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Understanding and quantifying landscape structure – A review on relevant process characteristics, data models and landscape metrics

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ABSTRACT

For quantifying and modelling of landscape patterns, the patch matrix model (PMM) and the gradient model (GM) are fundamental concepts of landscape ecology. While the PMM model has been the backbone for our advances in landscape ecology, it may also hamper truly universal insights into process–pattern relationships.

The PMM describes landscape structures as a mosaic of discretely delineated homogenous areas. This requires simplifications and assumptions which may even result in errors which propagate through subsequent analyses and may reduce our ability to understand effects of landscape structure on ecological processes. Alternative approaches to represent landscape structure should therefore be evaluated. The GM represents continuous surface characteristics without arbitrary vegetation or land-use classification and therefore does not require delineation of discrete areas with sharp boundaries. The GM therefore lends itself to be a more realistic representation of a particular surface characteristic. In the paper PMM and GM are compared regarding their prospects and limitations. Suggestions are made regarding the potential use and implementation of both approaches for process–pattern analysis.

The ecological and anthropogenic process itself and its characteristics under investigation is decisive for: (i) the selection of discrete and/or continuous indicators, (ii) the type of the quantitative pattern analysis approach to be used (PMM/GM) and (iii) the data and the scale required in the analysis. Process characteristics and their effects on pattern characteristics in space and time are decisive for the applicability of the PMM or of the GM approach. A low hemeroby (high naturalness and low human pressure on landscapes) allows for high internal-heterogeneity in space and over time within patterns. Such landscapes can be captured with the GM approach. A high hemeroby reduces heterogeneity in space and time within patterns. For such landscapes we recommend the PMM model.

1. Quantitative approaches in landscape ecology

Recording and understanding landscape structures as well as modelling and forecasting changes thereof have long been the primary concerns of quantitative landscape ecology.

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The patch matrix model (PMM) was developed in the 1980s and describes landscape structures as a mosaic of discretely delineated homogenous areas (Forman and Godron, 1986; Wiens, 1989; McGarigal and Marks, 1995). The PMM therefore can be regarded as one of the first descriptive and conceptual models for landscape structures in landscape ecology. With the help of the PMM, landscape structures can be described in a simple and practical way by not just delineating homogeneous areas, but also by quantitatively assessing their spatial arrangement (landscape configuration) and their constituent diversity (composition). Numerous landscape indicators were developed to quantify different spatial and compositional aspects of PMM based landscape structures. This rather fast development of quantitative landscape ecology was further accelerated by continuously improved computer processing power and the resulting capability of processing increasingly large raster and vector data representing landscape structures.

In addition to the initially purely descriptive purpose of quantifying landscape structures (O'Neill et al., 1988; Turner, 1990; Riitters et al., 1995; McGarigal, 2002; Herzog and Lausch, 2001; Lausch and Herzog, 2002; Lang and Blaschke, 2007) attempts were made to identify potential relationships between landscape structures and spatiotemporal biotic and abiotic processes within the landscape (Turner, 1989), such as the spread of species or populations and biodiversity (Mühlner et al., 2010; Walz and Syrbe, 2013) or effect of soil characteristics on vegetation patterns distributions (Schmidtlein et al., 2012; Lausch et al., 2013a). As a result, the quantification of landscape structures based on PMM was increasingly used for assessing and planning landscapes (Syrbe et al., 2007), quantification of landscape functions (Bolliger et al., 2007; Bolliger and Kienast, 2010) or quantification of ecosystem services (Syrbe and Walz, 2012).

This speedy development fostered enthusiasm in quantitative landscape ecology and led to a spirit of optimism or even "research euphoria" in landscape ecology at the start of the 1980s and 1990s. Yet what was increasingly overlooked was the fact that the underlying PMM is only a very simplified conceptual model of real landscapes representing a very limited aspect of the underlying reality. In addition, the PMM was reduced to available or interpretable data or land use classes and thus essentially represents the human view of real landscapes. Despite these deficits, ardent attempts were made to explain just about all spatio-temporal processes with PMM-based landscape structures, even though the ecological basis or the fundamental understanding were often lacking.

Despite the absence of truly meaningful insights and consistent, robust results, the PMM-based quantitative landscape ecology was continually being endorsed by researchers especially as a result of the advancement in remote sensing (RS) and geographical information systems (GIS).

More than 20 years after the introduction of the PMM, the initial euphoria gives way to growing scepticism surrounding the principal suitability of the PMM as a universal approach for quantitative landscape structure analysis (Kupfer, 2012). While many studies (Uuemaa et al., 2013) were able to find relationships between landscape structures and ecological processes, most of those have little statistical significance, very limited explanatory value and do not translate into a causal understanding of the underlying mechanisms (Li and Wu, 2004; Bailey et al., 2007a, 2010). Furthermore, connections and relationships from different studies often contradicted each other, resulting in an increasing lack of consistent and generalizable insight.

The lack of emerging generalities or universal patterns in those relationships between landscape structure and ecological processes certainly has many reasons. The scientific literature covering this particular field reveals frequent use of ambiguous terminology, missing definitions of key concepts (e.g., fragmentation), lack of proper and consistent quantification of those concepts, not enough variability in the underlying landscape structures (predictor variables), errors and their propagation in the development of PMM as well as negligence of all variables not represented by the PMM. This situation is definitely not satisfactory and can hardly be resolved or changed solely with greater computation power or technological advances and the resulting benefits in remote sensing data collection and geographical data processing.

This reflection on the state-of-being of quantitative landscape ecology gives raise to the following questions:

- What are the causes for the virtual absence of general and universal insights in quantitative landscape ecology?
- What role does the PMM play for the interpretation of relationships between processes and landscape structures and vice versa?
- Has quantitative landscape ecology based on the PMM really "failed" or are we just looking in the wrong direction?
- What are the limitations of the PMM and how do they influence and restrict progress in quantitative landscape ecology?
- Is the PMM based representation of landscape structure suitable for all data, research questions and hypotheses?
- Are there alternative or complimentary approaches to the PMM? If yes, under what conditions could they be used?

