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RESEARCH ARTICLE

Integrating landscape ecology and the assessment of ecosystem services in the study of karst areas

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Abstract

Context A landscape is defined as a "system of ecosystems" and this is a model in which karst areas can easily be integrated. In karst areas, much of the connectivity between the units of the landscape is underground, with aquifers and caves forming a continuous layered tissue. However, underground environments are among the least studied landscapes on Earth because of limited accessibility and the difficulty of performing surveys.

Objectives The aim of this paper is to provide a conceptual framework for applying principles of landscape ecology to research on karst environments.

Methods By adapting the standard patch-corridor-matrix model to a 3d model, the main issues that need to be addressed were identified. These include identifying the main morphological (surface and underground) karst features; determining the landscape structure through its features, composition, and configuration; and developing adequate indices.

Results The landscape spatial structure of different karst areas influences fundamental ecological functions and biodiversity patterns. Determining how structure, biodiversity, and functions relate reveals important insights into the functioning of karst systems. Emphasizing the provisioning of ecosystem services is essential in supporting the concept that karst regions are vital for human well-being because they host valuable resources and fundamental ecosystem processes. The paper discusses how this framework helps address anthropogenic impacts and conservation issues on karst.

Conclusions The potential of applying a landscape approach to karst systems lies in developing models that provide ecological information relevant to understanding karst systems and understanding their implications for natural resources management.

Keywords Subterranean biology · Subterranean habitats · Caves · Landscape pattern · Sustainability

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Introduction

Karst environments are systems with peculiar geomorphological and hydrogeological characteristics and are considered some of Earth's most fragile natural systems (Brinkmann and Parise 2012). Karst areas represent approximately 15% of the world's terrestrial zones, and they host valuable resources such as water, soil, and vegetation, providing habitats for several animal species, both epigean and hypogean, many of them being rare or endemic (Ford and Williams 2007; Williams 2008; Mammola et al. 2019). Simultaneously, almost 17% of the human population lives in karst areas, and 25% of them rely on groundwater (Ford and Williams 2007; Goldscheider et al. 2020), making these areas very valuable.

Terrestrial systems are generally represented as a mosaic of *surface elements*, but in karst areas the three-dimensional development of underground environments has a strong ecological relationship with the surface. In karst environments, a large part of the connectivity between the landscape units extends underground, with aquifer systems and empty spaces forming a continuous tissue developed on several levels (Helf and Olson 2017). A "system of ecosystems," as the landscape is defined (Forman 1995a), is a model in which karst systems, and in particular underground karst, can easily be integrated. Accepting this model would allow the development of a holistic approach that involves rethinking the protection of caves, which should not be considered isolated environmental units, as defined in many environmental policies. For example, the EU Habitats Directive is the main European legislative framework for the conservation of habitats (Directive 1992/43/EEC) and governs the protection of caves as a distinct and self-contained habitat, distinguishing them from the rest of the karst landscape ("Caves not open to the public," Natura 2000 code: 8310; "Fields of lava and natural excavations," Natura 2000 code: 8320; "Submerged or partially submerged sea caves," Natura 2000 code: 8330).

National or regional cave registers are a typical tool used to designate caves and are sometimes available as online databases or publications (see, e.g., Price 2014; Ferrario and Tognini 2016). Cave registers are usually systematic collections of information about the location and characteristics of caves, and they are the basis for protection measures in the territory. The term "cave," however, is variably defined in different countries and by different authors. The International Union of Speleology (https://www.uis-speleo.org/) defines caves eligible to be cataloged in official registers as cavities with a horizontal or vertical development exceeding 5 m and a planimetric development /entrance width ratio > 1, provided they are large enough for human beings to enter. This is a human-based, or cavers' definition; from a geological point of view, caves are connected voids formed by different "underground processes" (excluding rock primary porosity), whatever their dimensions. Caves can therefore be defined by their genesis (i.e., created by mechanical processes such as collapse or erosion, by chemical dissolution, by volcanic processes, etc.). Despite these differences, the common theme linking the various kinds of cavities is their interest to human explorers and their use as habitat by cave-adapted organisms (White and Culver 2011). Whatever definition of caves is adopted, considering caves as "single elements" is insufficient for their protection, as this hampers the capacity to implement effective conservation of these environments and associated resources.

It has sometimes been assumed that caves are isolated elements because populations of cave-adapted organisms can be extremely isolated (Culver 1970; Snowman et al. 2010; Balogh et al. 2020), although there is growing evidence of extensive gene flow between karst systems (Buhay and Crandall 2005). Cave entrances are critical for human access, they typically occur as a chance intersection of an evolving underground environment with the surface (Culver and Pipan 2019) and represent only a small portion of a cave system. In fact, cave entrances can be too small for human access or be absent. As an extreme example, caves without entrances include the Scot Hollow Cave in West Virginia (Lane et al. 2018) and the Pestera Movile Cave in Romania (Sarbu et al. 2019), and many other caves with no entrance have been discovered by drilling or mining activities. The network of fissures, joints, and bedding planes, the epikarst, the interstitial habitats, the shallow subterranean habitats, and the "*milieu souterrain superficiel*" (see Box 1 Glossary) should be considered together with caves and other underground voids, as they contribute to the complex system of a karst landscape.

Given the vulnerability of these environments and the complex interconnections between karst landscape elements, it is crucial to shift the attention to the landscape level. This paper discusses how landscape ecology can contribute to the study and conservation of karst areas, paying specific attention to the underground domain. It addresses the classification of karst landscape elements and how landscape metrics could be further developed for a better description of karst landscapes and considers the fundamental aspect of the relationships between landscape structure, biodiversity, and ecosystem functioning. Finally, it discusses the ecosystem services of karst areas and the implications for karst conservation.

