Advancing Landscape and Seascape Ecology from a 2D to a 3D Science

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Landscape ecology has fundamentally changed the way ecologists view the world through a greater understanding of the links between spatial patterns and ecological processes. Until recently, landscape ecology has been largely a two-dimensional (2D) science focused on the spatial patterning of 2D planar surfaces rather than three-dimensional (3D) structures. Advances in high-resolution remote sensing technologies, such as laser altimetry, acoustic sensors, and photogrammetry now provide the capability to map complex ecosystem structure in three dimensions, creating more structurally realistic models of the environment. In the present article, we focus on high-resolution 3D structure, using terrestrial and marine examples to illustrate how state-of-the-art advances in landscape ecology achieved through novel data fusion, spatial analysis, and geovisualization of environmental data can provide new ecological insights. These examples provide a look to the future in landscape and seascape ecology, where continued progress toward a multidimensional science will fundamentally shift the way we view, explore, and conceptualize the world.

Keywords: habitat complexity, lidar, photogrammetry, remote sensing, 3D visualization

Landscape ecology, the study of spatial patterning and its ecological consequences, has markedly changed the way we understand and manage ecosystems (Wiens 2009). Over the past quarter century, landscape ecology has seen a meteoric rise from humble beginnings, in which it received much skepticism, to being its own distinct discipline, which is now pervasive throughout mainstream ecology (Turner 2005). Although the application of concepts and techniques from landscape ecology has greatly expanded our understanding of the relationship between organisms and the geometry of their landscapes—and, more recently, seascapes—the discipline is being revolutionized by the rapid advances in geospatial technologies and ecological informatics (D'Urban Jackson et al. 2020). Advances in high-resolution remote sensing systems and data processing are allowing us to quantitatively model the complex surface of the Earth, both above and below water, with greater detail and accuracy than ever before. In addition, biotelemetry devices (e.g., geotags, GPS collars, acoustic transmitters) that track individual animal movements in time and space (Tracey et al. 2014, Williams et al. 2020), combined with spatial analytical tools, provide an unprecedented opportunity to investigate the ecological importance of multidimensional landscapes and seascapes (Wedding et al. 2011).

Traditionally, landscape ecology concepts and techniques have been based on a two-dimensional (2D) view of the Earth, by which we mean a flat or planar surface, often conceptualized as a patch mosaic (Forman and Godron 1981) but sometimes as a continuous gradient (Cushman et al. 2010). As such, quantification of landscape structure has been dominated by the application of patch-based spatial pattern metrics applied to 2D maps (Lausch et al. 2015)—for example, land cover and habitat maps represented as spatial mosaics of discrete and internally homogenous patches. Developing largely from analyses of aerial photographs and Landsat data, the study of the ecological causes and consequences of 2D spatial patterning in landscape ecology has contributed greatly to our ecological knowledge (Newton et al. 2009). Landscape ecology studies, however, have often lacked, as well as overlooked, opportunities to incorporate important vertical variability across surface terrains when linking spatial structure to ecological function and change (Kent 2009, McGarigal et al. 2009, Lecours et al. 2016). Although low-to-moderate-resolution digital elevation models (DEMs) have been used for decades to provide insight into the 3D nature of landscapes, technological advances in remote sensing, data processing, and modeling that enable a 3D landscape ecology are accelerating a shift in research attention to the challenges of integrating and interpreting more of the true multidimensional complexity that exists in nature (Lausch et al. 2015, Frazier et al. 2019). In contrast to the conventional 2D planar surfaces, landscapes and benthic seascapes (and to a lesser extent pelagic seascapes) are increasingly represented as continuously varying spatial gradients, such as digital terrains and true 3D volumetric models (box 1; Lausch et al. 2015). Such

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Box 1. Shifting from 2D patch matrix to 3D gradient models in landscape ecology.

