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Landscape heterogeneity: concepts, quantification, challenges and future perspectives

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Summary

The intrinsic complexity, variety of concepts and numerous ways to quantify landscape heterogeneity (LH) may hamper a better understanding of how its components relate to ecological phenomena. Our study is the first to synthesize understanding of this concept and to provide the state of the art on the subject based on a comprehensive systematic literature review of 661 articles published between 1982 and 2019. Definitions, terminologies and measurements of LH were diverse and conflicting. Most articles (534 out of 661) did not provide any definition for LH, and we found great variation among the studies that did. According to our review, only 10 studies measured the effects of different land-cover types on biotic or abiotic processes (functional LH). The remaining 651 studies measured physical attributes of the landscape without mentioning that different land-cover types may impact biotic and abiotic processes differently (structural LH). The metrics most frequently used to represent LH were the Shannon diversity index and proportion of land-cover type. Most metrics used as proxies of LH also coincided with those used to represent non-heterogeneity metrics, such as fragmentation and connectivity. We identify knowledge gaps, indicate future perspectives and propose guidelines that should be addressed when researching LH.

Introduction

Landscape ecology is closely linked to the concept of landscape heterogeneity (LH), which is the qualitative or quantitative variation of landscape elements (Box 1; Risser 1987, Li & Reynolds 1994, 1995, Pickett & Cadenasso 1995, Turner et al. 2001, Fahrig et al. 2011). LH has two main components: composition and configuration. The variety of land-cover types, known as compositional LH (Li & Reynolds 1995), provides different environmental conditions (e.g., light incidence and temperature) and resource availability (e.g., shelter and food) for organisms, while the spatial arrangement of land-cover types, or configurational LH (Box 1), influences the magnitude of processes that occur within and between patches (Li & Reynolds 1995). Hence, compositional and configurational LH affect several biotic and abiotic processes, including species diversity (Regolin et al. 2020), movement of individuals (Romero et al. 2009), predation (Kauffman et al. 2007), pest control (Gardiner et al. 2009), pollination (Boscolo et al. 2017), nutrient cycling (LeClare et al. 2020) and fire occurrence (Vega-García & Chuvieco 2006). Humans may also be influenced by LH, such as in the provision of urban ecosystems services (Hamstead et al. 2016) and in terms of human wellbeing (Finder et al. 1999).

LH can be further described under structural and functional perspectives. Structural LH considers the attributes of a landscape, regardless of the effects that different land-cover types have on biotic and abiotic processes. The choice of the structural components is usually based on prior knowledge or assumptions regarding the studied organism. This type of approach usually assumes that metrics such as number of patches and edge extent are sufficient to characterize landscapes (Li & Reynolds 1995, Fahrig et al. 2011). The lack of clearly stated assumptions and the ecological processes that they represent can lead to the mistaken conclusion that the attributes of the landscape are solely responsible for the patterns found and not proxies of an underlying ecological process. Conversely, functional LH considers how different land-cover types affect a target species or biological group or how they influence abiotic processes such as nutrient flow (Li & Reynolds 1995, Fahrig et al. 2011). In other words, the realization of biological

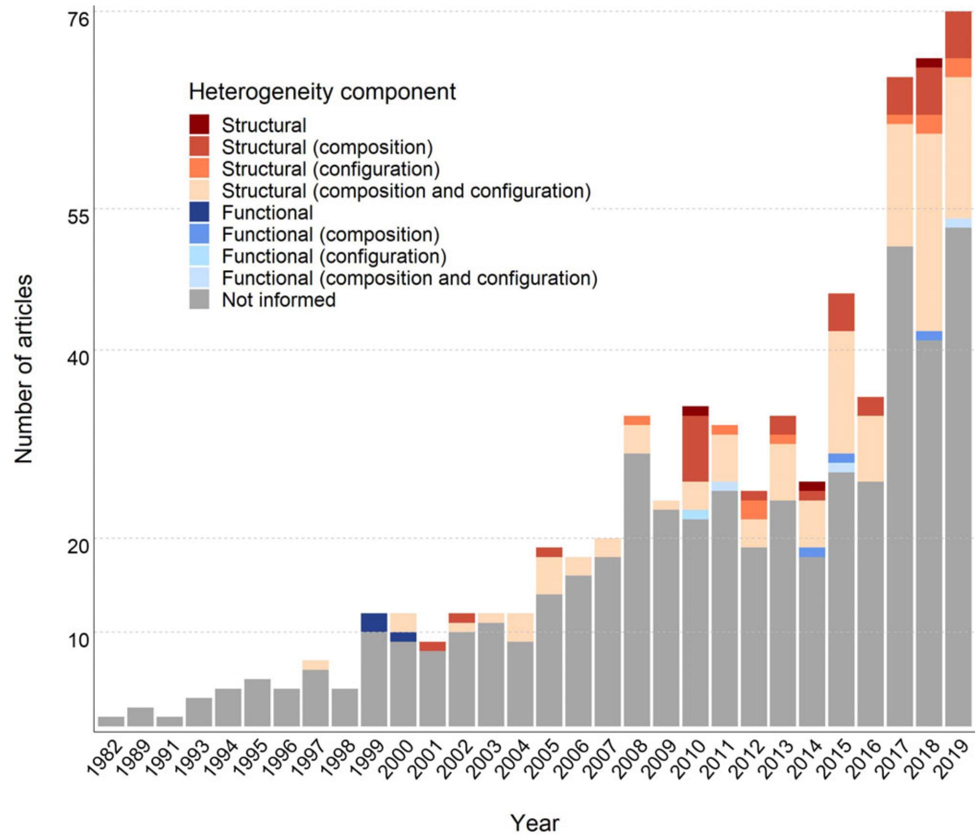

Fig. 1. Number of articles per year that addressed landscape heterogeneity. Coloured bars indicate the proportion of articles in which authors stated that distinct types of heterogeneity (compositional/configurational; structural/functional) were measured – see definitions and a discussion of these terms in Box 1. The type of heterogeneity was attributed only when authors explicitly stated them.

processes will depend on how organisms 'perceive' the environment, and consequently this will be influenced by the variation in the functional LH.