In 2005, McGarigal and Cushman introduced the gradient model (GM) as an alternative representation of landscape structure. Instead of delineating homogeneous and discrete areas, the GM represents landscape structure on the basis of continuous data in which the only discrete unit is a pixel or grid cell in a raster based data model. Such continuous data has always been the output of remote sensing information, including digital cameras with ever higher resolutions of smaller pixels. Therefore the introduction of the GM into landscape ecology was not an entirely new concept. The novelty results in discovering GM as an alternative representation of landscape structure and in encouraging its quantification and subsequent relation to ecological processes, similar as landscape metrics based on PMM were used before. The GM seemed intriguing, because it does not require human biased assumptions about land-cover types (their borders) but is based on raw data as observed by different sensors–similar like a picture taken by a digital camera. While a picture is still a "model" of reality, it represents much more attributes of the real object compared to a reduced e.g. 8 colour simplification of the same. Since remote sensing technology uses multiple sensors capturing reflections of a broad range of visible and non-visible frequencies, GM based landscape representations contain much more information and are therefore a much more realistic representation of landscapes. The question is, whether continuous data lend themselves to similar quantitative approaches as landscape indices do for the PMM. Without quantifying GM based landscape structures the merit of GM to quantitative landscape ecology might be limited. Nevertheless, the introduction of GM was to some extend being heralded as a "new era" in quantitative landscape ecology. Still, GM's have to prove that they can overcome the limitations of the PMM's and it remains to be seen if we can derive new and more consistent insights using GM based landscape representations.

We need to explore if GM can help us to better understand, quantify and model landscape structure and in particular the effects of ecological processes on landscape structure and vice versa. Also, we need to investigate if GM's should replace PMM's, or if both models can coexist side by side, serving different purposes and complimenting each other.

The goal of this paper is to take a critical look at the use of PMM and GM in quantitative landscape ecology. Our specific objectives are: (1) to explain the differences between PMM and GM, (2) to identify major research areas for process–pattern interactions (PPI) in landscapes, (3) to identify criteria in support of selecting appropriate data, quantitative methods and PMM or GM in landscape ecological analyses and (4) to emphasize possibilities for applying both quantitative and qualitative approaches landscape ecological research, landscape assessment, and regional planning.

2. Quantifying landscape patterns

The structure of a landscape emerges from the characteristics of the individual elements of an ecosystem and their spatial configuration. According to Forman and Godron (1981, 1986) and Turner

(1989) these elements of a landscape determine the distribution of energy, material, and species in a landscape.

Characteristics of landscape patterns, such as the configuration and composition of elements – often also characterized as spatial or landscape heterogeneity–influence ecological processes and the resulting biodiversity with profound impacts on the functioning of ecological and socio-economic systems (Forman and Godron, 1986; Cushman et al., 2010). Vice versa, all of those affected spatio-temporal processes in turn impact and determine landscape patterns. To understand such process–pattern interactions and to formalize them in models, the composition and configuration of spatial patterns – landscape structure – needs to be quantified.

2.1. Patch matrix model – PMM

In the patch matrix model (PMM), as presented by Forman and Godron (1981, 1986), landscape structure is reduced to three principal elements: matrix, corridor and patches (Fig. 1a). While this conceptual model originated in North America, it was soon endorsed and applied by scientists all over the world. Blaschke (2006) argues that, in contradiction to the anthropocentric arguments developed in favour of the natural capital paradigm (Haines-Young, 2000), the PMM model of Forman (1995) offers much that is of value to landscape ecology. He suggests that the PMM may provide the key to understanding land use systems and changes thereof by means of using and interpreting quantitative landscape indicators. In other words, the claim here is "landscape configuration as perceived by the PMM approach matters".

Patches represent homogenous areas of a certain land-cover or land-use type with their own individual characteristics, such as shape or size (Forman and Godron, 1986; McGarigal and Marks, 1995) and ecological functions, such as isolation for populations (Wiens, 1989). The spatial arrangement of patches of various land-cover types in a landscape results in a characteristic landscape structure (Forman, 1995), which has also been called patch mosaic (Turner, 1989). Landscape structure or landscape pattern emerge from composition and configuration of patches. Landscape composition refers to the number, proportional frequency and variety of land-cover types of patches. Landscape configuration addresses the spatial aspects of the patch mosaic, such as the size and shape of patches as well as their spatial arrangement within a landscape (Fig. 1a).

The PMM model also refers to the matrix, which is the dominant background land use/land cover type of a landscape. The PMM therefore implicitly declares patches as habitat patches and is therefore essentially a species specific concept. Forman and Godron (1986) envisioned landscapes to be represented by habitat patches interspersed with smaller stepping stones and connected with corridors – all of those embedded within the inhabitable matrix. The motivation of the PMM was therefore driven by species conservation and not by an anthropocentric perspective. Nevertheless, the simplicity of the PMM, its compatibility with data models in geographical information systems (polygons) and the availability of remotely sensed data along with established classification schemes led to a widespread use of the PMM well beyond its intended purpose. It is noteworthy that the PMM approach is limited to a two-dimensional representation of landscape structures, although efforts have been made by Hoechstetter et al. (2008) and Stupariu et al. (2010) to incorporate higher dimensions into the PMM based landscape representation. Another limitation of the PMM approach results from the necessary delineations of patches by discrete boundaries. In reality, however, sharp boundaries between adjacent land-cover types are rare. Instead, gradual changes or ecotones are more common. The primary compromise between the pragmatic convenience of PMM's and reality lies in its oversimplification of landscape structure. While simplification is an inherent characteristic of any model, its suitability for explaining or understanding reality should be validated by how much variation a model can explain or how well predictions made from a model align with observed changes in reality. If a model cannot stand up to these tests then it fails to represent those factors which are important to the question of interest. The PMM is no exception. Many relationships between PMM based landscape indicators and ecological response variables have been weak and inconsistent. The reason must not necessarily be the model itself, but the underlying data and classification schemes. Translating reflection values of remote sensors into vegetation or land-use classes is error prone and limited by resolution, time of observation, scale and our ability to ground truth remotely sensed data. Averages across large areas are often used and extrapolated across arbitrarily delineated patches. Therefore, there is often a fairly significant discrepancy between PMM based land-cover maps and the real landscape. These discrepancies are often neglected in subsequent analyses but might be the reason for the limited insights we derived from PMM based quantitative landscape ecology so far.