The patch-matrix model along with its associated pattern metrics have been central to the way that landscape ecology has advanced our understanding of pattern–process relationships. The patch-matrix model offers a simplified representation of surface patterns through a mosaic of internally homogeneous patches with discrete boundaries (figure 1). The recent resurgence of interest in a 3D representation of landscape structure, including the gradient model derived from continuum theory (Fischer and Lindenmayer 2006, McGarigal et al. 2009) is an attempt to broaden the perception of spatial heterogeneity in landscape ecology and ultimately to recognize species-specific responses and to better integrate ecological process-based variables (Lausch et al. 2015). The continuum model recognizes that a range of ecological processes may affect habitat suitability for different species through time, in a spatially continuous and potentially complex way. An additional benefit of the gradient approach to modeling spatial pattern is that it retains the captured heterogeneity and avoids subjectivity associated with boundary delineation and thematic designation associated with categorical habitat maps. Terrains, defined by spatial variation in elevation, are gradient models that can be quantitatively characterized with morphological metrics such as slope, aspect, curvature, and rugosity. These terrain metrics provide insight into the development of landscapes and seascapes over geologic timescales. Terrain also drives ecological variation on contemporary timescales, such as through the modification of microhabitat, surface hydrology, current flows, and biogenic structure. Terrain effects on faunal and floral composition, as well as ecosystem processes, are often substantial but difficult to account for using field measurements alone. As a result, there has long been a need for terrain-explicit ecological study, and 3D mapping continues to substantially contribute to this effort.

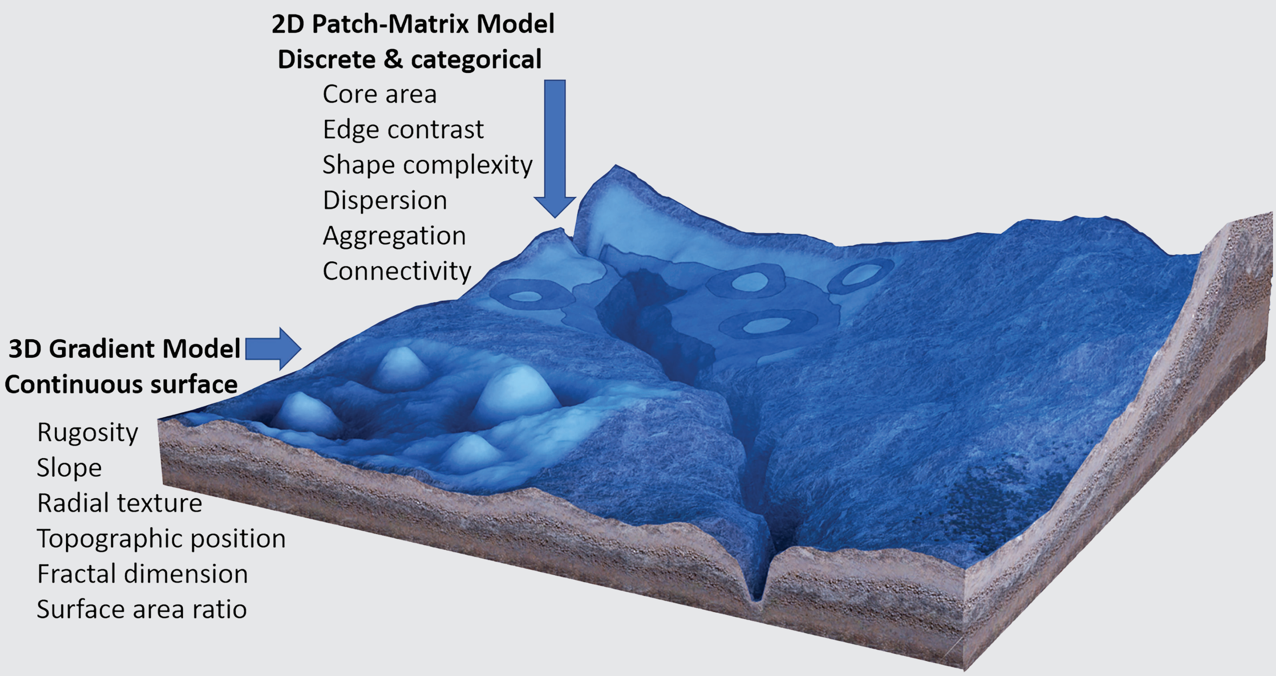

Figure 1. Earth surfaces represented as spatial constructs based on landscape ecology conceptual models. The patch-matrix model is quantified by patch metrics, and the gradient model is quantified by surface metrics (adapted from Pittman 2018).

3D representations enable quantification of ecologically important spatial variables, such as topographic complexity and surface morphology that influence the spatiotemporal dynamics of terrestrial and aquatic environments (Lecours et al. 2016, Zellweger et al. 2019). A rapidly emerging cross-cutting challenge in landscape and seascape ecology is the ecological interpretation of surface patterns across spatial and temporal scales, including the prediction of changes to those patterns and the ecological and social consequences.