Landscapes may be evaluated according to their physical attributes (structural LH) combined with their compositional and/or configurational aspects, such as the proportion of land-cover types and edge extents (Fig. 1, 'Structural (composition and configuration)'; Duflot et al. 2014). Similarly, landscapes can be described by considering the effects of different land-cover types on biotic and abiotic processes (functional LH) combined with their compositional and/or configurational aspects (Fig. 1, 'Functional (composition and configuration)'; Perović et al. 2015). Therefore, LH can be perceived, studied and represented according to several perspectives depending on the subject motivating the research and on the study target (see examples of the different components of LH and a conceptual scheme in Box 1).

Different mechanisms and hypotheses underlie how LH could affect biodiversity patterns. Distinct land-cover types may influence the ability of organisms to exploit different yet essential resources. This process, called 'landscape complementation', is affected by the heterogeneity of land-cover types and the spatial arrangement of different patches in landscapes, as both can influence the mobility of organisms (Dunning et al. 1992). LH may have a positive effect on species richness and abundance for several taxonomic groups (Benton et al. 2003). However, as LH increases, patch sizes of habitats tend to decrease, with the patches eventually becoming so small that they may not provide sufficient resources to organisms and thus might no longer sustain viable populations (Duelli 1997). This suggests that the occurrence of overall taxa is greatest at intermediate levels of LH and, thus, the intermediate disturbance hypothesis would drive the species richness–LH relationship (Fahrig et al. 2011, Redon et al. 2014).

The complexity of the topic may prevent us from gaining a clear understanding of which LH components and perspectives have been assessed in empirical research (Tscharntke et al. 2012). Moreover, different methods for quantifying LH may yield different results, which may hinder the construction of a more robust body of knowledge in the field and, consequently, environmental decision-making. Li and Reynolds (1995) highlighted that the difficulty in defining and quantifying LH originates in the concept itself, which is usually related to specific research questions and data types. Despite the relevance of LH and the increasing number of publications addressing this topic over the last four decades, a synthesis of the LH literature is still needed. Unlike other reviews of the effects of LH on animal diversity (Tews et al. 2004), ours is the first to synthesize the knowledge and provide the state of the art on the subject based on a comprehensive systematic literature review. Specifically, we: (1) identify how LH is defined and quantified; (2) identify the scope of studies and biological response variables investigated in relation to LH; (3) identify the spatial scales most used; and (4) provide a summary of knowledge gaps, indicating future perspectives and proposing guidelines that should be followed when researching LH. We hypothesized that the definitions and metrics used to quantify LH will vary across studies, making comparisons across studies and general conclusions harder to draw (Hodges 2008). We further hypothesized that the scale and variables used to measure LH are not clearly stated (Jackson & Fahrig 2015). Lastly, we hypothesized that the scattered definitions and lack of consistency among studies weaken the real understanding of LH in biodiversity and landscape conservation. To address these issues, we propose guidelines to help with strengthening the outcomes of LH studies.

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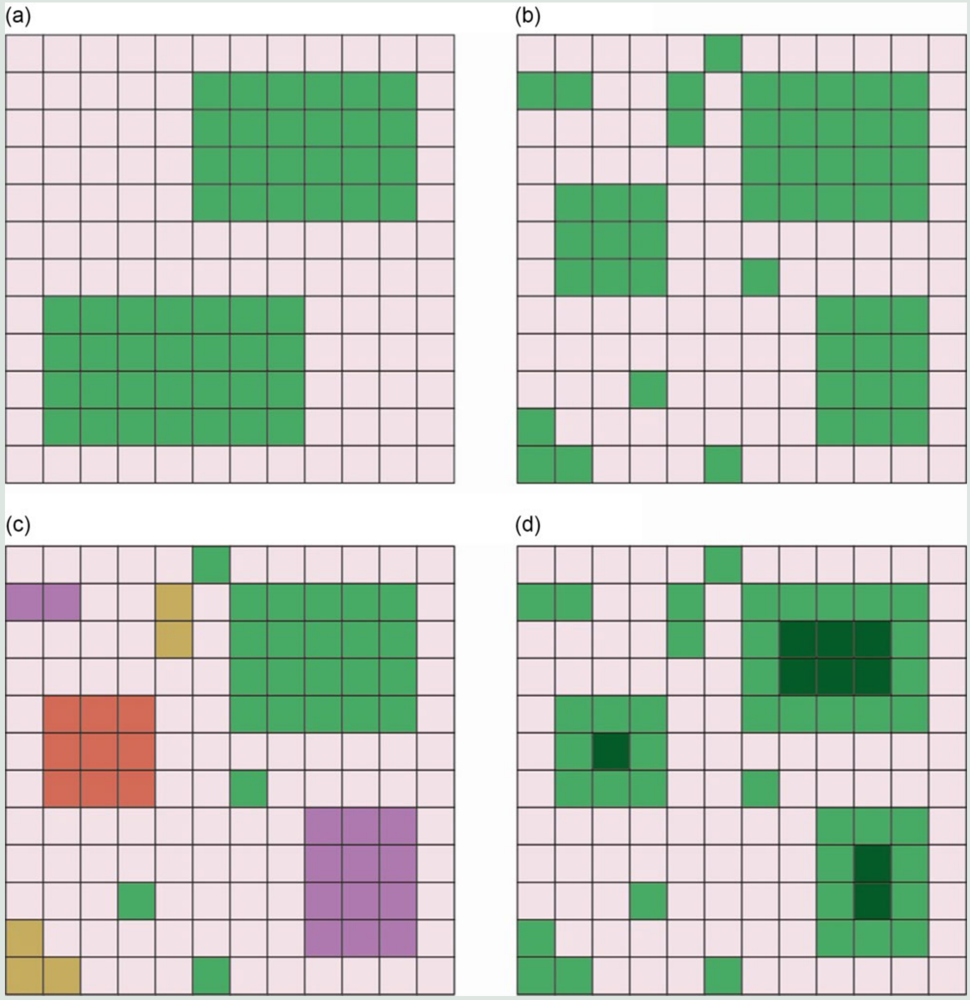
Box 1. Schematic representation of the different dimensions of landscape heterogeneity (LH).