BOX 1 Glossary

Bedding planes: The surfaces separating a layer of a sedimentary rock from the preceding and successive one

Blind and dry valleys: A blind valley is a river valley originating abruptly from a karst output or spring; a dry valley is a river valley in which the water disappears underground via a stream sink or swallet, or by leakage to a cave below

Epigean: Pertaining to the surface domain

Epikarst: The uppermost weathered zone of carbonate rocks

Habitat biophysical structure: The physical structure of a habitat consisting of biotic elements such as vegetation and abiotic elements such as rocks, sediments, and minerals deposits

Hypogean: Pertaining to the domain below the epigean (also called underground or subterranean)

Interstitial habitats: Voids between sand or fine gravel grains that can be filled with water

Joint: A planar or gently-curving crack separating two parts of once continuous rock

Karst: A geologic region characterized by layers of carbonate (limestone and dolostone) rocks affected by karst processes (mainly chemical dissolution) pierced by dolines and underlain by caves and underground streams

MSS (*Milieu Souterrain Superficiel*): Underground network of empty air-filled voids and cracks developing within multiple layers of rock fragments (also called superficial underground compartment, Juberthie and Delay 1981)

Planimetric surface: A surface with representation only of the relative horizontal positions of elements, without topographic elements (i.e. elevation)

Sinkholes: Depressions in the ground that have no natural external surface drainage and where rainfall collects and typically drains into the subsurface. They are also called dolines and can be formed either by chemical dissolution processes associated with infiltrating rainwaters or by the collapse and breakdown of pre-existing caves

Speleothems: Cave formations of mineral deposits and cave sediments (e.g., stalactites, stalagmites, flowstone covering sediments.)

Spring: A natural flow of underground water from rock or soil onto the land surface or into a surface water body

SSHs (*Shallow Subterranean Habitats*): Aphotic subterranean habitats relatively close to the surface and consisting of the spaces between rocks. These habitats are more variable than caves, with a pronounced annual temperature cycle and a higher availability of organic matter. They contain species modified for subterranean life and species unique to these habitats, and are important gateways to the subterranean domain (Culver and Pipan 2014)

Vadose: Underground condition where voids are mainly air-filled, and only partly or occasionally water-filled. This zone is also known as the unsaturated zone. In the vadose zone, speleogenesis is mainly the result of free-running water from the surface. Vadose cave passages are typically underground canyons, vertical shafts, or domepits

Applying principles of landscape ecology to karst environments

Defining elements, mosaics and spatial patterns

A first step in describing a landscape is to identify its elements (Zonneveld 1989; Table 1). Karst landscapes occur when dissolution is the primary agent modeling the landscape (Culver and Pipan 2019). Because of dissolution, these landscapes have distinct features

Table 1 Morphological elements of the karst landscape in its different zones with indication of dominant processes and hydrology (see Fig. 1 for schematic representation karst landscape features)

Catchment zone	
Morphological elements:	Dominant processes:
- Covered or sub-soil karst: solution, drawdown and suffosion dolines, sub-soil *Karren* (*Rundkarren*), *dent de dragon* (sub-soil pinnacles), karst corridors (*bogaz, zanjon*);	Chemical and biochemical corrosion, erosion, rainwater infiltration by diffuse and concentrated inflow, recharge by allogenic streams
- Uncovered or bare karst: micro and macro *Karren*, collapse dolines and shafts;	Hydrology:
- Macroforms and surface karst landscapes: dry valleys, dolines, uvala, cockpit karst, polygonal karst, cone karst, pinnacle and *tsingy* karst, *mogotes/ fengkong* karst, tower or *fenglin* karst, *clints and grikes* karst, ruiniform terrains, *giant grikeland*s, karstic canyons	Diffuse and/or concentrated inflow of surface waters, transfer to the endo-karst
Epikarst zone	
Morphological elements:	Dominant processes:
- Fractures and joints widened by dissolution, micro-conduits network	Chemical corrosion, diffuse karstic enlargement of fractures and joints, slow percolation to the underlying vadose zone
	Hydrology:
	Slow percolation to the endo-karst; casual concentrated flow through the largest micro-conduits
Unsaturated or vadose zone	
Morphological elements:	Dominant processes:
- Domepits and shafts created by slowly percolating water, waterfall shafts, underground canyons, breakdown rooms, vadose modification of phreatic morphologies, physical deposits (allogenic and autigenic sediments, snow and ice close to the entrances), chemical deposits (speleothems and cave minerals)	Mechanical erosion by flowing waters, condensation-corrosion processes, breakdown and gravity-related collapse processes, sediments and speleothems deposition
	Hydrology:
	Difference between fossil and hydrologically active zone/caves
	Dripping and progressive concentration of water flows; underground streams, waterfalls and lakes; rapid transfer of infiltrating waters to the phreatic zone
Epiphreatic or floodwater zone	
Morphological elements:	Dominant processes:
- Galleries and other water-filled zone corrosion morphologies, sediments deposition, corrosion and erosion of pre-existing speleothems, temporary or permanent lakes, temporary sumps and water-filled passages	Dominant mixing corrosion processes, some erosion processes, deposition and disturbance of sediments, some speleothems formation and erosion
	Hydrology:
	Rising of water from the phreatic zone, temporary flooding of cave passages, rapid water transfer to overflow springs, short water storage time
Saturated or phreatic zone	
Morphological elements:	Dominant processes:
- Underwater, or phreatic galleries, phreatic corrosion microforms	Chemical corrosion
	Hydrology:
	In the epiphreatic zone, slow water transfer to perennial springs (eventually buried); in the deep phreatic zone, very slow flowing waters, long term storage in the aquifer
	Very poor or nonexistent water auto-purification processes, but active processes of pollutant dilution, pollutant diffusion and progressive accumulation of pollutant flowing from the vadose or epiphreatic zone
Springs	

Table 1 continued

Morphological elements:	Dominant processes:
- Cave springs, blind valleys, temporary, perennial and overflow springs, buried springs. Dominant erosion morphologies, sometimes disturbance or re-deposition of pre-existing sediments, some speleothems formation in rarely active overflow springs	Mechanical erosion by flowing waters, some sediment transport and deposition Hydrology: Surface out-coming of underground waters