For years, elevation information was derived through stereo pairs or radar interferometry that were of low spatial resolution and infrequent coverage. Today, however, 3D terrain data are widely available for many regions of the world, including global land coverage, in the form of DEMs, digital bathymetric models, and digital surface models, enabling the multiscale exploration and quantification of surface morphology for terrestrial and subaquatic terrains (i.e., lake or sea-bed bathymetry;

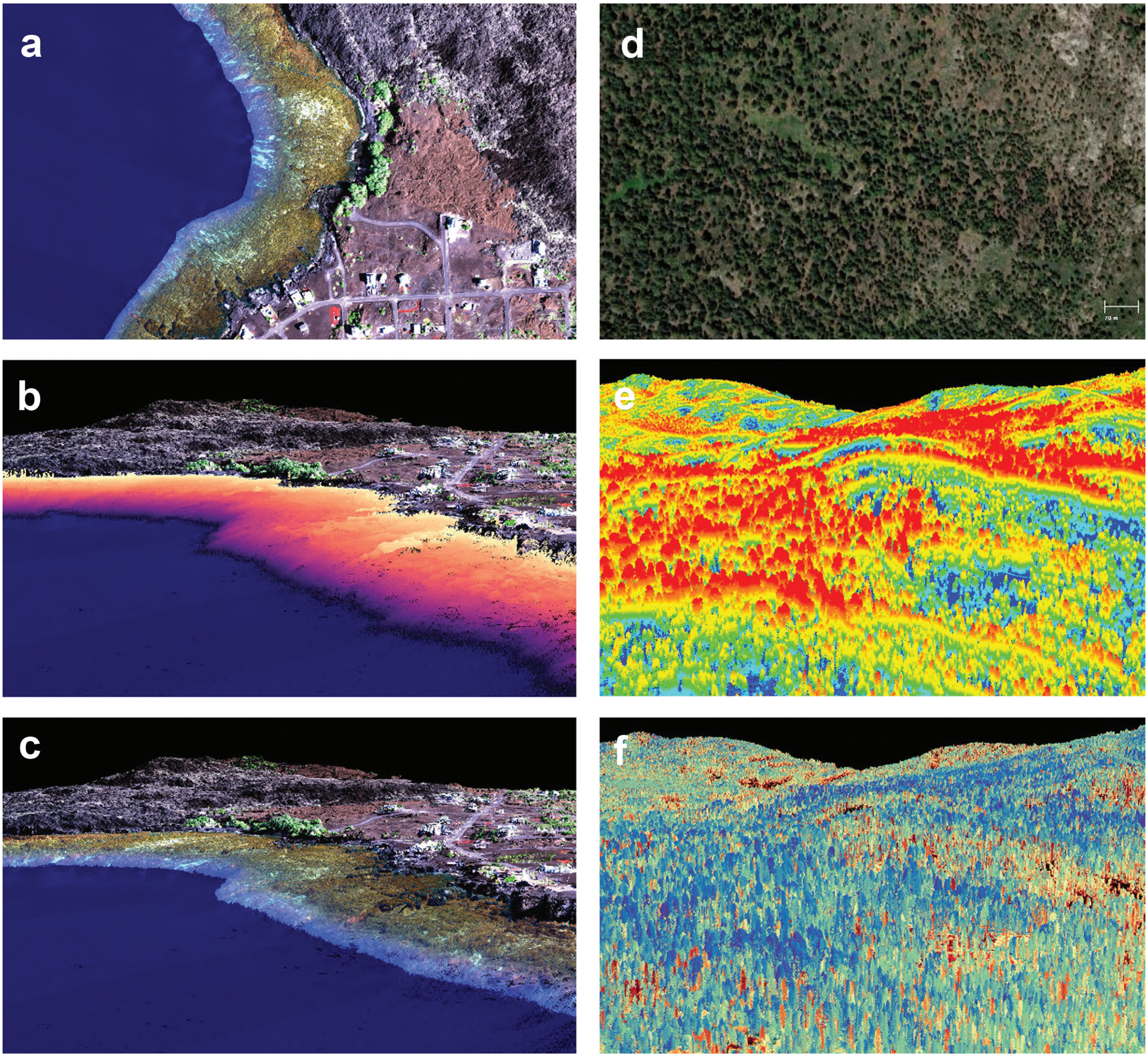

Figure 2. Examples of 2D and 3D data in Papa Bay, Hawaii and Sequoia National Park in California. (a) 2D three-color Global Airborne Observatory (GAO) image over Papa Bay, Hawaii, (b) 3D seamless land–sea terrain showing lidar-derived bathymetry and (c) ocean floor color (with water removed via models), (d) 2D three-color Google Earth imagery of a forest in Sequoia National Park, (e) 3D model of tree height from lidar data for the same region, and (f) canopy water content measured with GAO spectroscopy.