Each square represents a pixel of a categorical mapping (i.e., the smallest possible mapping unit in which pixels of the same colour have the same categorical value). The four landscapes (a–d) represent patches of land-cover types (coloured pixels) and a matrix (light grey pixels). The area occupied by the matrix and the patches is the same in all four landscapes; however, the components values (composition and configuration) and perspectives (structural and functional) differ. Landscape (a) has the same compositional LH (diversity of land-cover types) as (b), but landscape (b) shows a more complex spatial patterning than (a) and, consequently, higher values of configurational LH. In landscape (c), pixels of different colours represent different land-cover types. Therefore, compositional LH in landscape (c) is higher than that in (b), even though both have the same configurational LH. Landscape (d) has the same land-cover types as landscape (b); however, it is represented under the 'perception' of a species for which edge-pixels (i.e., pixels that have direct contact with the matrix; light green pixels) have lower habitat suitability than pixels that are not in contact with the matrix (core pixels; dark green). The difference in suitability between edge–core areas may affect the occurrence of a given species and may be described as different land-cover classes. Areas located in patch edges may be affected by the surrounding matrix; thus, differences in environmental conditions (e.g., light incidence and temperature) between fragments (core and edge) could be expected (Turner et al. 2001). These differences could affect vegetation structure, species occurrence, ecological interactions, and several other biotic and abiotic processes, which in landscape ecology, are widely known as edge effects (Turner et al. 2001). In summary, in contrast with landscape (b), in which only the structural perspective is considered, landscape (d) exemplifies functional LH, in which edge effects are considered for a given species. Another way to analyse the landscape from a functional perspective would be to assign different weights in the analyses that are concerned with the effects of different land-cover types (c). These weights could vary according to the biological group or abiotic factors, so that for a given species some type of land cover can provide more (or fewer) resources and, thus, influence a certain ecological process.

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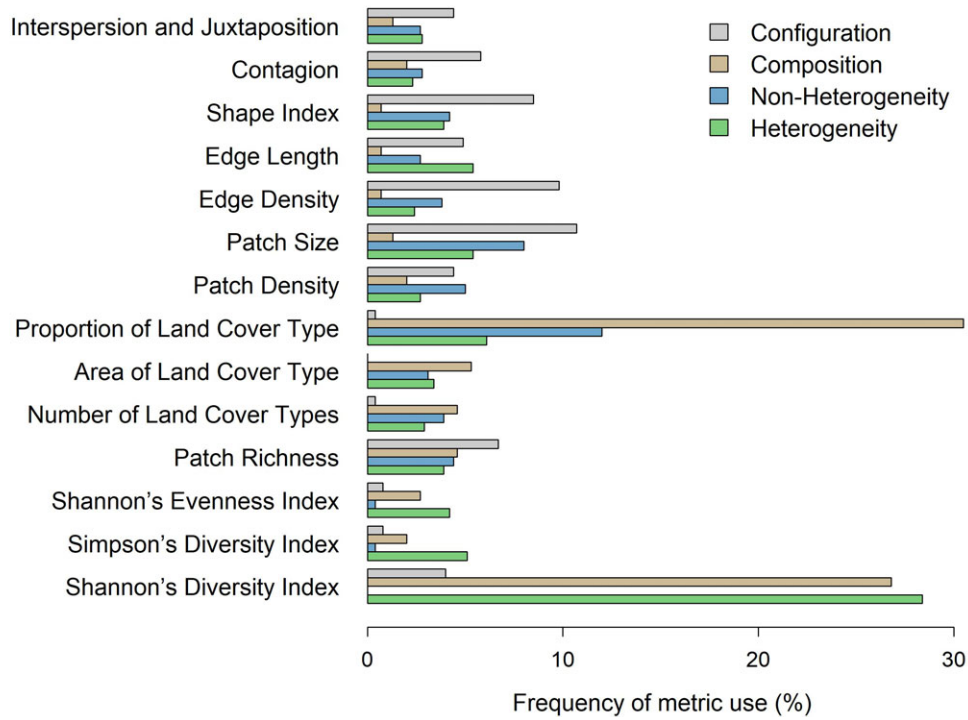

Fig. 2. The 10 most frequently used metrics assigned by the authors as proxies of landscape heterogeneity (green bars) and of other landscape aspects unrelated to landscape heterogeneity (blue bars). The percentage of studies in which each metric was considered as a proxy for configurational landscape heterogeneity are indicated by grey bars and for compositional landscape heterogeneity by light brown bars. Note that the summed numbers do not correspond to the total amount of articles reviewed (661) as the quantity of metrics employed varied among studies.