2.2. Gradient model – GM

The increasing awareness of the limitations in establishing significant, robust and generalizable relationships between PMM based landscape indicators and ecological response variables (Tischendorf, 2001; Li and Wu, 2004; McGarigal and Cushman, 2005) motivated the search for alternative approaches in support of quantifying landscape structure. These efforts resulted in the development and recognition of the gradient model (GM) by Müller (1998), McGarigal and Cushman (2005) and McGarigal et al. (2009). The GM represents landscape structure as continuous data based on a raster or grid based data model. Therefore, each cell or pixel of the grid becomes the smallest homogenous and discrete spatial unit allowing for a seemingly continuous change of characteristics within a landscape (Fig. 1b). The GM does not make any further assumptions about the shape, size and configuration of homogenous areas, which also excludes the need for delineating and defining arbitrary sharp boundaries between such areas. The GM also implicitly allows for a three dimensional representation of landscape structure, the third dimension being embedded in the range of the value of a particular variable, such as habitat suitability, elevation or soil moisture. A GM representation of a landscape can be derived by two approaches. First, by analysing gradients of landscape variables from categorical land-cover maps, and second, by using continuous field variables usually originating from remote sensors (Cushman et al., 2010).

Gradient analysis of categorical maps can be achieved by means of the moving window approach (McGarigal and Cushman, 2005). This approach moves a window of a certain shape and size across a raster map and respectively assigns the value of a landscape metric calculated within that window to the cell over which the window is centred. Therefore the value of each cell of the resulting GM raster map represents the particular characteristics as captured by the chosen landscape metric within the extent of the window. The size of the window can be regarded as the scale of interest with respect to the value of interest of each single cell in the resulting GM raster map. A good example for GM based landscape representations are habitat suitability maps for single species. Depending on the home or dispersal range, such habitat suitability maps present a continuous surface or gradient of habitat suitability within a landscape.

On the other hand, GM representations of landscapes correspond to raw output from remote sensors. Such maps are similar like digital images in which each pixel represents the reflectance value of a certain frequency. A good example is the Normalized Difference Vegetation Index (NDVI) as an indicator for the amount of green vegetation. Likewise, topography or aspect lend themselves

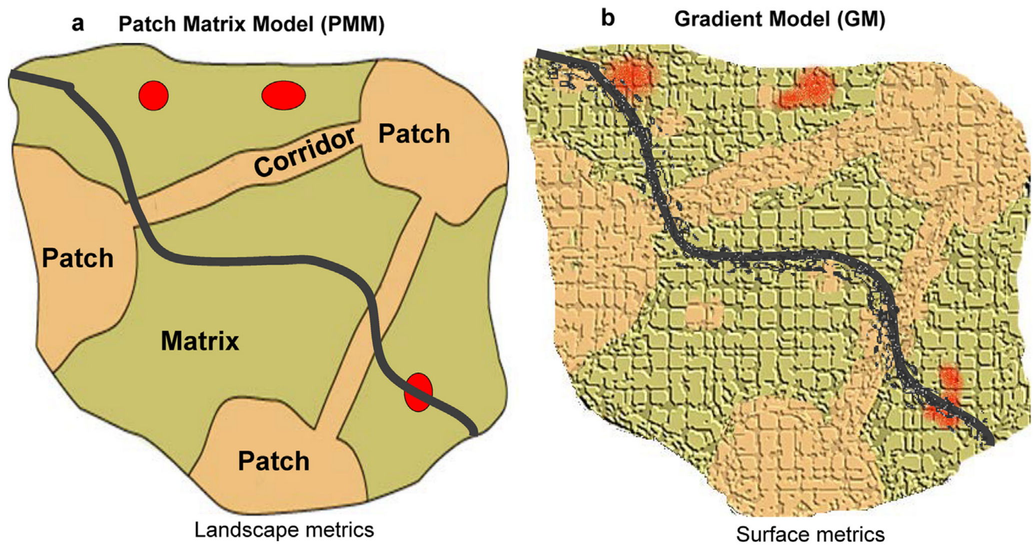

Fig. 1. Representation of landscape structure: (a) Patch matrix model (PMM), (b) Gradient model (GM).

to continuous surface maps and are best represented in raster format.

Overall, the GM based approach requires fewer or no assumptions compared to the PMM and allows for a more realistic representation of real landscapes. GM based models, however, usually present only one variable of interest – such as elevation or habitat suitability or green vegetation density – of a landscape. This corresponds to one land-cover type or category in the PMM. The advantage, however, lies in the continuity of the variable values. Multiple GM based models can be overlaid and potentially aggregated to represent different aspects of a real landscape in one GM map. The drawback of GM landscape representations is the difficulty of "extracting" or calculating landscape metrics from continuous surface maps. The quantification of pattern characteristics is less straight-forward compared to PMM based landscape metrics. Furthermore, interpreting results obtained from such GM based landscape metrics can be difficult. For example, if we found a positive relationship between the variation in NDVI and biodiversity in a landscape, it would be difficult to directly apply this finding practically. This is primarily due to the fact that GM based variables represent mostly emerging surface characteristics, such as NDVI or habitat suitability, which can only indirectly be controlled by landscape management.

3. Pros and cons of the patch matrix model and the gradient model

In an effort to evaluate the use of approaches for quantifying and understanding landscape patterns, a comparison of the potential and limitations of PMM and GM is needed. Table 1 lists the advantages and drawbacks of both approaches for quantifying landscape patterns.

4. Effects of processes on landscape patterns and vice versa

4.1. Natural processes and environmental conditions

Changes in the biochemical and structural–geometrical reactions within plants have a profound impact on vegetation patterns. Such changes are caused by processes and factors like: (1) Soil properties including depth, texture, chemistry, moisture patterns, composition and heterogeneity (Lausch et al., 2013, 2013b); (2) the spatial arrangement of different plant species (Asner et al., 2012);

Table 1
Advantages and disadvantages of patch matrix model (PMM) vs. gradient model (GM) in quantifying landscape patterns and understanding process-pattern interactions.