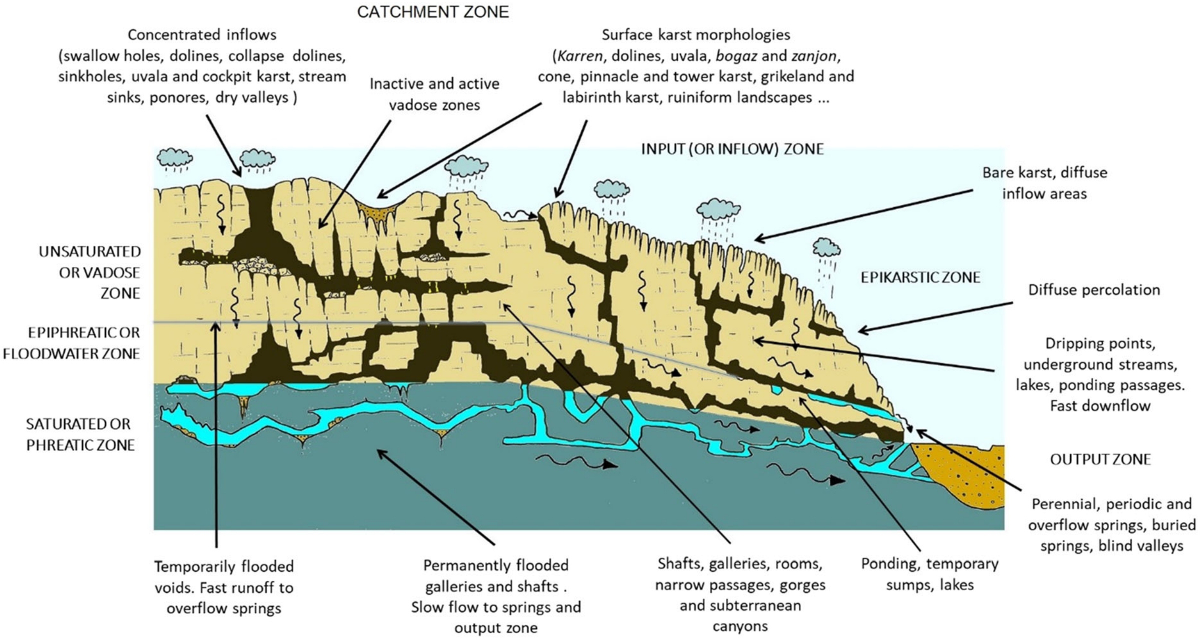


Fig. 1 Schematic representation of a karst landscape with surface and underground features

such as caves, sinkholes, springs, blind and dry valleys, and many others (Fig. 1, Box 1). Although karst elements are mainly created by chemical processes of rock dissolution, physical, biological, and microbiological processes also contribute to karst evolution. Indeed, karst environments are not the passive result of a reaction between water and rock, but they are the product of dynamic interactions between rock and a continuous flux of energy and matter in and out of caves (water, air, nutrients, etc.) at varying scales of impact. When describing a karst area, each element in the landscape can be characterized by recording specific features such as type, size, shape, origin, location, and function. The characterization of elements and their location in space leads to the definition of a mosaic of elements composing the landscape. By characterizing the karst landscape as an arrangement of various elements, fundamental landscape properties can be determined, such as composition, diversity of patch types, spatial configuration, fractal dimension, and arrangement complexity (Fig. 1). This helps describe landscape and elements patterns, scale, connectivity, networks, circuitry, or mesh size (McGarigal 2014), which are important features when analyzing landscape-scale ecological processes in an environment. For example, water drainage in karst is affected by several elements in the landscape, such as topographical features, water and topographic gradients, characteristics of input in the catchment area (diffuse/concentrated inflow) and the output zone (springs), and the characteristics and development of caves systems. Species dispersal is another landscape-scale process affected by the connectivity of elements and the presence and position of barriers (Verhoeven et al. 2017). Ecosystems are not isolated systems and cannot be understood without considering the flow of energy and material across their boundaries. Considering ecosystems as “open” systems requires an understanding of how mosaics of ecosystems interact and are spatially organized to affect ecological exchanges and ecosystem processes.

Scale

The identification of the appropriate scale of analysis is a core question in subterranean biology. The theory of scale and hierarchy is a key framework for understanding pattern-process relationships and became the basis for landscape ecology (Turner et al. 2001; Cushman et al. 2010), but it has rarely been applied to karst environments. Most studies focus on fine-scale features such as springs or caves (Herrando-Pea et al. 2008) and only rarely consider the whole karst basin as the scale of analysis. The relevant scale depends on the research aims and the system itself, as different problems require distinct scales of analysis and a multi-scale method is often required. Cave or microhabitat approaches may be useful for answering questions related to specific fauna requirements or adaptation (e.g., Ficetola et al. 2018), but an examination at the drainage system scale is required to address hydrological and macroecological issues and to understand how the links between multiple elements determine the processes occurring across the whole system.

Researchers in subterranean biology have been slow to take up the conceptual framework of the ecosystem (Odum 1953) mainly because of uncertainty related to the definition of size, inputs, and outputs of the subterranean ecosystems (Culver and Pipan 2019). This barrier has been partially overcome by studies showing the importance of drainage system-level analyses (Rouch 1977; Simon et al. 2007; Schneider et al. 2011). In a pioneering study, Gibert (1986) estimated the hydrological balance of an entire karst basin in France by reporting water evapotranspiration, runoff, infiltration, and output as a percentage of precipitation in the study area, revealing that infiltration was more than twice the surface runoff and was related to the ratio of basin covered by soluble or insoluble rock. He also estimated the yearly flux of components such as organic matter, indicating the relationship between the organic carbon entering and leaving the system (Gibert 1986). Nevertheless, studies assessing the flow across the whole drainage system remain scarce (examples include Jones 1997, on the karst hydrologic budget and Simon et al. 2007, on organic carbon flow).