Review methods

We performed a comprehensive search in the Web of Science database (clarivate.com/webofsciencegroup) using the following keywords and Boolean operator search criteria: 'landscape heterogeneity' OR 'landscape diversity' OR 'landscape homogeneity' OR 'landscape simplification' OR 'spatial heterogeneity' OR 'functional heterogeneity' OR 'temporal heterogeneity' OR 'structural heterogeneity' AND 'landscape'. We restricted the search to the following research areas: 'Ecology', 'Environmental Sciences', 'Biodiversity Conservation', 'Geography Physical', 'Forestry', 'Remote Sensing', 'Environmental Studies', 'Plant Sciences', 'Zoology', 'Agriculture Multidisciplinary', 'Marine Freshwater Biology' and 'Biology'. We restricted the search to a publication date of the end of 2019 (Fig. 1), which resulted in 2879 articles. As we were interested in heterogeneity measurements, we only considered articles in which authors had claimed to have quantified LH, and after carefully reading all 2879 articles (mainly the title and abstract but, in some cases, the full text), 661 publications were eligible for our analysis.

To characterize the definitions and measurements, we extracted from each study (1) the LH definitions given, (2) the LH components investigated (compositional/configurational), (3) the LH perspectives investigated (structural/functional; Box 1) and (4) the metrics used as proxies of LH. We also recorded (5) the research topic (including taxonomic groups and level of biological organization) and (6) the spatial scale used. The definitions and types of metrics accounted for in this study were only considered when explicitly referred to by the authors to avoid misinterpretations and subjectivity.

The landscape metrics, scope of the studies and variables related to LH were, in general, specific to each study. Therefore, to synthesize the information, we grouped similar terms in the same class; for instance, 'proportion of pasture' was classified as 'proportion of land-cover type' (Fig. 2). Definitions of LH were also synthesized (Appendix S1 & Tables S1 & S2); for example, when configurational LH was defined as 'the degree of spatial complexity of the landscape pattern' (Fahrig et al. 2015), we classified it as 'heterogeneity in spatial arrangement of land-cover types' (Appendix S1 & Table S2). To ensure consistency, only the first author (VT) performed these classifications.

We determined five extent classes based on the smallest analytical unit of landscape scale, namely polygons from which LH metrics were extracted: (1) local, when studies sampled local landscape scales (usually small regular polygons, such as squares and circles) – studies were considered local even if different landscape scales (polygons) were spread over larger areas (e.g., crop fields spread over a country); (2) regional, when studies were based on regional maps that were smaller than a country but larger than a local unit (e.g., a watershed or a province); (3) national (territory of a whole country); (4) continental (whole continent); and (5) global (entire world). The extent classes were considered to be different from the scale of the study. For example, if LH metrics were extracted from circles surrounding sampling sites spread across a country, the extent class was defined as 'local', although the study could be considered as being national in scale.

We only assigned articles as having structural/functional or compositional/configurational measures of LH when these were explicitly stated by the authors. Similarly, we did not assume which metric was used to quantify LH or non-heterogeneity aspects unless this was explicitly stated in the study (even for the most often used metrics, such as the Shannon diversity index; McGarigal et al. 2009). Additionally, to provide an overview of other descriptive aspects of LH studies, we also extracted data on the terms most used to refer to LH, geographical coverage (e.g., countries, biomes), spatial and temporal aspects (pixel size, timescale and number of temporal observations) and the landscape models (heterogeneous mosaic, binary or continuous model). For descriptive information, see Appendix S1.

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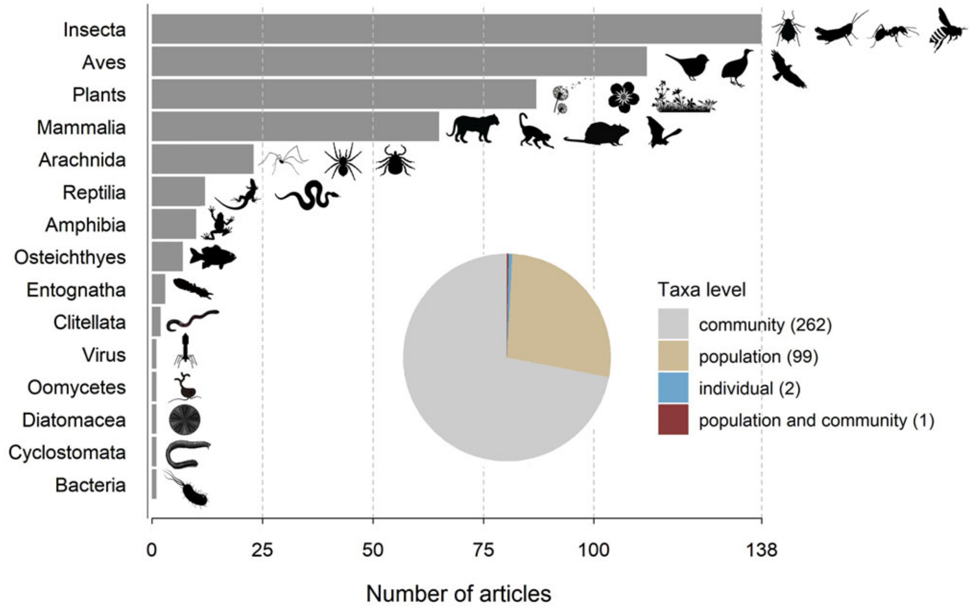

Fig. 3. Frequency with which different taxonomic groups were used as a dependent variable in studies that measured landscape heterogeneity. The pie chart indicates the proportion of the level of organization of the taxa studied. Note that the summed numbers do not correspond to the total amount of articles reviewed (661) as the quantity of metrics employed varied among studies.