Patch matrix model – PMM

Advantages

- Approach is straightforward, understandable and easy to use (Turner, 2005; Cushman et al., 2008)
- Well-developed and widely understood quantitative techniques (McGarigal et al., 2009)
- If patches represent a species habitat then realistic representation of how organisms of that species interact with the landscape (Cushman et al., 2010)
- Easy and straight-forward quantification of pattern characteristics by means of landscape metrics
- Moderate computational requirements

Disadvantages

- Discretization leads to the loss of internal heterogeneity within patches, which may result in loss of important ecological information (McGarigal et al., 2009)
- Unrealistic sharp boundaries between patches, no definition of transition zones between land-cover types possible
- Classification schemes of land cover/land use have a great influence on quantitative results in landscape ecology
- Different classifications and data depth influence quantitative analyses (Wickham et al., 1997; Bailey et. al., 2007b)
- Sensitivity of selected landscape pattern metrics to land-cover misclassifications (Wickham et al., 1997)
- Different landscape extents lead to non-comparable quantifications between landscape segments (Lausch and Herzog, 2002; Bailey et al., 2007b)
- Lack of established standards for classifying land-cover types

Gradient model – GM

Advantages

- No lack of information due to simplification, aggregation and assumptions
- No assumptions about delineating homogenous areas and sharp boundaries (Cushman et al., 2010)
- Powerful geostatistical and multivariate methods applicable

Robust and flexible method for organism-centered analysis (McGarigal and Cushman, 2005)

- New remote sensing data (hyperspectral data) offers an enormous data source in application of GM

Disadvantages

- Requires extensive GIS and remote sensing expertise
- Less intuitive than PMM
- Generates complex and large data volumes, highly multidimensional
- Multiple layers require the use of advanced spatial data mining techniques (Lausch et al., 2014)
- GM require high data storage and powerful computing capacity
- Lack of standardized continuous surface metrics

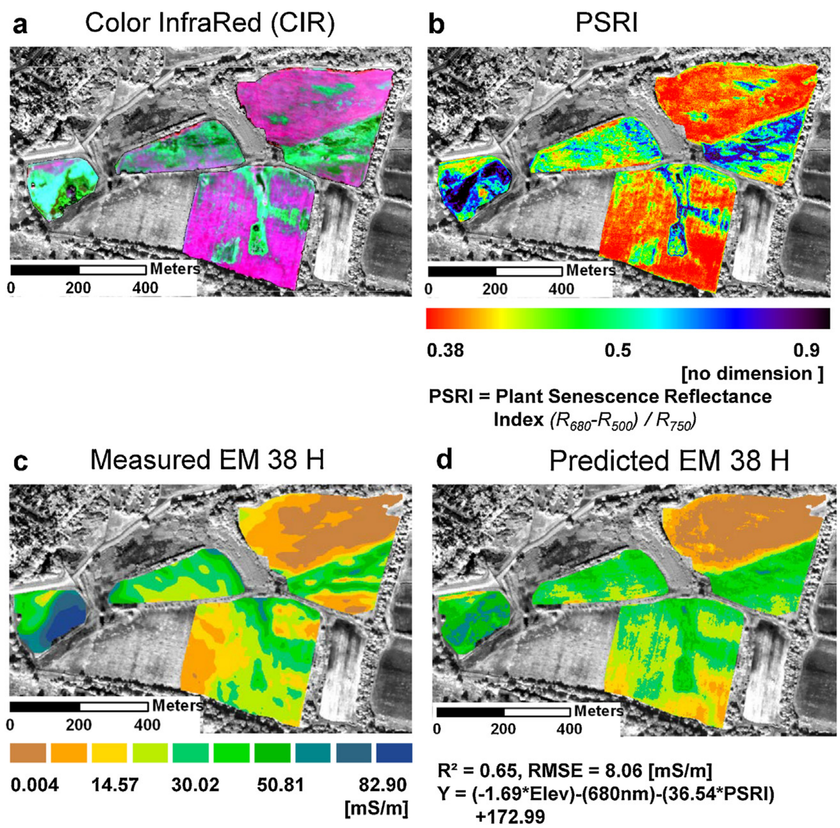

Fig. 2. Derivation of soil pattern properties/moisture patterns – electrical conductivity (σ_a) measure with EM 38 H – electromagnetic (EM) of vegetation patterns with hyperspectral remote sensing data: (a) vegetation patterns from hyperspectral AISA-DUAL data, displayed in colour infrared (CIR), (b) quantification of the vegetation patterns based on PSRI – Plant Senescence Reflectance Index, (c) measured soil moisture based on electrical conductivity (σ_a) measure with EM 38 H, (d) prediction of soil properties/moisture patterns based on hyperspectral vegetation characteristics
(modified after Lausch et al., 2013b).

(3) inter- and intra-species competition amongst plant species that lead to biochemical–biophysical properties of vegetation and (4) plant strategy types (Liira et al., 2008; Schmidtlein et al., 2012). Other relevant factors include: (5) ecological and environmental stress factors on vegetation (Carter and Knapp, 2001); (6) changes to vegetation through seasonal biorhythm and phenology (Asner et al., 2012); (7) short-term dynamic brought about by disturbances in vegetation patterns (Feilhauer and Schmidtlein, 2011); (8) disturbance regimes activated by humans or nature (Turner, 2010) and (9) human management strategies or human pressure on vegetation.

4.1.1. *Vegetation as an indicator for environmental conditions*

A functional connection between soil properties, moisture and vegetation patterns is something that can already be seen in data from aerial photographs. This connection allows using remotely sensed vegetation patterns as a proxy for the variability and heterogeneity of local characteristics, such as soil properties and moisture patterns (Lausch et al., 2013b). With high spatial and spectral resolution data like Airborne Imaging Spectrometer (AISA), the spectral response of vegetation as a function of soil properties and soil moisture patterns can be studied (Lausch et al., 2013, 2013b). The basis for the pattern formation of vegetation here includes the biochemical, physical and structural changes of plants compared with different soil conditions and moisture patterns (Fig. 2).