Three-dimensional spatial metrics and their representation

The landscape is modeled as a patch-corridor-matrix planimetric surface (Forman 1995b), and it is therefore difficult to fit aspects of three-dimensional patterns into this concept. The necessity of considering a third vertical dimension in landscape analysis has been often highlighted (Hoechstetter et al. 2008; Wu et al. 2017). The two-dimensional representation limits the analysis because it does not allow the inclusion of ecologically meaningful structures, with a consequent loss of valuable information about landscape heterogeneity. Considering the three-dimensional geometries of areas opens up perspectives for a more realistic representation of structure elements (Hoechstetter et al. 2006). However, current studies mainly refer to surface terrain features such as roughness, landform, relief, or the vertical structure of vegetation (topography- or elevation-related features) (Dorner et al. 2002; Mücke et al. 2010). In karst areas, key information may be lost due to an inability to describe the landscape structure with appropriate three-dimensional metrics, and this is a particular problem for underground environments. For example, a flooded gallery should be characterized not just by its length and width but also by its height, sinuosity (i.e., curvilinear, rectilinear, ramiform—see Palmer 2012), volume (which may stock water), and wall roughness, and by the sediments and deposits that totally or partly choke it. Furthermore, elements of the underground environment occur at a given depth, and a z-value associated with the x and y coordinates is needed to determine their location in the space. Hence, it is essential to develop adequate metrics—which do not yet exist for karst areas—to capture the 3D-features of the elements. These metrics would provide a more realistic assessment of the landscape’s spatial structure, thus assisting a better understanding of karst patterns and processes (Stupariu et al. 2010). Subterranean environments require more sophisticated analysis methods than the 3D-landscape characterizations of the Earth’s surface performed using remote sensing

(Blaschke et al. 2004; Hoechstetter et al. 2008). Remote sensing is impossible in the subterranean domain, and new techniques are needed to overcome this limitation. Some of these have been tested, such as geophysical exploration combined with 3D laser scanning (Ba et al. 2020) or electrical resistivity tomography (Sono et al. 2020), but these techniques are generally expensive and need refinement before they can be broadly adopted.

Advantages and limitations in the study of underground environments

Karst landscapes have some peculiarities that assist or limit the investigation of the systems themselves. Factors making underground environments easier to study than their surface counterparts include the stability of many features and the fact that biotic characteristics are determined by a limited number of factors, such as distance from the surface and water availability. The distance from the surface determines temperature, light, and nutrient availability, while water is a primary driver for the occurrence of organisms and determines the movements of both biotic (species) and abiotic (sediments, nutrients) masses (Schneider et al. 2011; Lunghi et al. 2017; Ficetola et al. 2018). Moreover, underground environments have species-poor biotic communities because only a limited number of specialized species can thrive in these extreme environments (Romero 2009), which can make their description easier. Consequently, trophic networks are simpler (Gibert and Deharveng 2002), with primary producers and herbivores often missing and decomposers, predators, or parasites well represented (Mohr and Poulson 1966).

Limitations in investigating underground environments are related to difficulties in exploring, mapping, and collecting accurate data on geology, hydrology (Jeannin et al. 2007), and biodiversity (Ficetola et al. 2019). Mapping these environments is the first prerequisite for a reliable representation of the landscape and its characteristics. Direct explorations of underground realm may be costly and challenging because they require sustained efforts and complex organizational structures to support the activities and can be time-consuming, with even caves of a modest size requiring multiple trips (White 2019; see Box 2 Cave surveying).

In addition to mapping the underground elements, correlating their elevation with aerial photographs and using elevation controls such as geographic surface benchmarks help build the final map projected onto topographic overlays (Kambesis 2007). Direct mapping of underground environments also allows the recording of important information such as groundwater drainage, water flow rate, streams confluence, and cave morphologies and the occurrence of animals, fossils, speleothems, cave minerals, and sediments, allowing a greater understanding of cave origins and evolution, which is essential for underground systems investigation.

Indirect methods can help underground mapping and partially overcome surveying difficulties. For example, information on hydrology can be derived from dye-tracing techniques: a non-toxic dye (typically a fluorescent dye such as Tinopal or Uranine) is injected into a sink or a cave stream, and its arrival time and concentration are recorded at specific output points (springs). This technique, combined with geological and hydrological data, allows the catchment area and the output points of a karst system to be defined, together with throughput rates and recharge and storage amounts, to evaluate the system's vulnerability to pollutants. Indirect investigations may also involve air tracing, air pressure, temperature, and flow measurements in multi-entrance caves systems, to evaluate fluxes throughout the cave and energy exchanges with the surface. Indirect methods usually require physical cave exploration for sampling. Integrating direct exploration and indirect approaches may be helpful, and thus the possibility of using landscape surface characteristics to infer underground structures needs to be investigated. For example, spring outflow hydrograph and chemograph analysis, which correlates discharge, temperature, and water chemistry variations of a karst spring with input/rainfall in the catchment area, can help evaluate the degree of karstification and the main characteristics of a karst drainage system (e.g., large karst conduits drainage, i.e., well-karstified aquifers, versus diffuse drainage through poorly karstified joints, i.e., fissured aquifers) (Ford and Williams 2007).

Box 2 Cave surveying

Cave exploration requires the physical entering of cave passages, which can be narrow, vertical, wet, muddy, choked with boulders or sediment, or even completely water-filled. Cave surveying can therefore be very challenging, and very few electronic and automatic instruments work in such tough conditions. Hand clinometers, compasses and tape are still commonly used; cave drawings are handmade by surveyors, who normally work in teams of three as a minimum; and the data are later transformed into maps and sketches, so that surveying a long and complex cave system can be a very time-consuming activity. In a wide, horizontal, and easy cave, surveys normally require 8 to 10 h for every 500 m length, but in a difficult cave with vertical shafts or very narrow passages, the surveying speed is much slower and it may take several days to explore just a few meters. In recent years, new materials, equipment, and technologies have made cave exploration easier. The greatest improvement in the exploration of submerged caves has come from rebreathing, a diving technology that reduces the volume and weight of scuba tanks, thus increasing the explorer's autonomy. The rebreather technology has allowed distances and depths to be reached that were previously unthinkable. However, cave exploration remains extremely challenging and dangerous.