Landscape heterogeneity in the literature: definitions and important terms

Our review spanned 37 years (1982–2019), with gaps from 1983 to 1988 and from 1990 to 1992. The number of publications on LH has increased over the years since the first publication in 1982 (Fig. 1), but at different rates over time. Most articles (534 out of 661) did not provide any definition of LH, and we found great variation among the studies that did provide definitions. For instance, the spatial component of the landscape was not considered in some articles, and authors stated, for example, that 'landscape diversity can be considered an attribute of landscape health and landscape stability' (Yeh & Huang 2009), or LH was defined under specific conditions to comply with the goals (e.g., the 'number of vegetation types in 500 m radius of site'; Pereoglou et al. 2016). Among all studies that defined LH (n = 127), 24.4% considered both compositional and configurational components by explicitly stating the investigated components in the definitions (e.g., the 'spatial variation of the composition and configuration of landscapes'; Li et al. 2015) or implicitly stating them (e.g., the 'land-cover types and their spatial arrangements'; Singh et al. 2017). Lastly, only two articles considered temporal aspects in their definitions (Deutschewitz et al. 2003, Wang et al. 2017).

Among all 127 articles with a LH definition, 51 different references were cited, with 52.7% of the articles citing at least one reference. The most cited references were Fahrig et al. (2011; n = 16), followed by Li and Reynolds (1995; n = 9) and Li and Reynolds (1994; n = 5). These three references consider LH as the compositional and configurational variability of landscapes. However, some studies adapted the original definitions from these references, as in Corro et al. (2019), who defined LH as 'the number and amount of land uses' while citing Fahrig et al. (2011). Although this definition is contained in the reference, it considers only one aspect of LH described by Fahrig et al. (2011).

There are striking differences between studies that measured LH under the structural and functional perspectives. We found only 10 (0.01%) studies that explicitly stated that functional LH was measured, with the definition of functional LH consistently used. For instance, Azevedo et al. (2000) assigned weights to forest patches according to their regeneration time, with higher weights assigned to older patches as they would offer more resources for birds. In contrast, 158 (24%) studies measured structural LH, but only three explicitly provided a definition of the term (Mairota et al. 2013, Fahrig et al. 2015, Ye et al. 2015).

From the seven publications that used biological variables in functional LH articles, only one studied a community (Perović et al. 2015). In contrast, from the 102 articles that used biological variables in structural LH studies, 80 investigated communities and 22 studied populations (Fig. 3). Concerning LH components, most articles (75%) did not state whether they measured compositional or configurational LH (Appendix S1 & Fig. S1), even though they employed metrics commonly used as proxies for these components. In 17.4% of the reviewed articles, the authors explicitly state that both compositional and configurational LH were analysed, while in 5.4% and in 1.6% of the articles, only compositional or configurational attributes of landscapes were measured, respectively. Fahrig et al. (2011), the most cited reference, defined compositional LH as 'the number and proportions of land cover types' and configurational LH as 'the spatial arrangement' of them. However, we found 10 distinct definitions of compositional LH in 46 articles that cited Fahrig et al. (2011; Appendix S1 & Tables S1 & S2).

Landscape metrics quantifying and representing landscape heterogeneity

A total of 203 metrics were used to measure LH, while 238 were used to measure other landscape features (e.g., fragmentation and connectivity). The metrics most frequently used to represent LH were the Shannon diversity index and proportion of land-cover type (Fig. 2). Most metrics used as proxies of LH also coincided with those used to represent non-heterogeneity metrics (Fig. 2). For instance, although 'number of land cover types' and 'patch richness' commonly quantify LH (McGarigal & Marks 1994), we found that most studies employed them to measure other landscape features (Fig. 2). Regarding compositional heterogeneity, the metrics most commonly used were those describing

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the amounts of different land-cover types (e.g., 'proportion and number of land cover types') and the number and proportional abundance of patch types in the landscape. For configurational LH, the metrics most frequently used were 'patch size' and 'edge density' (Fig. 2), which were also applied by different authors as proxies for different types of LH. For instance, the 'proportion of a land-cover type' was considered as both structural and compositional LH and as both a heterogeneity and non-heterogeneity metric (Fig. 2). This result highlights the difficulty in interpreting the type of LH authors aimed to address when it is not explicitly stated.

Studies also used remote-sensing metrics as proxies of canopy-cover quality, including the normalized difference vegetation index, the enhanced vegetation index and semivariograms (Garrigues et al. 2008, Horning et al. 2010). These parameters can summarize the distribution of biophysical properties of the vegetation and are good indicators of heterogeneity over landscapes, making them suitable proxies for LH as long as pixel values are used instead of categorical maps (Garzia et al. 2018, Sugai et al. 2019), although it is worth mentioning that this can be true if pixel values are measured and not averaged. However, 27.5% of the articles did not specify the metric used to represent LH.