figure 2a–2f; Lecours et al. 2016, Florinsky 2017). For instance, open access to global land elevation data from NASA's Shuttle Radar Topography Mission, advances in satellite and ship-derived bathymetry and ongoing progress in the bathymetric mapping of the global ocean (e.g., Seabed 2030; Wölfl et al. 2019) are providing reliable data for enhanced environmental monitoring and ecological investigation on land and sea (Amatulli et al. 2018, Lyons et al. 2020). But, in general, information about the landscape and seascape in the vertical dimension has been underused in ecology, in part because of limited data availability, uncertainty around data quality, the coarse grain nature of the data, the dominance of 2D conceptual models, and the specialist analytical ability required for 3D data processing. What has been achieved, however, demonstrates that the integration, or fusion, of 3D information with other remotely sensed data across a range of spatial and temporal scales holds great potential

Box 2. What is lidar?

Lidar (for *light detection and ranging*) is an active optical sensor technique using a pulsed laser for measuring ranges (distance to surfaces) through the time taken to return reflected energy to the instrument (Weitkamp 2005). An airborne lidar sensor for terrain mapping generally consists of three operational components in addition to the laser ranger, a scanning mirror for directing the laser pulse, a GPS antenna and receiver for providing absolute position, and an inertial measurement unit for providing aircraft orientation. By mounting the lidar platform on an airborne platform, the forward motion of the aircraft and laser scanner allow mapping of the Earth's surface across space (figure 3).

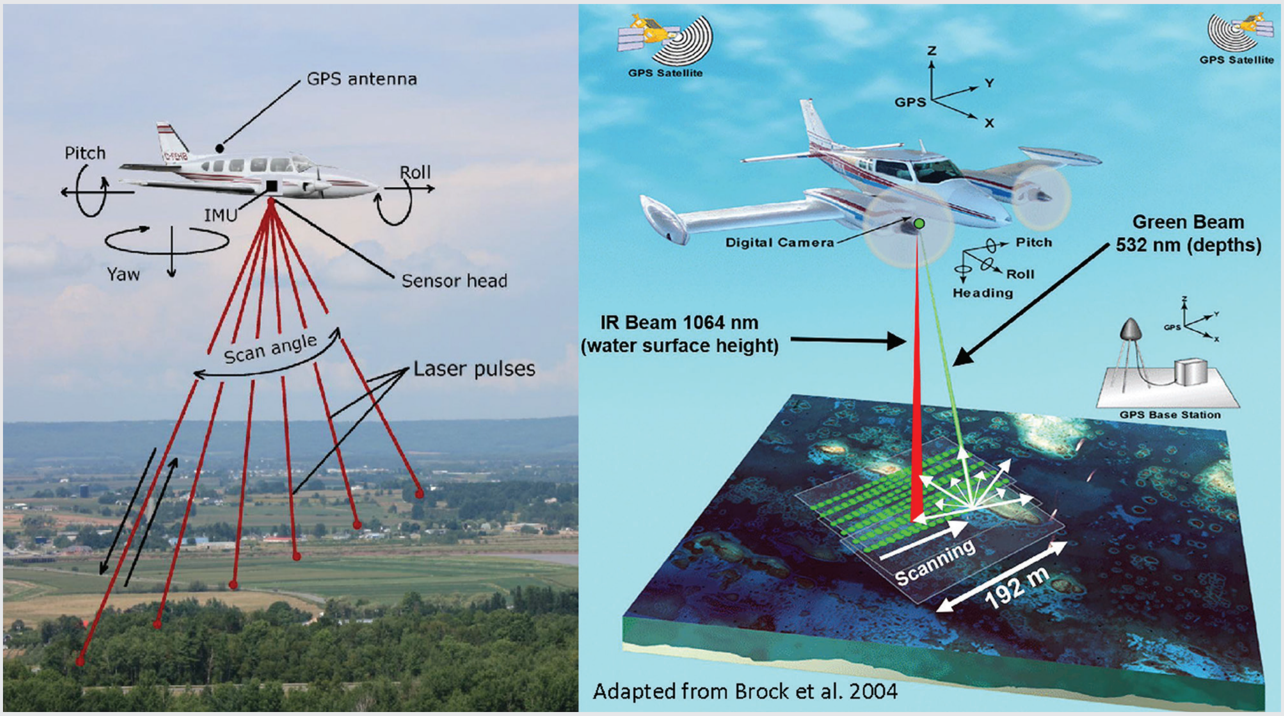

Figure 3. Schematic of a lidar sensor installed on a fixed wing airborne platform collecting observations.