Integrating landscape ecology and assessment of ecosystem services in the study of karst areas

Landscape ecology is based on the principle that ecosystem composition, structure, and function partially depend on the spatial and temporal context of the ecosystem (i.e., its landscape context) so that ecological observations at any location are affected by its boundary conditions—that is, by what is around. This approach has been applied to various natural and anthropogenic landscapes, from tropical regions to agricultural areas and urban areas to deep oceans (Naveh and Lieberman 2013; Young et al. 2017). This paper proposes a framework to integrate landscape ecology principles (elements, mosaics, patterns, disturbances) with the study of karst areas, particularly the subterranean dimension (Fig. 2).

Biodiversity in karst landscapes

Ecological and evolutionary factors determine biodiversity in karst environments. Karst age, the cave's origin, past climate events (e.g., glaciation), and biogeographic processes have shaped the distribution of organisms, and the interplay between these factors is complex (see Mammola et al. 2015). The current distribution of organisms in underground environments largely depends on nutrient availability, water supply, light, or niche differentiation (Christman and Culver 2001; Lunghi et al. 2014). Subterranean species generally have narrow distribution ranges, which results in high spatial turnover in species composition across regions, with clusters of spatially structured populations that may evolve into new species (Zagmajster et al. 2018; Ficetola et al. 2020). The high endemism levels are related to the fragmentation of the subterranean habitats in karst landscapes and the long-term persistence and relative stability of subterranean environments (Gibert and Deharveng 2002). In this context, the analysis of habitat patch distribution can illuminate the evolutionary processes caused by the isolation of populations (Chiari et al. 2012).

Much of underground biodiversity is yet to be described (Manenti and Pezzoli 2019; Ficetola et al. 2019). In addition to identifying species, the modeling of their distribution in subterranean environments is a further task of primary importance (Mammola 2018). How organisms interact with the landscape depends on their needs and on the characteristics of the landscape itself. Landscape elements can represent both barriers and corridors for movement. Some cave organisms need to live in underground habitats for their entire life cycle (troglobites and stygobites), while others enter or live in caves for specific needs (troglophiles). The movements of these organisms are determined by landscape characteristics. The composition of the matrix and how patches are arranged within the space may determine isolation (Chiari et al. 2012) or aggregation (Biswas 2010) of animal populations, and this influences genetic exchanges and interspecific interactions, which have consequences for the survival of populations. It has been observed that the extinction of cave-dwelling metapopulations depends on the

