranken et al (2015)

Table 4 (continued)

Theory [1]	First reference(s) [2*]	Components of theory development 			Additional references [3]
D.4 Percolation theory	Broadbent and Hammersley (1957) Percolation processes	> Neutral landscape models characterised by a two-dimensional percolating network were constructed based on percolation theory in order to analyse the patterns generated, thereby creating a basis for comparison with and benchmarking of empirical landscapes.	> Based on percolation theory, a range of approaches to analysis of categorial spatial data were developed, making it possible to model degrees of fragmentation and resulting patchiness of the landscape and critical percolation thresholds by which patches are defined and delineated.	> Percolation theory was developed to describe physical properties of gels and polymers and diffusion processes in crystals, emphasising the connectivity within stochastically generated structures.	(b) Flory (1941), Stockmayer (1944), Stauffer (1985), Grimmet (1989) (c) Gardner et al. (1987), O'Neill et al. (1988), Turner and Gardner (2001), Gardber and Walters (2002), Ritters et al. (2007) Antrop (2021)
D.5 Hierarchy theory	Simon (1962) The Architecture of Complexity	> Hierarchy theory was used in a broad array of contexts within landscape ecology to model and observe scales in time and space, including the ordering of nested hierarchical levels.	> A new paradigm for ecological analysis was formulated based on hierarchy theory, focusing on the relationship between hierarchy and scale and its importance for pattern-process-scale relationships in ecological and human-environmental systems.	> A theory of hierarchy was proposed, explaining complexity as a form of a hierarchy in order to grasp the organisation of social, biological and physical systems defined as being composed of interrelated subsystems, each being hierarchically structured.	(b) Simon and Ando (1961), Simon (1976, 1994) (c) MacArthur (1972), Allen and Starr (1982), MacKay and Jan (1984), O'Neill et al. (1986, 1988), Urban et al. (1987), Naveh (2000a)n, O'Neill (2005), Wu (2013b), Millington (2021)
D.6 Fuzzy set theory	Zadeh (1965) Fuzzy sets	> Fuzzy knowledge-based models were introduced as mathematical models for soil surveying, land evaluation and in ecological research to advance descriptive power beyond classical classifications.	> Fuzzy logic was applied widely in landscape ecology to handle uncertainties in the spatial classification of complex continuous datasets. This inspired the development of conceptual models for ecotones, transitions and gradient zones.	> A mathematical theory of fuzzy sets was formulated, describing how elements have a degree or probability of membership to a certain group rather than a simple categorial and/or binary relationship.	(c) Salski (1992), Burrough (1989; 1992), Kacewicz (1994), Marsili-Libelli (1991), Sybre (1999)
D.7 Fractal dimension	Mandelbrot (1967) How Long Is the Coast of Britain? Statistical Self-Similarity and Fractional Dimension	> Fractal geometry was used as to formulate landscape metrics employed to quantify the shape complexity of objects and spatial patterns, as well as to quantify and model spatial-ecological correlations.	> Fractal metrics were used to model landscape patterns as a way to determine and quantify degrees of human influence on landscape patterns inferred from shape complexity.	> A theory of fractal geometry was proposed, emphasizing how ideal geometrical figures represent natural bodies exhibiting self-similarity in each of their parts in ways that can be observed when amplifying their form, making it possible to quantify shape complexity.	(b) Mandelbrot (1977), Burrough (1981) (c) Krummel et al. (1987), O'Neill et al. (1988), Loehle (Loehle 1990), Li (2000b)

Table 4 (continued)

Theory [1]	First reference(s) [2*]	Components of theory development (Observations and actions → Insights applied across contexts → Generally applicable theory)			Additional references [3]
D.8 Sense of place theory	Lefebvre (1974) La production de l'espace Tuan (1977) Space and Place: The Perspective of Experience	> Concepts of place stimulated new types of analysis within landscape ecology, building on distinctions between place and space inspired by the work of Lefebvre and Tuan. Here the "betweenness" of places was a point of emphasis, as the place concept was used to explore meeting points between subjective and objective, situated and desituated aspects of landscape.	> Place as well as parallel concepts such as sense of place and place attachment became an integrated part of landscape research, practice, planning and policy, forming a conceptual basis for research into communities, polities and social groups inhabiting landscapes, including processes of place-making and capacity building affecting them.	> The concept of place was used to denote meaningful sites linking geographies with people through experiences and practices, engagements, modes of being in the world and lived geographies, building on previous meanings of place as location and as a setting for morphological processes which extend back in time to antiquity.	(a) Lefebre, H. (1991) The production of space (c) Entrikin (1991), Hunziker et al. (2007), Saar and Palang (2009), Primdahl et al. (2018), Olwig (2019)

[1] Names given to theories are based on a compromise between original titles if indicated by the author(s) and how the theory is understood today.