The fundamental subsystem within a lidar sensor is the laser (light amplification by stimulated emission of radiation) ranger, which exploits properties of laser technology to measure the distance between the sensor and a target. Contemporary terrestrial lidar systems use ranging lasers operating in the near-infrared portion of the electromagnetic spectrum because of the reflective properties, minimal interference from ambient energy sources and eye safety considerations (Wehr and Lohr 1999). Typical lidar systems are capable of producing and recording over 500,000 pulses per second (500 kilohertz), which achieves a dense sample of the terrain. Lasers emitting energy from this portion of the electromagnetic spectrum tend to produce strong reflections from dry snow and vegetation, weaker returns from concrete and asphalt, and limited penetration of water.

Bathymetric applications typically use laser pulses in the near infrared (NIR) frequency as well the green frequency (half NIR, 532 nanometers). Bathymetry is obtained by differencing the range in NIR returns reflected from the water surface and the green returns, which penetrate to the seafloor.

Multiple returns and the full waveform increase the ability to discern and characterize surface complexity. Lidar systems are now carried on space satellites. For example, NASA's Ice, Cloud, and Land Elevation (ICESat-2) carries the ATLAS (Advanced Topographic Laser Altimeter System), a green wavelength, photon-counting lidar, for the global measurement and monitoring of terrestrial and shallow water terrain elevation with a primary focus on the cryosphere (Parrish et al. 2019).

to provide new ecological insights (Davies and Asner 2014, Calder et al. 2020).

The development of air, water, and space-borne lidar (for *light detection and ranging*; box 2; Lefsky et al. 2002), the ability to fuse lidar with other remotely sensed data, and the proliferation of low-cost aerial and water-borne vehicles capable of carrying multiple optical and acoustic sensors (Anderson and Gaston 2013, Wölfl et al. 2019) provides an opportunity to significantly enhance our ability to quantify 3D patterning in biological, geological, and anthropogenic components of the environment. For example, ultrahigh-density laser scanning from low altitude drones can resolve plant stem, leaves, and branch structures in 3D over large areas at relatively low cost to measure biomass, morphological traits, and structural change (Kellner et al. 2019). Image processing techniques such as structure from motion (SfM) and multiview stereo photogrammetry allow the creation of fine scale (millimeters to centimeters of spatial resolution) 3D surface models from 2D photographs and photo mosaics that are receiving rapid uptake with diverse applications in ecology and ecosystem monitoring (D'Urban Jackson et al. 2020). SfM is being applied to a wide variety of ecosystems, such as studying spatially and temporally heterogeneous forest canopies and semiarid ecosystems (Cunliffe et al. 2016), grasslands (Cooper et al. 2017), coral reefs (Casella et al. 2017), and mangroves (Feliciano et al. 2014). Introduction of 3D-capable data sources has wide ranging implications for ecological applications and estimating ecological processes, including carbon sequestration, quantifying habitat structure, mapping ecosystem services, and measuring and modeling consequences of climate change (Asner et al. 2012). For example, 3D models of vegetation structure can efficiently identify vegetation types, estimate above ground biomass and carbon storage, and enhance understanding of ecological functions (Cunliffe et al. 2016). In the marine environment, lidar and multibeam sonar derived terrain models combined with machine learning have enabled high performance predictive mapping of marine species and biodiversity at increasingly fine spatial scales (Pittman and Brown 2011, Wedding et al. 2019). Finally, as a monitoring tool, timely repeat collections of data to map 3D terrains can help operationalize adaptive ecosystem-based management (Camarretta et al. 2020). Given such widespread value and importance, we present examples of 3D data applications in terrestrial and marine environments to illustrate how state-of-the-art advances in landscape and seascape ecology have been achieved through novel data fusion, spatial analysis, and visualization of environmental data.