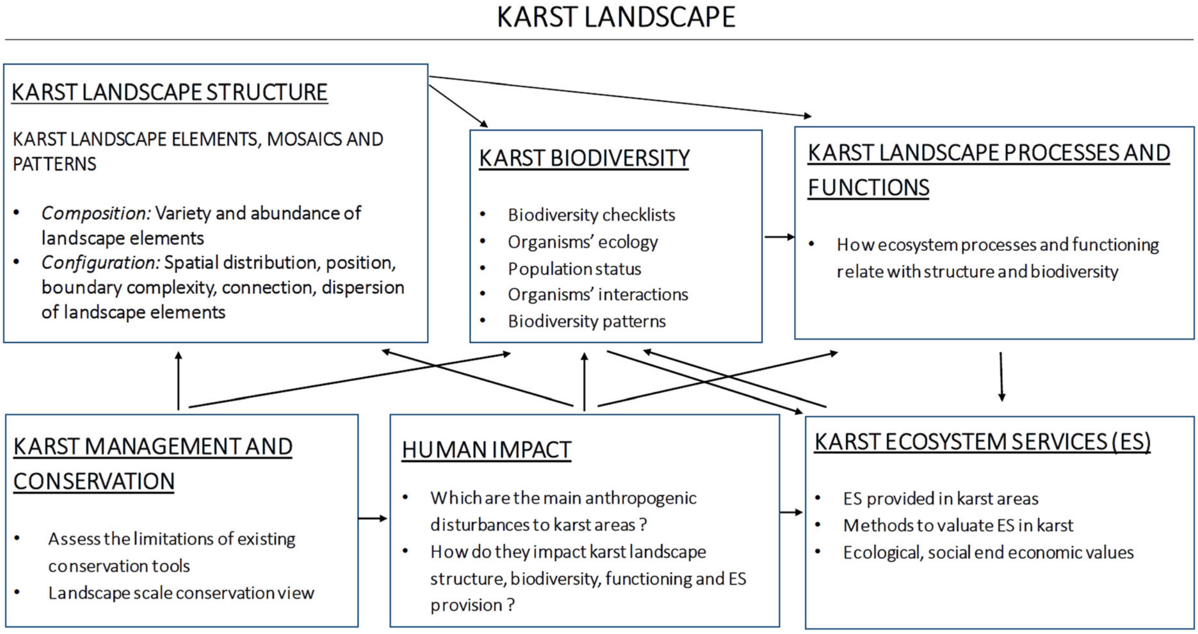


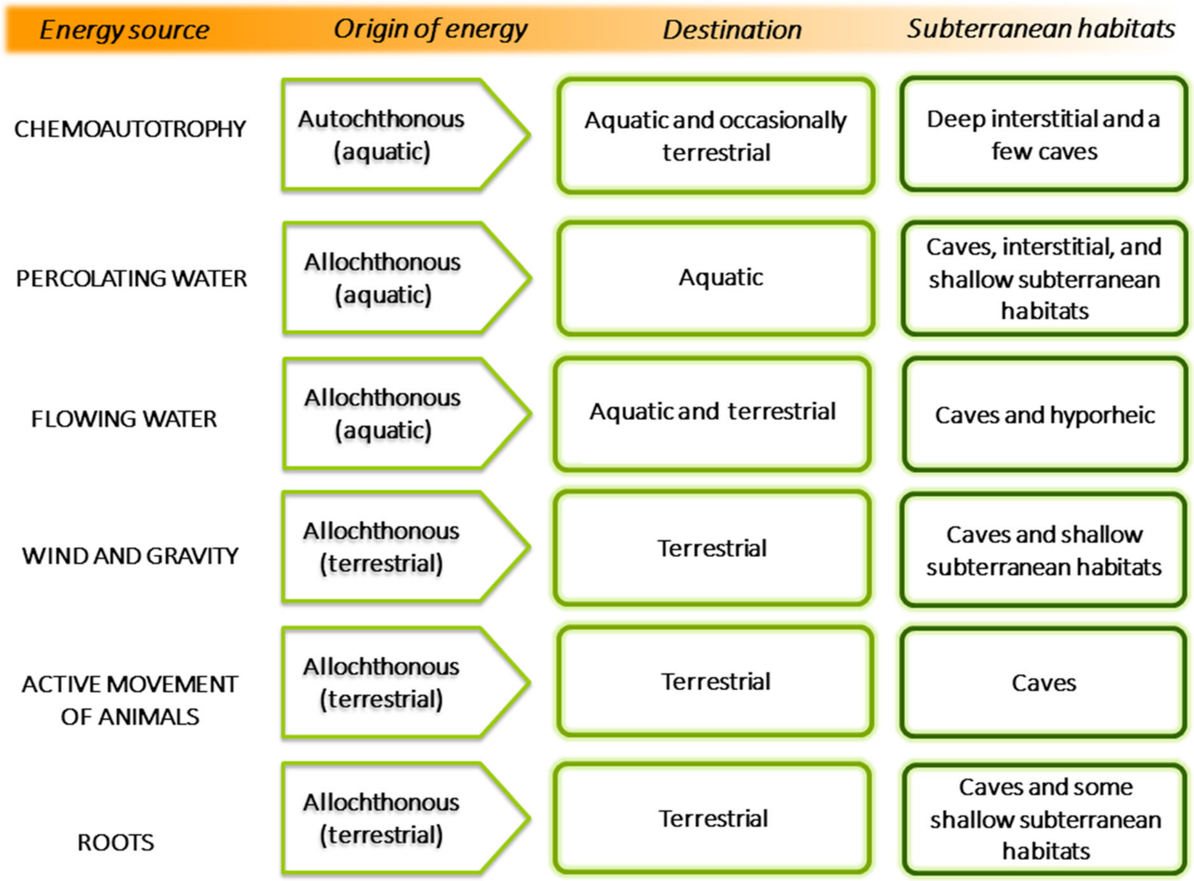
Fig. 2 Framework to integrate landscape ecology and the assessment of ecosystem services (ES) in the study of karst areas (arrows indicate 'effect', either positively or negatively)

complexity of the network, particularly on the size and spatial arrangement of habitat patches, together with species movement (Campbell Grant 2011).

There is a growing interest in relationships between subterranean habitats and biodiversity (Zagmajster et al. 2018). The diversity of subterranean species is determined by the interplay between productivity, habitat availability, spatial heterogeneity, energy production, and climate suitability (Eme et al. 2015). The overall diversity tends to be higher in regions characterized by high surface productivity (Culver et al. 2006) and high density of caves (this can be an effect of higher habitat availability, or of better sampling) (Christman and Culver 2001; Christman and Zagmajster 2012; Ficetola et al. 2014; Niemiller et al. 2021). However, additional factors can increase the richness of subterranean species, including habitat heterogeneity (Sket et al. 2004) and regional species richness (Malard et al. 2009), highlighting the importance of landscape context in biodiversity patterns. Nevertheless, biodiversity patterns are also influenced by subterranean dispersal (Culver and Pipan 2019), which is determined by the arrangement and types of landscape elements. Understanding the connectivity of landscapes requires data on specific dispersal behaviors and pathways in subterranean systems that are often lacking. For large animals such as bats, the general capacity of permeation in a landscape is known, and barriers are readily detectable (Furey and Racey 2016), but for terrestrial arthropods, water-dwelling animals and microorganisms, there is not enough knowledge available.

Landscape structure and ecosystem function in karst environments

The relationship between ecological functions and spatial patterns is a key theme of landscape ecology that helps inform land management practices. This approach may also shed light on the functioning of karst landscapes. In karst landscapes, material and energy flows follow complex pathways that are not always fully understood. Generally, water occurs at the surface and enters the subterranean system at the rock-soil interface, following vertical and horizontal pathways (e.g., Helf and Olson 2017). The biophysical structure of habitats influences many ecological processes. Water flow, water storage, rock erosion and dissolution, speleothems and sediment deposition, organic matter accumulation, nutrient flow, rate of photosynthesis close to the entrances, air-flow, organisms' niche availability, and organisms' movements



Energy source	Origin of energy	Destination	Subterranean habitats
CHEMOAUTOTROPHY	Autochthonous (aquatic)	Aquatic and occasionally terrestrial	Deep interstitial and a few caves
PERCOLATING WATER	Allochthonous (aquatic)	Aquatic	Caves, interstitial, and shallow subterranean habitats
FLOWING WATER	Allochthonous (aquatic)	Aquatic and terrestrial	Caves and hyporheic
WIND AND GRAVITY	Allochthonous (terrestrial)	Terrestrial	Caves and shallow subterranean habitats
ACTIVE MOVEMENT OF ANIMALS	Allochthonous (terrestrial)	Terrestrial	Caves
ROOTS	Allochthonous (terrestrial)	Terrestrial	Caves and some shallow subterranean habitats

Fig. 3 Classification of sources and origins of energy and their destinations in subterranean environments (source: Culver and Pipan 2019)

(Lunghi et al. 2017) are all examples of these processes. A general pattern of the source of energy and its destination in subterranean habitats is presented in Fig. 3. Temporal and spatial dynamics are also fundamental factors (Turner 1990). For example, flooding dynamics determine community changes and affect the overall flux of materials such as sediments or organic matter (Simon and Benfield 2001). Moreover, karst landscapes are formed by geochemical processes that are generally ongoing because of water flow, and the morphology of the rocks is therefore reshaped continuously as a result of continuous dissolution, new rock formation, or changes in hydrological regimes.