[2] In some cases, a single author or group of authors introduced the concept in question. In cases where a broader array of researchers contributed, a comprehensive selection of works is referenced.

[3] Additional references include (a) English translations of the original work when relevant, (b) other works related to the theory and later developments including antecedents to the theory, and (c) publications about the theory as well as applications and further development within landscape ecology. See the reference list for full references.

* In some cases, theories were developed in parallel by multiple authors, often over prolonged periods of time. In these cases, the earliest publication that we know of is included.

biological organisation, and across spatial and temporal scales.“ (Hartvigsen et al. 1998; see also Preiser et al. 2018).

Another example is the concept of sustainable yields and the first notion of sustainability of plant communities, ecosystems, and productive systems (e.g. wood production (von Carlowitz 1713). In the post-war period, concepts of sustainability and sustainable development were reconfigured, defined in the so-called Brundtland report, and widely used today (United Nations and World Commission on Environment and Development 1987). Subsequent work in landscape ecology contributed with spatially explicit models of sustainability (C.1), often emphasising interdisciplinary, inclusive perspectives on sustainability linking social and ecological factors (Potschin and Haines-Young 2006; Selman 2012). As such, theories of human-induced environmental changes and linkages between social-ecological transformations and development were central to the earliest landscape ecologists. On this basis, increasingly advanced theories of socio-ecological interaction were developed and applied within the field, particularly in the later part of the 20th century (since the 1970s) when the ecological crisis and environmental management became key issues in the field, motivating a closer inspection on how people engage with the landscape and how landscapes structure human life, lifestyles and economies (Opdam et al. 2018; Wu 2021).

Group D: theory derived from application of existing general concepts in new empirical contexts

The fourth mode of theory generation (Table 4) is characterised by research processes taking their point of departure in established generally applicable theories, primarily formulated in other research fields, which are applied in a spatially explicit context, after which a theoretical contribution is formulated within landscape ecology. Concepts, models and methods derived from mathematics, computer science, physics and associated fields form an essential source of inspiration for this type of theoretical development. Concepts such as heterogeneity, functionality, complexity and organisation are examples that are also applied when studying cultural landscapes. Based on this type of inspiration, landscape ecologists have developed a wide range of spatial analysis approaches

that have later been used across the sciences. Examples include analysis approaches based on information theory (D.3), percolation theory (D.4), hierarchy theory (D.5), fuzzy set theory (D.6) and fractal dimensions (D.7).

One of the foundations for this line of research was the mathematical theory of communication as formulated by Shannon (1948), where the concept of entropy is used to quantify the information of a set of possible messages (Brillouin 1962; Gallager 2001). From the 1950s onwards, information entropy as used in the information theory (D.3) was widely applied in landscape ecology to quantify population and species diversity (Margalef 1958; Phipps 1981b), to model spatial heterogeneity (Phipps 1981a; Baudry and Burel 1985), and to quantify the information content of maps in relation to landscape classifications (Kilchenmann 1971, 1973; Kwakernaak 1984). With the further development of computer sciences, spatial statistics and GIS, the Shannon diversity index became a widely used landscape metric indicating the diversity and heterogeneity of spatial and ecological phenomena (Margalef 1958; Vranken et al. 2015). Percolation theory (D.4) represents another example of this. Research based on the conceptualisation of the theory by Flory (1941) as further developed by Stockmayer (1944), Broadbent and Hammersley (1957) formulated a general theory of percolation describing the physical properties of gels and polymers and diffusion processes in crystals based on connectivity in the generated structures. The first known application in a landscape ecological context was to model the propagation of forest fires (MacKay and Jan 1984). The percolation theory also inspired Gardner et al. (1987) to construct neutral landscape models in order to analyse the generated patterns and their percolating network, which has been applied in numerous cases in landscape ecology since (Gardner and O'Neill 1991; O'Neill et al. 1992; Gardner and Walters 2002; Riitters et al. 2007). These insights were applied in different research contexts by using the patch-corridor-matrix model (B.4), where percolation theory relates the connectedness of the matrix to the area occupied by patches (Forman 1979). In a similar way, the hierarchy theory (D.5) was developed as a general theory based on insights from management science, economics, physiology, biology and mathematics (Wu 2013b). Herbert A. Simon formulated the theory to explain complexity as a form of hierarchy, defining a hierarchic system as "a system that is composed of interrelated subsystems, each of the latter being, in turn, hierarchical in structure until we reach some lowest level of elementary subsystem" (Simon 1962). This principle led to different applications in a spatial and ecological context, including the ordering of nested hierarchical levels, which has proven to be a robust framework for understanding scale and hierarchy in space and time. Thus the general hierarchy theory became useful for the understanding of ecological and human-environmental systems characterised as "both a self-contained whole to its subordinated subsystems and a dependent part of its supersystem" (Naveh 2000a) and for which the principles of hierarchy and scale are essential factors (Millington 2021).