Scope of landscape heterogeneity studies

Most articles (45%) addressed the effects of LH on biodiversity patterns, while others addressed biodiversity-related topics, such as agricultural yield (12.7%), human-induced changes (4.7%), ecosystem services (3.2%) and conservation (1.5%; Appendix S1 & Fig. S2). These last research topics addressed LH by evaluating natural landscape patterns and/or by quantifying how these patterns changed in space and time. Approximately 24% of the articles evaluated LH without accounting for any response variable, being treated as 'landscape analysis' (Appendix S1 & Fig. S2). For example, studies aimed at identifying sites with high LH (Perko et al. 2017), analysed landscape changes over the years (Li et al. 2005) or proposed approaches to quantify LH (Hamstead et al. 2016).

Biological response variables related to landscape heterogeneity

Biological data were used in 55.5% of the articles, with the most frequent response variables being species richness (18.4% of all variables), species abundance (11.3%) and species diversity (7%; Appendix S1 & Fig. S2). The biological groups most frequently studied were insects (27.5%), birds (24.0%), plants (18.7%) and mammals (14.0%; Fig. 3), reflecting a general taxonomic bias in biodiversity research worldwide (Troudet et al. 2017). Regarding the biological level of organization, our results revealed that communities are far more commonly used response variables (72.2% of studies that used biological data) than populations or individuals (Fig. 3).

Scale and extent

Most studies used local-extent analyses (57.5%), followed by regional (33.7%), national (6.2%) and continental extents (2.3%), and there was only one global mapping analysis. Wider-extent studies investigated, for example, changes in LH over different time periods in a watershed (classified as regional extent; Wang & Wang 2013). Despite its importance, as we hypothesized, 3.9% of studies did not inform on which spatial scale (mapping polygons size) was employed for mapping. From those that evaluated landscape delimitations based on circles, squares and/or rectangles and used a single landscape scale, 70% did not justify the choice of the scale used. For the remaining 30% that did justify the scale employed, more than half (66%) chose the scale based on the biology of the studied organism. For most biological groups, the local was the most frequently employed scale, except for vertebrates, which demonstrated a larger contribution of regional and national extents (Appendix S1 & Fig. S3). Circular buffers were the most frequent delimitation within all biological groups (Appendix S1 & Fig. S3). Only 25% of studies used more than one scale, such as several circular buffer sizes, and most multiscale studies were conducted at local extents (Appendix S1 & Fig. S3; further details on the landscape and temporal scales and extents are provided in the Supplementary Material).

Inconsistencies, knowledge gaps and future perspectives

The literature related to LH may be inserted into a wider context of ecological research concerned with understanding the role of heterogeneity in determining ecological patterns (Stein et al. 2014). Given the concurrence of LH with current scenarios of climate change, land conversion, destruction of natural areas and biodiversity loss (Barnosky et al. 2011), research accounting for such challenges is extremely relevant to supporting the development of conservation strategies and evaluating existing conservation plans. A conceivable strategy to guarantee the integrity of ecological processes and the long-term conservation of species is to preserve patches of natural vegetation embedded in heterogeneous landscapes (Benton et al. 2003, Perfecto & Vandermeer 2010).

There is an imbalance of the taxonomic groups studied (Fig. 3). Except for most insect species, some of the most-studied groups (birds, plants and mammals) comprise 'charismatic species', which are often used as 'umbrella species' in conservation actions (Barua 2011). In most studies, insects were used as the focal group, mainly because they are taxonomically diverse, occupy almost all terrestrial environments, are widely used as bioindicators, have medical or veterinary relevance and are agricultural and forestry pests (Hill 1997). Focusing on underrepresented groups, such as reptiles, amphibians, invertebrates other than insects and microorganisms, should be a major concern in future studies. By reducing taxonomic bias, knowledge gaps related to the role that LH plays in governing ecological processes and biodiversity patterns (species occurrence, richness and abundance) could be narrowed. Furthermore, at the landscape level, key ecosystem processes can be driven by many understudied taxa, and valuable ecological processes will remain unknown if LH studies remain focused on the same taxonomic groups. For example, chelonians (turtles) could account for a significant portion of seed dispersal in terrestrial environments (Falcón et al. 2020); hence, understanding how they are distributed and how they move in heterogeneous landscapes could be relevant for ecological restoration.

Additionally, the level of organization of these groups and the mechanisms governing such organization are influenced in distinct ways by LH. Species coexistence, persistence and diversification should govern the main ecological mechanisms that regulate broad patterns (e.g., species distribution) across ecological systems. For instance, positive correlations between LH and bird richness may result from a dependence of the taxa on similar environmental variables or on different but spatially covariant variables (Kissling et al. 2007). Therefore, searching for a causal inference in LH