Biodiversity influences ecosystem functioning and determines many fundamental ecosystem processes, including water purification or nutrient cycling (Mace et al. 2012). However, it is still largely unknown how biodiversity sustains ecosystem functions and services in karst areas. Certainly, functional diversity is central to understand ecosystems functioning. It can be measured by the diversity of functional traits of a community and is of primary ecological importance because it influences ecosystem dynamics, stability, productivity, nutrient balance, and other aspects of ecosystem functioning (Tilman 2001; Cadotte et al. 2011). Functional diversity can explain variation in ecosystem function even when species diversity does not, thus offering crucial insights (Cadotte et al. 2011). The functional diversity of subterranean environments has rarely been studied, but it can reveal unexpected patterns. Confounding the expectation of lower functional diversity in such a harsh environment, Fernandes et al. (2016) demonstrated that cave isopods (Oniscidea) show higher functional diversity compared to surface taxa, possibly because they find more suitable conditions, including lower predation pressures and greater water availability, and this promotes their distribution and diversification. Knowing the functional diversity of organisms is fundamental because it is one of the most effective predictors of ecosystem functioning (Song et al. 2014). The growing availability of theoretical and technical frameworks and the development of trait databases for animals and microorganisms enable a greater understanding of underground functional diversity (Moretti et al. 2017; Nguyen et al. 2016; White et al. 2020), but there is still a significant gap in knowledge concerning the traits and ecology of cave organisms.

Karst ecosystem services

Ecosystem services (ES) are defined as the goods and services deriving from ecosystems that contribute, directly or indirectly, to human well-being (MEA 2005). The recognition, evaluation, and monitoring of these benefits may offer new empirical and conceptual tools that can be combined with more traditional approaches (e.g., the establishment of protected areas and endangered species protection) to support the management of natural systems and promote sustainable human development (Müller et al. 2010). For these reasons, an integrated assessment of the ES of karst environments should be a primary goal for conservation. The almost total absence of such studies makes such assessments urgent (however, see ES approach to karst areas by Žujo and Marinšek 2012; Quine et al. 2017; Wang et al. 2019). This paper provides a list of *potential* ES provided by karst areas, indicated separately for surface and underground environments (Table 2). Underground karst supports many services, providing water and genetic material from species, regulating water fluxes and chemical and biological conditions, transforming biochemical and physical inputs, and regulating and maintaining abiotic and biotic factors overall. Other important services deriving from underground environments are related to the cultural dimension of humans and, although undervalued, cultural ecosystem services are essential for human health and well-being (Bratman et al. 2019). Cultural benefits derived from the exploitation of natural environments include outdoor and recreational activities and the aesthetic appeal of calcareous forms, fossils, and underground spaces. Furthermore, cave settings encourage social gatherings and human interactions both for sport and scientific purposes, and interactions with the natural environment shape people's sense of personal identity. The physical, mental, and cultural enrichment that can be achieved in caves makes them some of the most intriguing environments on Earth (Fig. 4).

Several studies have reported that the evaluation of ES is an effective practical strategy for environment conservation. It is used to prioritize key biodiversity areas for conservation (Shrestha et al. 2021), to identify conflicts between nature conservation and human societies (Setälä et al. 2014; Bezák et al. 2017), and to inform conservation planning (Mitchell et al. 2021). These insights can be included in strategic environmental assessments (tools supporting decision-making to make sustainable territorial plans; Semeraro et al. 2021) or can even be integrated into economic decision-making (Banerjee et al. 2020; Yang et al. 2020). Finally, the ES approach ensures that the complex relationships between nature and humans are clearly understood and explicitly stated, promoting solutions that balance the existence of human societies with nature (Luck et al. 2009; Beaumont et al. 2017). However, the current measures of services fail to capture adequately the benefits humans derive from karst areas.

Human impact and opportunities for karst conservation

Landscape dynamics occur over temporal and spatial scales: evolution and geological processes act over long timespans, colonization and reproductive processes act over medium to short timescales, and local disturbance processes can have immediate consequences. Among local disturbances there is the human impact that can alter landscape context and biodiversity. Impacts on underground environments and processes include land use and land cover change, pollution of soil and water, water pumping, mining and quarrying exploitation, rock excavation for underground infrastructures, modifications of conditions of underground water drainage, and disturbance and poaching of fauna.

While human activities can foster conservation in the subterranean environment, they can also determine impacts if not correctly managed. For example, cave tourism and caving entail people entering caves, which are extremely fragile environments. Direct experience

Table 2 Ecosystem services (ES) provided by karst areas: "Section" reports the main groups under which ES are divided; "Division" reports the type of ecosystem services

Section	Division	Description	Literature examples for karst areas	Surface	Underground
Provisioning (Biotic)	Biomass	Any crops and fruits grown for nutritional purposes, livestock, food and materials from wild plants and animals, plants and animals materials used as a source of energy	Allocca et al. (2018), Bonsall et al. (2016), Coxon (2011), Huang et al. (2008)	●	
	Genetic material from all biota	Genetic material from wild plants, fungi or algae; Seed collection; The genetic information stored in wild animals	Riddle et al. (2018), Yoshizawa et al. (2018), Magnabosco et al. (2018), Culver and Pipan (2014)	●	●
Provisioning (Abiotic)	Water	Drinking water, surface water that we can use for different purposes other than drinking, water that can be used as a source of energy, natural inorganic materials that can be used as an energy source (in some areas of the world)	Griebler and Avramov (2015), Siebert et al. (2012), Ford and Williams (2007)	●	●
Regulation and Maintenance (Biotic)	Transformation of biochemical or physical inputs to ecosystems	Mediation of pollutants or toxic substances of anthropogenic origin by organic processes such as decomposing pollutants; Reducing noise and visual screening	Heinz et al. (2009), Iannace and Trematerra (2014)	●	●
	Regulation of physical, chemical, biological conditions	Regulation of baseline flows and extreme events such as control of soil erosion, buffering mass movement (avalanches), control of water flow (flood, coast protection), protection from wind	Guerra et al. (2017)	●	●
		Lifecycle maintenance and habitat: Maintaining nursery populations and habitats for species spending at least part of their life cycle underground (including gene pool protection)		●	●
		Pests and invasive species control, diseases control	Kunz et al. (2011), Medellín et al. (2017)	●	●
		Regulation of soil quality, ensuring soils formation and development, decomposition and fixing processes of organic matter	Wang et al. (2019)	●	●
		Control of the chemical quality of fresh- and salt water by biological processes	Zhang et al. (2016), Pronk et al. (2009)	●	●
		Regulation of global climate through chemical composition of atmosphere and oceans, regulation of the physical and chemical quality of air for people	Cao et al. (2018), Cao et al. (2016), Jianhua et al. (2012)	●	●