Comparable effects on plants are also caused by a number of environmental stressors. The most important functional changes as a result of stress that can be detected with remote sensing techniques are: Changes in content of photosynthetic active pigments and cellulose, photosynthetic activity, intra- and extracellular water content in plants as well as changes to the transpiration behaviour in plants which affect leaf positioning and geometry, stomatal distribution and protective measures like leaf hair and cuticles (Swatantran et al., 2011; Hernández-Clemente et al., 2011). The continuous variation of those vegetation characteristics is often neglected and then ignored after classifying a certain area into a "land-cover" type in support of a PMM representation of landscape structure. A resulting land-cover type merely represents the average vegetation characteristic across the delineated area at a certain point in time. We can assume from phenology that this vegetation will remain the primary cover type for a certain period of time, but succession in natural systems may also change that. We therefore need to be aware of those processes affecting the vegetation patterns we observe and in turn affect ecological processes, such as biodiversity or dispersal. Most of this awareness and information is lost once a static land-cover type has been established by classification methods and is therefore not available in a homogeneous patch of the PMM.

4.1.2. *Plant species "under the microscope"*

The latest developments of optical remote sensing techniques feature hyperspectral sensors like HyMAP, ARES and AISA. HySpex with a high spectral resolution of 400–2500 nm and often 100–500 spectral channels marks the next generation of optical remote sensing techniques for quantifying vegetation patterns. With their high spectral resolution, the variability and temporal dynamics of spatial patterns based on changes in biochemical–biophysical vegetation characteristics can be observed, measured and quantified. These new developments in technology lead to a new research area focused on quantitative vegetation modelling based on the

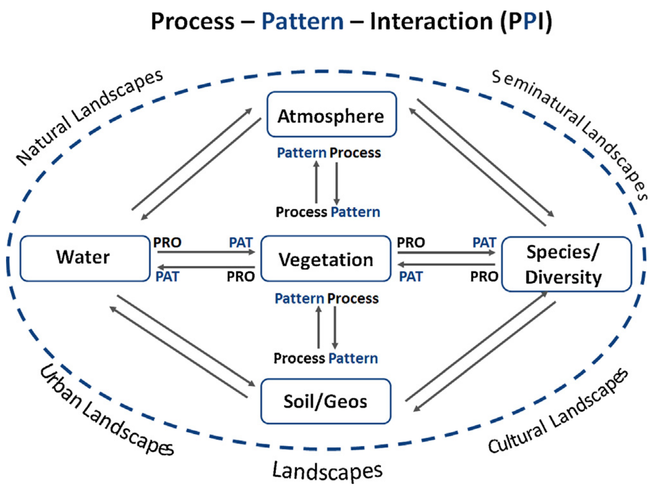

Fig. 3. Process–pattern interactions (PPI) in landscapes.

biochemical–biophysical vegetation stoichiometry, known as the "spectranomics approach" (Asner et al., 2009, 2012). Asner et al. (2012) developed and proposed a "fingerprint for each species" (http://spectranomics.stanford.edu/Spectranomics_Database) based on the biochemical–structural properties of plants. With the help of this new approach, the effects of functional reactions to stress and environmental changes on vegetation patterns can be analyzed in addition to the phylogenetic tree of species based on the "morpho-taxonomic and bar coding information".

Furthermore, using comparable data and approaches, Schmidtlein et al. (2012) studied vegetation patterns as reactions of plant species in plant communities to specific local characteristics. Feilhauer et al. (2014) used a multi-sensor approach to map 2000 natural habitat types and quantified a continuous floristic composition and floristic gradient based on hyperspectral remote sensing data. Furthermore, Feilhauer and Schmidtlein (2011) were able to demonstrate that, based on intermittent hyperspectral remote sensing data, vegetation patterns based on canopy reflectance can be studied (Fig. 3).

4.1.3. Effects of landscape structure on species

Landscape structure may affect various aspects of organisms' behaviours, population dynamics and biodiversity (Fig. 3). Therefore, landscape patterns are used to understand and quantify (1) the movements of animals, such as foraging, dispersal, migration or home ranges, (2) the effect of habitat configuration on population persistence (Deutschewitz et al., 2003). The latter commonly involves (3) habitat suitability analysis (Billeter et al., 2008) and (4) investigating population and meta-population dynamics. Finally, (5) landscape structure is central to effects of biodiversity and biological heterogeneity on complexity (Cushman and Huettmann, 2010). The number of studies addressing effects of landscape structure and in particular habitat configuration on animal species is growing fast (Simova and Gdulova, 2012; Uuemaa et al., 2013; Syrbe et al., 2013). Many of those studies address the loss and fragmentation of species' habitats with detrimental effects on fitness, reproduction and survival (Lang and Blaschke, 2007) and led to the development of new landscape metrics (e.g. Jaeger, 2000) to support consistent quantification of habitat fragmentation independent of habitat amount.

A review by Uuemaa et al. (2011) confirmed that landscape structure may affect the distribution of insects, amphibians, mammals and birds. Uuemaa et al. (2011) were able to prove that for virtually every species a very simple set of landscape metrics is sufficient to explain such distribution patterns. How strong and meaningful such relationships between landscape metrics and species distributions are, depends on both the spatial and thematic resolution of the remotely sensed data, and on the characteristics of the species.

4.2. Anthropogenic forces on landscape structure

Another important focus of quantitative landscape ecology relates to effects of human activity on landscape patterns, which can and should be considered a process shaping landscape structure similar like natural disturbances or succession (Riitters et al., 2002). Landscape changes by human activity are constrained by the "primary landscape structure" which is a result of the geographical situation, topology, soil characteristics, local climate and vegetation composition (Walz, 2001). In most of Europe human activity resulted in a "secondary landscape structure" (Meyer, 1997) or "cultural landscapes". These human dominated landscape structures are distinctly different from natural areas and are often the result of thousands of years of transformation processes, such as large scale clear cutting, mining or agriculture (Bastian and Bernhardt, 1993). Changes in land-use policies can also have drastic effects on landscape patterns (Kienast, 1993; Lambin et al., 2001; Kuemmerle et al., 2008). For example reforms in the European Union had and will have effects on landscape structures. Another driver for landscape changes are new technologies and last but no least human approaches to food production. Organic or biodynamic farming – while still at grass-roots level – already changes agricultural landscape structures around the world. All of those human dominated processes lead to distinctive and continuous changes in landscape composition and configuration as well as qualitative characteristics of landscape patterns.