In a similar way, key concepts from social theory and theory stemming from within the humanities were applied within landscape research to study the relationship between human agency and societies on the one hand and landscape on the other hand (Field et al. 2003; Farina 2009b; Wu 2010). Based on this inspiration, landscape research supported the development of theories emphasising the place of people in environments, often emphasising a research agenda focused on achieving standardised methods for the assessment of cultural environments, places, heritage and landscape character (Hobbs 1997; Hölting et al. 2020b). This later became a primary source of inspiration for research taking place in adjacent fields such as the environmental humanities, environmental history, environmental anthropology, environmental sociology and environmental psychology. Examples of theories in this group are the Gestalt theory (D.1), the theory of landscape character (D.2) and the sense of place theory (D.8). A good illustration of this mode of theory development is the theory of landscape character, which has its point of departure in a general concept of "character" dating back to antiquity, denoting the particular, identifying qualities of an object or person (Garber 2020). Since the early 19th century, this concept was used to describe landscapes, for example in the descriptions of Macculloch (1824) of the character of the Highlands and Western Isles of Scotland "containing descriptions of their scenery and antiquities, with an account of the political history and ancient manners, and of the origin, language, agriculture, economy, music, present condition of the people etc." The concept of landscape character has

since become increasingly popular in research concerned with land use assessment and conservation, mainly since the 1980s when standardised methods for landscape characterisation were applied first in England and Scotland and later in other countries and regions. As such, approaches based on theoretical notions of landscape character have now matured and developed to form a coherent framework for sustainable, integrated planning and policy that is widely used in the Western world (Fairclough et al. 2018a; Simensen et al. 2018).

Discussion

Common characteristics of landscape ecological theories

Comparing landscape ecological theories makes it clear that they have a number of characteristics in common. All the theories lift spatial aspects of the phenomena studied to analytical primacy. A clear focus on spatial differentiation and spatial units of analysis predominates, based on which relationships with other facets of research objects and other phenomena groups are then investigated. Another common denominator is that a large number of theories were formulated in the context of solution-oriented research focusing on nature, biodiversity and ecosystem health, wildlife- and land management (theories 1 A-3-5-8-9-10-11-12-13, B4-5-7 & C1-3-4). Interest in sustainability and nature conservation alongside scientific curiosity in understanding it is a widespread feature among landscape ecological thinkers. This combination forms a basis for widely held motivations to investigate relationships between nature and humans. Looking at the type of empirical material collected in these theories, it is clear that many contributors to theory in landscape ecology formed their seminal experiences by engaging in ecosystem monitoring, rural land management, woodcraft, range management, expedition work, conservation and cognate forms of direct engagement with nature. It is also characteristic, especially for theories in groups A and B, that there is an explicit interest in working with research topics at a spatial and temporal scale that matches the perception and agency of humans. For these contributors, fieldwork is highly valued and understood to provide a unique form of access to the complexity of ecologies in landscapes, combining vertical and horizontal perspectives on areas under study (all theories of groups A and B). In contrast, other theories are characterised by being based mainly on a combination of mathematical theory, quantitative modelling and computer simulation in alliance with remote sensing and GIS technologies, typically at scales larger than the human scale (theories B4, D3-4-5-6-7 and A2-13). Lastly, it is characteristic of the field that there is a pronounced emphasis on connections, interrelationships and wholes. Landscape ecological thinking is ripe with successful attempts to overstep conceptual, disciplinary and sectorial boundaries among others, connecting seemingly disparate or unrelated phenomena groups or variables (all theories in groups A and B, C2-3-4, D1-2-5). It is clear from the review that considerable emphasis is put on investigating "wholes" rather than subsections of phenomena and that analysis strategies are designed to avoid set categories and linear, unidirectional modes of reasoning.

Sequences, breaks and continuities of theory development in landscape ecology

The review illustrates that the field has a broad array of well-defined theories, constituting a continuous accumulation of knowledge about landscape phenomena since the early 19th century. Different phases can be identified. In the late 18th to the mid-19th century, when the scientific field of landscape research emerged, seminal concepts of spatially situated ecologies formulated by von Humboldt (1805; 1808), Darwin (1839, 1859) and others formed a source of stimulus for the later development of landscape ecology. These concepts inspired the first of a series of approaches to landscape ecological theory formulation emerging in the 1920 and 1930s when an advanced spatial ecological mode of reasoning was defined, supported in part by the new bird's eye perspective of aerial imagery used to study landscapes revealing the holistic character of the landscape as described Troll 1939a); Sauer (1925); Granö (1929) among others. These approaches emphasise spatial and ecological logics in all types of landscapes and are still in place today (Freeman et al. 2015; Simensen et al. 2018; Cassar 2019; Lovell et al. 2021).