Table 2 continued

Section	Division	Description	Literature examples for karst areas	Surface	Underground
Regulation & Maintenance (Abiotic)	Transformation of biochemical or physical inputs to ecosystems	Mediation of pollutants, toxics and other nuisances by abiotic processes: dilution of pollutants by freshwater, filtration, sequestration, storage, accumulation; mediation of nuisances by abiotic structures or processes		●	●
	Regulation of physical, chemical, biological conditions	Regulation of baseline flows and extreme events: mass flows, liquid flows, gaseous flows		●	●
		Regulation of life conditions by the maintenance of physical, chemical and abiotic conditions	Zhang et al. (2007)	●	●
Cultural (Biotic)	Direct, in-situ and outdoor interactions with living systems that depend on presence in the environmental setting	Physical and experiential interactions with natural environment, enjoyment through active/immersive interactions and passive/observational interactions: sport and recreation, watching plants and animals, using nature to destress		●	●
		Intellectual interactions with natural environment: investigating nature, studying nature, which enable education and training	Wang et al. (2019), Mammola (2018), Groves et al. (2018), Soares and Niemiller (2013), Reboleira et al. (2011), Stokes et al. (2010), Juan et al. (2010)	●	●
		Characteristics of living systems that are resonant in terms of culture or heritage	Robert (2017), Algeo (2004)	●	●
		Characteristics of living systems that enable aesthetic experiences		●	●
	Indirect, remote, often indoor interactions with living systems that do not require presence in the environmental setting	Elements of living systems having symbolic meaning (like national or local emblem) or sacred or religious meaning (spiritual importance for people); nature used to make films or to write books	Doorne (2000), Buffetrille (1998)	●	●
		Other biotic characteristics having a non-use value: characteristics or features of living systems that we think have an intrinsic, existence or bequest value		●	●

Table 2 continued

Section	Division	Description	Literature examples for karst areas	Surface	Underground
Cultural (Abiotic)	Direct, in-situ and outdoor interactions with natural physical systems that depend on presence in the environmental setting	Physical, experiential, intellectual, representative interactions with natural abiotic components of the environment: ecotourism, recreation	Groves et al. (2015), Parise (2011), Kim et al. (2008), Safarabadi and Shahzeidi (2015)	●	●
	Indirect, remote, often indoor interactions with physical systems that do not require presence in the environmental setting	Spiritual, symbolic and other interactions with the abiotic components of the natural environment having values of identity, cultural meaning; Bequest value for future generations	Smith (2004)	●	●

In the table a brief description of the services is reported as defined by the Common International Classification of Ecosystem Services and some examples of these services are described for karst areas. Surface and underground are intended as *potential* ES provision, depending respectively on land use type for aboveground karst and underground specific characteristics for belowground (simplified from CICES V 5.1 classification; Haines-Young and Potschin-Young 2018)

of subterranean environments enhances people's awareness, ecological knowledge, and connection to nature, and this can result in respectful behavior and environmental stewardship. At the same time, tourists may negatively impact cave habitats by changing microhabitat availability (e.g., with light or the creation of pathways), continuous treading, the introduction of alien species, acoustic pollution, and direct disturbance resulting from people touching speleothems and animals (Mammola et al. 2017). Similarly, caving is fundamental for exploring the underground environment, recording biodiversity data or enhancing speleologists' knowledge, and caving associations are often the first promoters of cave protection. However, this activity can be invasive if cavers' behavior is not regulated. Luckily, most cavers and speleologists regulate their activities, abandoning explorations if there is a danger of damaging speleothems or preventing visits to bat-inhabited caves when the bats are hibernating or nursing. However, the trade-offs between cave exploitation by humans and cave protection can be complex and require careful evaluation.

Despite the close dependence humans on karst, protection policies are often absent, incomplete, or ineffective at the landscape scale. As karst systems are intrinsically fragile environments with high connectivity among their elements, they would benefit from a landscape conservation approach that goes beyond the conservation of single caves or single cave species. Local conservation actions are effective on small scale but do not prevent landscape-level threats. This shift in perspective from "the site" to "the site embedded in a landscape" has profound implications for management. Landscape knowledge is the fundamental requirement when defining conservation priorities and regulating activities that may influence the landscape, and this can only be achieved by undertaking comprehensive landscape studies. For example, the European Landscape Convention has established landscape quality objectives and consequent recommended actions that could serve as models for other countries (Déjeant-Pons 2006). It is important to include social perceptions of landscapes and manage trade-offs between human activities and karst protection, ensuring the safeguarding of both. This aspect is of particular importance, as strengthening relationships between populations and their surroundings underpins sustainable development (Makhzoumi et al. 2011).

Conclusion

The potential of applying a landscape approach to karst systems lies both in developing models that provide ecological information relevant to the understanding of karst systems (spatial heterogeneity, ecological connectivity, ecosystem functionality) and in understanding the possible implications for resource management. A landscape ecology approach enables an understanding of the dynamics of the karst regions

Fig. 4 **a** Surface limestone landscape with typical karst morphology (Monte Grignone, Italy; photo by C. Canedoli); **b** Underground environment with narrow passages and calcite speleothems (Antro delle Gallerie, Valganna, Italy; photo by D. Corengia); **c** Cave diving exploration in a flooded passage about 300 m from the cave entrance (Sorgente del Torregione, Italy; photo by D. Corengia); **d** Cave fauna (gen. *Polydesmus,* photo by D. Corengia); **e** Cave polluted with garbage (grotta della Selva, Italy; photo by F. Merisio); **f** Tourism activity in caves (Buco del corno, Italy; photo by A. Ferrario)

and provides a rationale for improving their management and conservation. An adequate understanding of structure, biodiversity, and functioning of karstic systems and a greater awareness of their value through the quantification of benefits derived by humanity is of paramount importance for addressing the sustainable exploitation of the resources associated with them and promoting effective and large-scale conservation choices. The valorization of ecosystem services is here indicated as a way to implement karst protection for conservationists seeking to combine conservation and human development successfully.

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