5. How to appropriately quantify landscape structure?

For European agricultural landscapes, Bailey et al. (2007b) concluded that an intermediate thematic resolution was most suitable for predicting biodiversity. Landscape metrics with strong correlations to observed biodiversity included the largest patch index, edge density, nearest neighbour, proximity index and the Simpson's diversity index. The question remains, how meaningful such statistical relationships really are. For some species, whose habitat requirements and life cycles are well known, we are in a position to derive causation from correlation allowing for meaningful and practically relevant interpretations. For the many lesser known species, however, we may well find similar statistical relationships, but may have difficulties interpreting those (Bailey et al., 2007a). Furthermore, Uuemaa et al. (2011) also showed that a large part of the variation of the dependent variables can only be moderately well explained (Pearson's correlation coefficient of $<\pm 0.7$) with landscape metrics. Therefore landscape structure as represented by the PMM hardly ever fully accounts for the variation in ecological response variables. These limitations can be partly attributed to the PMM approach itself, the reduced amount of information resulting from aggregation and oversimplification, but also from potential misuse of PMM based landscape metrics (Tischendorf, 2001; Li and Wu, 2004).

We believe that these limitations can be overcome in some situations using the GM approach from remotely sensed data, which allows for a more realistic representation of vegetation patterns and resulting landscape structures including qualitative vegetation and habitat parameters. Considering and using GM based landscape models should help to improve our understanding of species–landscape interactions and, in particular, the effects of quantitative and qualitative vegetation characteristics on organisms, populations and biodiversity in general (Cushman et al., 2010).

Table 2
Classification of the degree of hemeroby and the corresponding degree of naturalness which affect the process–pattern interaction and therefore the internal heterogeneity (modified after Sukopp, 1976; Blume and Sukopp, 1976; Steinhardt et al., 1999; Klotz and Kühn, 2002).

Degree of hemeroby	Human impact	Degree of naturalness	Pattern changes in space/time	Internal heterogeneity	Borders/edges/ecotones	Indicators	Quantitative approach
Ahemerobic	Non	Natural	++++++	++++++	Soft	Continuous	GM
Oligohemerobic	Low	Close to natural	+++++	+++++			
Mesohemerobic		Semi-natural	++++	++++			
β-Euhemerobic (moderate)	Moderate	Relatively far from natural	+++	+++	Hard/soft	Continuous/discrete	GM/PMM
α-Euhemerobic		Far from natural	++	++			
Polyhemerobic	High	Close to artificial	+	+			
Metahemerobe (high)	Very high	Artificial	–	–	Hard	Discrete	PMM

5.1. Characteristics of processes affecting landscape patterns

When considering the applicability of quantitative models in landscape ecology, several principle questions need to be asked:

- Which processes affect patterns in landscapes?
- What are the quantitative characteristics of these ecological processes?
- How dynamic are vegetation patterns over time?
- What types of indicators are needed to quantify spatial and perhaps temporal characteristics of vegetation patterns?
- What is the best approach (PMM or GM) to represent and quantify landscape structure?
- What are the implications of those choices for generalizing and extrapolating the results of the analysis?

We therefore need to understand the processes affecting patterns. Steinhardt et al. (2012) emphasize the importance of understanding the scope, length, intensity and consistency of these processes. Furthermore, dominance, overlay and history of human pressures on the landscapes (hemeroby) also play a major role in shaping vegetation patterns and landscape structure. “The concept of hemeroby was originally developed for measuring human impacts on flora and vegetation. The term hemeroby, which was introduced by the botanist Jalas (1955), is derived from the Greek words hémeros (tamed, cultivated) and bíos (life). Later this concept was applied on whole ecosystems (Blume and Sukopp, 1976, p. 83; Sukopp, 1972, p. 113ff, Tables 2 and 3).

According to this, hemeroby can be understood as an integrative measure of the impact of all human intervention on ecosystems (Sukopp, 1976, p. 21; Walz and Stein, 2014, p. 279).

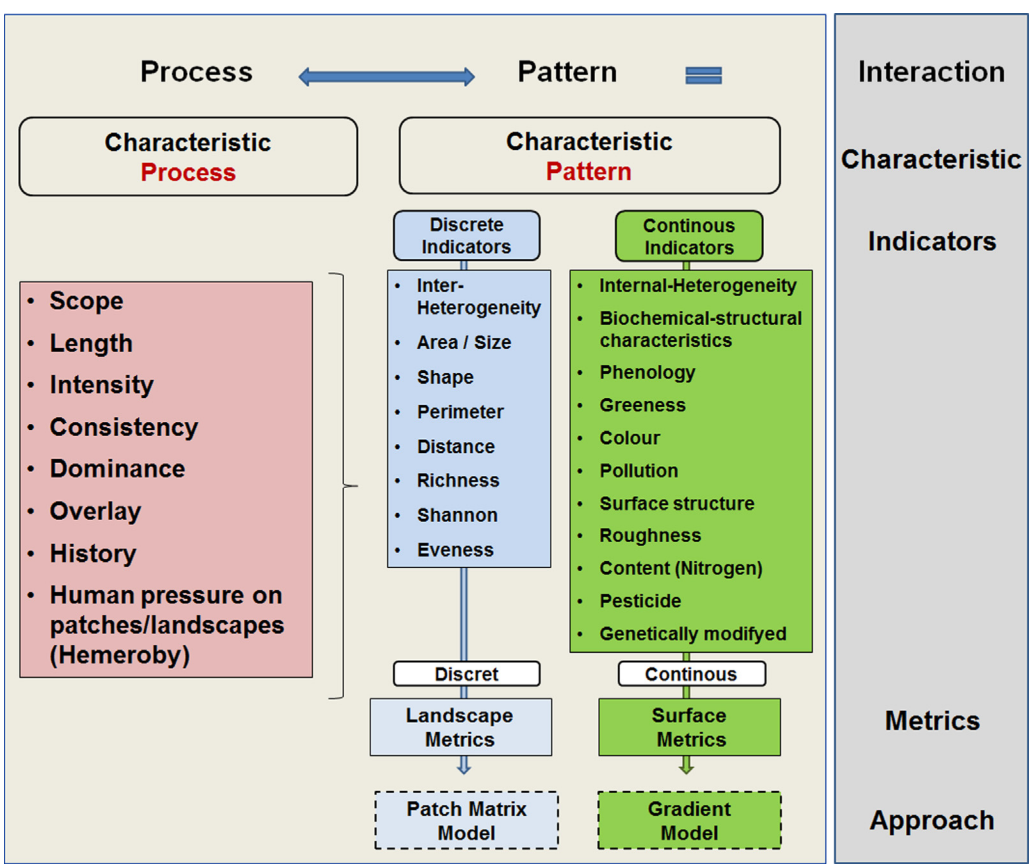

Fig. 4. Characteristic of the processes, discrete and continuous indicators in the process–pattern interactions.