The systemic approach can be observed since the 1930–1960s with the development of holism and

systems theory and the understanding of complexity and emergence, which later came to revolutionise the understanding of landscape (Smuts 1926; Shannon 1948; Von Bertalanffy 1950; Broadbent and Hammersley 1957; Simon 1962).

Similarly, the quantitative revolution that affected the field in the latter half of the 20th century led to fundamental changes in how landscape ecological research was conducted (Forman 2015; Antrop and Eetvelde 2017). This introduced quantitative modelling, spatial statistics, landscape indices and metrics (Cushman et al. 2008; Riitters 2019) and their applications in planning (Botequilha Leitão and Ahern 2002). This is still a rapidly growing approach engaged with the development of artificial intelligence and big data technologies to further landscape ecological research (Nowogrodzki 2020; Porter 2021; Remmel and Mitchell 2021).

The most current approach started in the 1990s–2000 with a call for holistic and transdisciplinary modes of research (Naveh 2000b) necessary for spatially explicit and multi-scale approaches to landscape sustainability (Potschin and Haines-Young 2006; Wu 2013c, 2021), multifunctionality (Wiggering et al. 2003; Brandt and Vejre 2004; Hölting et al. 2020b) and landscape ecological management (Lindenmayer et al. 2008; de Groot et al. 2010; Hersperger et al. 2021). This emphasises the necessity of social logics and theories in landscape ecology. Since these latest developments, the field has been characterised by a continuous process of refinement, advancement and reinterpretation of existing theories.

Looking ahead: trends of theory development in landscape ecology

It is interesting to observe that theories within landscape ecology did not replace each other as the field developed. In most cases we see a process of gradual accumulation of new theories alongside existing ones, each subjected to incremental refinement. As such, landscape ecology develops with a high degree of continuity and existing concepts are complementary to a larger extent than in competition with each other, indicating that theoretical multiplicity is an established practice within the field. However, there is currently little evidence of explicit, systematic reflection on this role of theory, especially with respect to concepts that today are taken for granted or have been "backgrounded" as shared reference points for researchers (Sudo 2014).

Theory serves researchers with a medium for transferring knowledge between empirical contexts seamlessly and iteratively in ways that adapt to observations made in local landscapes. A good example of a method to achieve this is middle range theory, originally proposed by Merton (1949) within sociology, which is currently gaining ground in landscape research and cognate fields (Meyfroidt et al. 2018; Schlüter et al. 2019). However, questions of transferability of findings between landscapes are challenging, as is the transfer of theoretical insights from landscape ecology to other fields (Francis and Antrop 2021). Concepts and models that could have been the subject of explicit theorising are transferred from context to context without clear reflection on the merits of doing so. As such, there is an apparent potential to improve conceptual precision by working more explicitly with theory in the field. Building on this observation, approaches to achieving improved processes of theory accumulation in landscape ecology could potentially take the form of a flexible conceptual toolbox of concepts and models rated and classified according to their empirical range and context of usefulness. This would constitute a new approach to theoretical synthesis aimed at encompassing the empirical diversity of cultural landscapes (and associated conceptual models) in a single theoretical framework, without imposing a unified language or vocabulary as such. Theory in this view would be multiform, with many alternative conceptions sitting side by side, resting on continuous cataloguing and assessment of the relevance of contributions relative to specific empirical conditions. This could be a vehicle for supporting the field in incorporating diversity in its subject matter, without losing a common foothold and instrument for coordination. An inclusive perspective on theory of this kind would reflect the actual diversity of theories within the field identified in this review and would likely support increased awareness of the role of theory in contemporary research. A more explicit, continuous way of working with theory of this kind would likely allow researchers better conditions for maintaining a critical awareness of the origin and relative relevance of theoretical concepts as these are being developed, brought to use and transferred between landscape contexts under study.

Conclusions

This article provides an overview of theories in landscape ecology applicable to the study of cultural landscapes. A literature review of theoretical contributions to landscape ecology was conducted. A total of 32 theories were selected and their pathways of development were described. Four modes of theory generation representing viable, tested transition pathways for the transfer of decontextualised knowledge in the field were identified. Theoretical work in landscape ecology was found to be characterised by (1) pursuing analysis strategies that lift spatial aspects of the phenomena studied to analytical primacy, achieving synthesis through the use of common spatial units; (2) promoting inclusive, interdisciplinary investigations of the relationship between humans and nature, linking social and ecological theories together; (3) maintaining a scale of analysis matching human perception and existence, making it possible to combine situated and desituated research practices; (4) continuously developing quantitative models to analyse spatial patterns and distributions of phenomena under study; (5) emphasising connections, interrelationships and wholes, employing analysis strategies designed to avoid classificational stability, set categories and linear, unidirectional modes of reasoning. Based on the review, a perspective on how to improve application of theory within the field was proposed.

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