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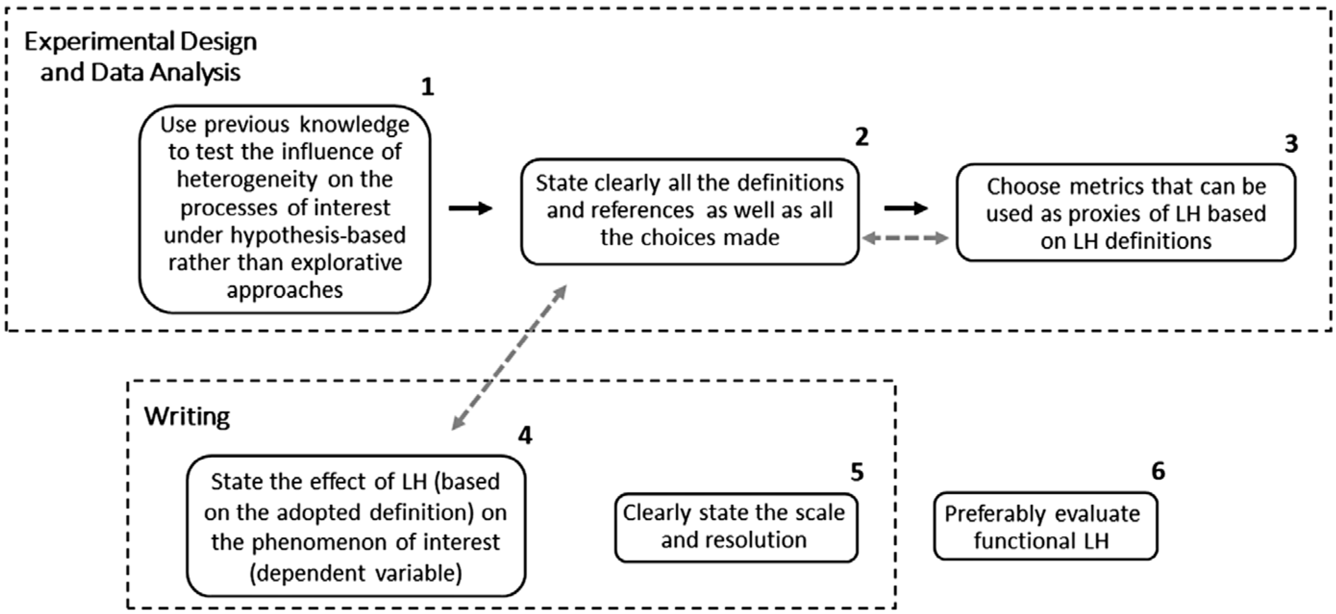

Fig. 4. Steps suggested for each stage in studies that aim to quantify landscape heterogeneity. Solid black arrows indicate the sequence of the steps that should be followed. The dashed grey arrows show that authors should go back to step 2 (stating definitions employed) when choosing the metrics (step 3) and when stating the effects of LH on the phenomenon of interest (step 4). These arrows also indicate that steps 2, 3 and 4 are directly related to each other. LH = landscape heterogeneity.

studies may help us to understand the mechanisms that promote biodiversity in heterogeneous landscapes, thus supporting practical conservation measures.

Movement and dispersal ability (Doherty & Driscoll 2018), habitat preference (Sánchez-Clavijo et al. 2019) and species interactions (Boscolo et al. 2017) are important factors affecting the response of every organism to LH. Given that communities are represented by a set of species with unique ecological requirements, responses of communities to LH often represent the output of countless ecological processes, meaning that determining the underlying ecological mechanisms is quite challenging (Wiens et al. 1993). Therefore, focusing on the functional dimension of landscapes could enable us to gain a better understanding of these mechanisms. Estimating the effects of different types of land cover on different species in a community may not be easy or feasible in most cases, and this may explain the fact that only one study used the functional perspective in a community study (Perović et al. 2015).

Few articles have explored the effects of LH on the spread of diseases (Suwonkerd et al. 2002, Overgaard et al. 2003; Appendix S1 & Fig. S2). Nonetheless, new diseases, such as that causing the COVID-19 pandemic, exemplify the urgency of understanding how landscape features, including LH, may affect the emergence and spread of such diseases.

Regarding the way in which authors refer to LH, the lack of clear definitions in 80.8% of studies and the inconsistencies in the terminology suggest that a fundamental shortfall of the literature on LH is due to an issue as basic as properly defining LH. As both composition and configuration components of LH may have different effects on biodiversity (Fahrig et al. 2011, Tscharntke et al. 2012), it is crucial to adequately classify, define and specify which component is being addressed. Determining the relative effects of composition and configuration allows for us to gain a better understanding of the mechanisms driving diversity patterns and further improve our strategies for landscape management (Duflot et al. 2017). Although most studies failed to specify the LH components analysed (Appendix S1 & Fig. S1), the proportion of published articles that specify it has nevertheless increased over the years (Fig. 1).

Most LH metrics were used interchangeably by different authors to represent compositional and/or configurational aspects (Fig. 2) as, theoretically, most metrics are proxies of both composition and configuration. For example, when calculating the Shannon diversity index, the number of patches and the proportion of different land-cover types in a given landscape are considered, as demonstrated in the following formula (Nagendra 2002): Shannon diversity index $= 1 - \sum i = 1Npi \times \ln pi$ where N is the number of land-cover types and pi is the proportional abundance of the ith land-cover type. This index is frequently used as a measure of landscape composition (Fig. 2). In turn, the number of patches is influenced by the degree of landscape fragmentation, which is related to its spatial arrangement (landscape configuration). Given the complex relationship between landscape composition and configuration, researchers should seek to minimize such interdependence when planning the experimental design of their studies.

Fragmented landscapes are commonly equated to heterogeneous landscapes and consequently the same metrics that are applied to quantify habitat loss or fragmentation *per se* have also been used to measure LH, and vice versa (e.g., patch and edge density and patch richness; Fig. 2). Because LH increases with more dispersed and intermixed land-cover types (Yaacobi et al. 2007), metrics referring to the spatial arrangement of single-class patches have also been used as proxies of LH, such as 'nearest-neighbour distance', 'interspersion–juxtaposition' and 'contagion index' (Šímová & Gdulová 2012).