Table 3
Description of landscape processes, origin and effects of processes on patterns, effects on heterogeneity in space and time, data and approach for quantifying process–pattern interactions with patch matrix model (PMM) or gradient model (GM).

Drivers and processes	Origin of process Dominant effects/reasons for patterns	Heterogeneity of patterns space/time	Data	Approach PMM/GM
Phenology	Seasonal and interannual variation of climate Changes in biochemical–biophysical vegetation characteristics	+/+++	Multitemporal remote sensing data (MODIS, Landsat TM), RapidEye, Sentinel Hyperspectral remote sensing data (HySpex, HyMAP, AISA, EnMAP)	GM
Stress on vegetation, fauna	Environmental stressors–fragmentation, noise, air pollution, soil disturbances, management strategies, species-competition Modification in biophysical properties and characteristics of flora and fauna Change of photosynthetic activity and pollination potential Change of cellulose content, cell water content Change of breeding behaviour and reproduction rate	+++/+++	RapidEye, Sentinel Hyperspectral remote sensing data (HySpex, HyMAP, AISA, EnMAP) Radar, thermal	GM
Species distribution	Environmental stressors – air temperature, air moisture content, rainwater amounts, wind speed, etc. Species distribution, adaptation, ecological strategy types of plant species	+++/+++	Rapid Eye, Sentinel Hyperspectral remote sensing data (HySpex, HyMAP, AISA, EnMAP), Thermal, Corine Data, Atkis data, Biotope data	PMM
Human management strategies	Landscape planning, economical strategies, laws and regulations, government policies, agricultural subsidies Crop rotation system, land-use intensity, pesticide, fertilization, river regulation	++/++	Landsat TM, Rapid Eye Hyperspectral remote sensing data	PMM
Urban development	Population and economic growth or decline Urban sprawl, land use perforation, densification, sealing	++/+	Landsat TM, SPOT, RapidEye, Sentinel, Thermal, In Europe: Urban Atlas, Corine Land Cover, different land use maps	PMM
Urban climate and climate change	Environmental stressors–air temperature, air moisture content, rainwater amounts, wind speed, etc. Urban heat island, superficial flooding, wind lanes	++/++	MODIS, Landsat TM Climate observation data, climate models	PMM/GM

Heterogeneity/patterns in space/time: +low, ++medium, +++ high
MODIS[b] – http://modis.gsfc.nasa.gov/
Landsat-TM[b] – Thematic Mapper, http://landsat.usgs.gov
RapidEye[b] – http://blackbridge.com/rapideye/
Sentinel[b] – http://www.esa.int/Our_Activities/Observing_the_Earth/Copernicus/Overview4
EnMap[b] – Environmental Mapping and Analysis Programme, Hyperspectral Satellite launch 2017, http://www.enmap.org/
HyMAP[a] – Hyperspectral Remote Sensor, Australia, HySpex[1] - Hyperspectral Camera, http://www.hyspex.no/
AISA[a] – Airborne Imaging Spectrometer For Application, http://www.spectralcameras.com/aisa
Corine Land cover data - http://www.eea.europa.eu/publications/COR0-landcover
Biotope data–Habitat maps usually originating from a combination of photo interpretation and fieldwork, e.g. http://www.wageningenur.nl/en/Expertise-Services/Research-Institutes/alterra/Projects/EBONE-2.htm

[a] Airborne.
[b] Spaceborne.

Combined, these natural and anthropogenic processes are the decisive factors that generate and shape vegetation patterns and their change over time. Fig. 4 illustrates the characteristic of these processes, discrete and continuous indicators in the process–pattern interactions.

5.2. Decision criteria for choosing the best model and data

Having two complimentary landscape representation models at hand requires criteria for choosing the most appropriate approach. We argue that processes and their characteristics in space and time creating and affecting landscape structures through vegetation patterns but also the purpose of the study and the research questions should be evaluated for choosing the best data model. Let us focus first on the importance of process characteristics, their spatial and temporal heterogeneity and hemeroby or naturalness of a landscape structure for the choice of the data model.

Landscapes under low human pressure (low hemeroby) can form highly dynamic and heterogeneous vegetation patterns. As we pointed out earlier, flowering and growth phenology can cause highly ephemeral heterogeneity in vegetation patterns due to annual changes in biochemical and structural vegetation properties. Low land-use intensity and therefore minimum human influence on the natural environment tends to result in high biodiversity (Blüthgen et al., 2012). This biodiversity in turn generates high temporal variability in vegetation patterns through a

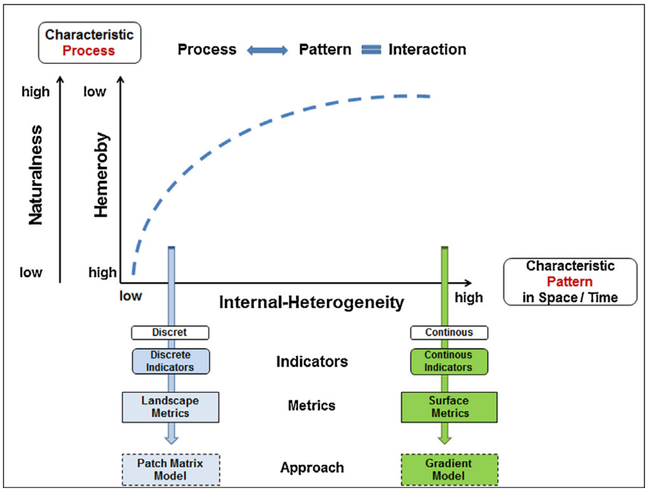

Fig. 5. Influence of process characteristics and their effects on pattern characteristics in space and time on the applicability of the patch matrix model (PMM) and of the gradient model (GM) for quantifying landscape patterns. A low hemeroby (high naturalness and low human pressure on landscapes) allows for high internal-heterogeneity in space and over time within patterns. Such landscapes can be captured with the GM approach. A high hemeroby reduces heterogeneity in space and time within patterns. For such landscapes we recommend the PM model.

diverse flowering and growth phenology over the year. Landscapes or areas with such a high degree of naturalness (or low value of hemeroby) should therefore preferably be represented using the GM approach (Fig. 5). For quantifying landscape structures with such a high transitory heterogeneity it is possible to draw on a number of continuous indicators such as the percentage of green, water content, morphology, vegetation geometry, or flowering phenology. If the GM approach is used, high-resolution geometric and spectral remote-sensing data such as RapidEye, the new Sentinel Remote Sensors or hyperspectral sensors like HyMAP (Australia) Hyperspectral Remote Sensor (Australia), AISA (Airborne Imaging Spectrometer For Application) or EnMap (Environmental Mapping and Analysis Programme) can be used.

On the other hand, high land-use intensity in urban and agricultural areas tends to control or fix vegetation patterns and landscape structure both in space and time. Such anthropogenic-dominated landscapes are primarily composed of homogenous areas with distinct boundaries. The resulting landscape structure is therefore best represented with the PMM approach, distinguishing patches of uniform land-cover or vegetation types delineated by sharp boundaries. Such patterns can be quantified by means of landscape metrics in support of expressing composition and configuration aspects of the landscape structure. Many of those landscape metrics have been applied in regional- and landscape planning, as well as for environmental assessments.

Finally, the purpose of a study requiring landscape structure to be modelled will also influence the choice of the appropriate data model. The PMM appeals by its simplified representation and similarity to conventional maps. It reflects how we – as humans – see and perceive landscape. The PMM also triggered the invention of numerous landscape metrics at landscape, land-cover or class and patch levels – all of which can be calculated rather easily and used as predictor variables in statistical models. Such numbers may also be used to track and monitor changes of spatial patterns over time or to compare configuration aspects of patterns across space and time. Most of all, however, the interpretation of analyses on PMM based landscape metrics is rather intuitive and simple. For instance, we know what average patch sizes or edge densities mean and can translate relationships with those variables into pragmatic and applied rules. This is more difficult if landscape structure was represented by the GM. Here, we do not have patches or discrete boundaries, which form the foundation for most of the landscape metrics available today. Instead, we need to derive quantitative information from continuous surface maps. From those we can calculate continuous indicators, such as averages or standard deviations of the variable of interest. For example, we can calculate the mean or standard deviation of NDVI or similar aggregates from a GM based landscape representation. The challenge remains on how to interpret such variables and their potential relationships with other ecological response variables. Much less standardization is possible and it remains to be discovered if a similar set of qualitative and quantitative landscape metrics can be derived from GM based landscape information. Table 3 gives an overview on drivers of landscape processes, their origin and effects on patterns, their effects on heterogeneity in space and time as well as the necessary data and approach for quantifying process–pattern interactions.

6. Conclusion and outlook

Understanding the heterogeneity of landscape patterns and their changes over time is important for comprehending and predicting the availability of food resources, habitat amount and fragmentation for animal species, biodiversity, and for environmental assessments in landscapes. Such landscape patterns are shaped and altered by ecological and anthropogenic processes.

Our paper attempts to explore the effects and mechanisms of ecological processes on landscape patterns and their dynamic changes over time. We identified natural processes and human land-use as two distinctive processes resulting in different characteristics of patterns in landscapes. The scope, length, intensity and consistency (Steinhardt et al., 2012) of these processes as well as the history and dominance of human pressure, which affects the degree of naturalness or hemeroby, must be examined to understand how they shape landscape patterns.

To this end we review two approaches for representing landscape structure as a result of vegetation pattern: the patch matrix model (PMM) and the gradient model (GM). Each model comes with its own set of assumptions, simplifications and quantitative potential. The characteristics of the processes shaping vegetation and landscape patterns are decisive for the use of either the PMM or the GM approach. In general, landscapes with a higher degree of naturalness (low hemeroby) and with a high temporal dynamic in vegetation patterns should be modelled using the GM approach. On the other hand, human-dominated landscape patterns, such as urban areas or agricultural landscapes lend themselves to a map like approach with discrete and homogenous areas separated by sharp and discrete boundaries – the PMM. Both models have different data requirements and allow for different quantification methods. Conventional landscape metrics, such as patch density or Shannon diversity can be calculated on PMM based landscape representations. GM based landscape representations allow for continuous surface metrics, such as the Normalized difference vegetation index or Slope (McGarigal et al., 2009).

We argue that the PMM approach as the backbone for most of our theoretical insights in quantitative landscape ecology also limits our progress due to the inherent simplifications and assumptions of the model itself. Although convenient and pragmatic, landscape heterogeneity and vegetation patterns rarely exist in the form of discrete and static patches with a finite set of vegetation or land-cover types. Still, we use PMM with confidence as a proxy to the real world, but often neglect the effects and propagation of errors and simplifications in our statistical and simulation models. Therefore we need to embrace alternative methods, such as the GM approach in support of building more realistic models in our efforts to understand how processes affect landscape patterns and vice versa. The GM approach is still regarded with scepticism, due to practical limitations arising from the need of high resolution data and comparatively complex analysis algorithms. Another challenge comes from the lack of universal landscape metrics as quantifiers for those continuous surfaces. More work is needed in support of developing indicators quantifying different aspects of spatial patterns in continuous surfaces. Last but not least, results derived from analyses based on the GM approach must be interpretable. Relationships between predictor variables, such as continuous surface metrics, and response variables do not always easily lend to intuitive interpretations. We still believe that endorsing the GM approach in quantitative landscape ecology, complimentary to the PMM approach, can and will enhance our understanding on how patterns and processes interact and ultimately benefit landscape ecology.

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