Guidelines to address landscape heterogeneity in ecological research

Our literature review provides insights into how to address LH by accounting for the distinct components and perspectives. We suggest six steps to be considered when assessing LH (Fig. 4):

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(1) Use previous knowledge to test the influence of heterogeneity on the processes of interest under hypothesis-based rather than exploratory approaches (Fig. 4). In our review, we identified studies in which the mechanism relating LH to biodiversity was unclear. The lack of a clearly stated mechanism prevents us from determining the likelihood of distinct ecological processes occurring (e.g., Marboutin & Aebischer 1996, Jeanneret et al. 2003). The processes of interest may also refer to an abiotic aspect involved in higher-level ecosystem processes. For instance, soil nutrients should vary less in landscapes situated in flat terrains in comparison to mountainous regions. Therefore, in areas of irregular terrain, landscape variables other than land-cover heterogeneity should be considered (Hu et al. 2019).
(2) The definition of LH and its components (composition and configuration) should be explicitly stated. Analysing LH without asserting and defining the components being addressed may hamper the comprehension of how landscape composition and configuration affect biotic and abiotic factors separately. This could lead to misunderstandings among researchers and the wider community, including stakeholders, and hinder advances in the field (Heink & Kowarik 2010). Few studies have analysed the effects of compositional and configurational LH separately. For instance, Perović et al. (2015) found that compositional LH in agricultural landscapes influenced the taxonomic diversity of butterflies, while configurational LH was mostly associated with their functional diversity. These are important findings for guiding landscape management in conservation plans, and future research should be concerned with the independent role of compositional and configurational LH. To avoid misinterpretations, we suggest using definitions and terms that are a consensus in the landscape ecology literature. Although ecological terms can be understood within the context in which they are used (Hodges 2008), clearly stating the definition being used may aid in understanding of the many aspects related to LH.
(3) Choose metrics that measure heterogeneity based on its implications for response variables. There are several methods for quantifying LH (Li & Reynolds 1994), and adequate metrics should represent the presumed effect on the ecological processes involved. Although heterogeneous landscapes are generally more fragmented in human-dominated regions, the use of metrics that are proxies of landscape fragmentation (e.g., patch and edge density and patch richness; Fig. 2) might not quantify LH in its totality. For example, a landscape with a high number of forest patches and high edge density (and therefore a high level of configurational LH) can have an uneven distribution of the forest patches in the different land-cover types, leading to a low value of compositional LH. In contrast, metrics that consider both the number and the proportion of landscape units, such as the Shannon and Simpson diversity indexes, might be more suitable, as they can represent both the configurational and the compositional aspects of LH (McGarigal & Marks 1994). As discussed, there are several ways to quantify LH components, and selecting metrics that quantify composition or configuration may be difficult. Therefore, researchers should clearly state which component is being addressed, the metrics being used as proxies of LH and the reasons why the predictors are expected to affect the response variable(s) chosen. Nonetheless, deciding on the appropriate metrics depends directly on the definition of LH and its components.
(4) To improve communication and provide adequate interpretations of results, authors should clearly state the effect of LH (based on the adopted definition) on the phenomenon of interest (dependent variable). The literature on LH is highly diverse and is already represented by hundreds of articles. However, we believe that a certain level of standardization of terminologies and concepts related to LH may enhance the ability of the scientific community to communicate such findings and translate the knowledge produced into decision-making actions.
(5) Clearly stating the scale and resolution used is fundamental when comparing and interpreting LH. The appropriate scale should be selected to represent the phenomenon of interest (e.g., species richness, fire incidence). For instance, Duflot et al. (2016) investigated the effects of LH on carabid beetles by establishing 1-km-edge squares based on the home range of the focal group. In addition, we suggest a multiscale approach to evaluate the scales of effect of the investigated parameters on dependent variables (Tscharntke et al. 2005, Jackson & Fahrig 2015), as the effect of LH on biodiversity at small scales (e.g., a local field) may be different from that at larger scales (Weibull et al. 2000, Chust et al. 2003). Moreover, studies that investigate LH over different time periods could benefit from employing the same scale and resolution to support comparisons over different periods. Although arbitrary delimitations may appear to have no scientific basis to assess ecological responses, LH measures in such extents are useful for supporting public policies related to biodiversity and ecosystem services such as watershed management (Qiu & Turner 2015).
(6) Research that focuses on the functional perspective of LH should be promoted. Because movement abilities and resource exploitation differ between taxonomic groups, functional components of landscapes provide useful approaches to investigate organisms from a functional perspective (Fahrig et al. 2011, Tscharntke et al. 2012). However, as functional LH requires information on how different land-cover types influence species demographic and behavioural processes, its application is not a trivial task. Moreover, subtle differences in land-cover types that are not apparent to humans and/or remote sensors may also affect species preferences and dispersal (Fahrig et al. 2011; Box 1). Despite the potential of functional LH to improve our understanding of how species interact with their environments, structural LH is easier to quantify as it uses a series of metrics that are commonly applied as proxies of biodiversity (Duelli 1997). The low number of studies that have employed a functional approach in LH analysis (Fig. 1) also indicates a research gap that should be addressed by future studies, especially as functional approaches can indicate how different land-cover types and their spatial arrangements affect both biotic and abiotic processes, such as species abundance and nutrient cycling.

By following these six suggested steps and considering the knowledge gaps identified, we believe that the literature on LH can become more cohesive and indicate more explicitly how patterns and processes are related to the different aspects of LH.

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