Measuring 3D structure

Three-dimensional structure can be readily quantified from DEMs derived from remotely sensed data (box 3). A wide range of metrics now exist for quantifying complex structure in digital surfaces with continuously varying height (i.e., surface gradients) and are beginning to demonstrate great utility in landscape and seascape ecology (McGarigal et al. 2012, Lecours et al. 2016). However, although some morphometrics (e.g., peak density, surface volume, and maximum peak height) have been considered analogous to some patch-mosaic metrics (e.g., patch density, percentage of landscape, and largest patch index; McGarigal 2013), it is becoming apparent that most surface metrics provide unique measures of terrain morphology, with many still lacking a meaningful ecological interpretation (Kedron et al. 2019).

The application of morphometrics has been most prevalent in the terrestrial environment, such as for quantifying forest structure (Lefsky et al. 2002, Hyde et al. 2005), modeling bird population density (Mason et al. 2003) and habitat (Wilsey et al. 2012), documenting ecological change to 3D forest community structure caused by invasive species (Asner et al. 2008), and comparing the effects of fire and herbivory on vegetation structure (Levick et al. 2009). It has been shown that animals respond directly and indirectly to 3D terrain and vegetation structure but with ecological responses varying both within and across species (Davies and Asner 2014). Likewise, in the marine environment, novel bathymetric measurements of the seafloor and ocean surface have led to new insights in marine animal ecology and have improved our understanding of coastal geomorphic change (Brock and Purkis 2009, Pittman and Brown 2011, Bouchet et al. 2015). Digital terrains offer great processing flexibility, facilitating exploration of scale effects through multiscale analyses with great promise in identifying focal scales and cross-scale interactions in ecological studies (Levin 1992, Pittman and Brown 2011, Lecours et al. 2016).

3D structural complexity in forest ecosystems

The architectural complexity of vegetation, particularly forests, and fine-scale field measurements of landscape topography have been incorporated into ecology for decades (MacArthur and MacArthur 1961, August 1983). Often readily measured proxies, such as diameter at breast height, stem height, or other morphological traits collected *in situ*, were generalized to stand level classes on the basis of species, allometric relationships, or spectral differences. With digital remote sensing, the vertical structure and other physical characteristics of vegetation have been measured and modeled by fusing data from active sensors (e.g., synthetic aperture radar) together with aerial images from passive optical sensors (Treuhaft et al. 2004). In addition, topographical information has been widely incorporated in ecological studies through species distribution modeling, the integration of geomorphometry with landscape ecology (Pike 2000, Ironside et al. 2018), and the analyses of relationships with landscape surface area estimates (Dorner et al. 2002).

Lidar now allows segmentation and classification of vertical vegetation structure at much finer horizontal and vertical resolutions than previously possible. Multiple measures of surface elevation and canopy structure allows characterization of ecosystem structural complexity, individual species morphology, improved bare earth elevation estimates, and the development of planimetric indices of vegetation canopy characteristics (Lefsky et al. 2002). Specifically, distributions of return locations in three dimensions (commonly referred to as *point clouds* in the lidar literature) representing

Box 3. Lidar-derived terrains and 3D surface models in ecology.

Remotely sensed data have been a cornerstone of landscape ecology, providing thematic maps of vegetation or land cover patterns, quantifying the spatial and temporal dynamics of biophysical states, and serving as inputs into social and biophysical models (Newton et al. 2009). Aerial photographs, multispectral and hyperspectral imagery, radar, and Lidar data have all been instrumental in deriving spatially explicit data relevant to ecological studies. Bare earth elevation data and 3D models of vegetation structure are increasingly being incorporated within landscape ecology studies to partition habitat suitability (Mason et al. 2003), to improve vegetation classifications (McCombs et al. 2003, Morris et al. 2005), and to improve areal estimates and associated patch metrics (Hoechstetter et al. 2008).

Bare-earth DEMs or digital terrain models provide estimates of the terrain elevation with vertical structures removed in the form of raster grids. Many useful topographic parameters can be created from DEMs (e.g., slope, aspect) that can provide insight into the topographic structure of the landscape and the resultant ecological patterns and processes. First-return DEMS, or digital surface models (DSMs; figure 4), are the surface elevation, including the tops of canopies, buildings, or ground where no features exist (Lloyd and Atkinson 2002, Andersen et al. 2006). DSMs can also be represented as full 3D landscape models with accurate measurements of ecosystem structure to which a wide range of animals respond, making these data effective predictors of biodiversity patterns (Davies and Asner 2014). Because of the flexibility of interpolation routines and availability of raw ground observations, lidar data can be used to create DEMs with varying horizontal resolution in order to address research involving scale dependent environmental variables (Anderson et al. 2005), and the ability to perform multiscale analysis is critical in many landscape ecology studies. The appropriate DEM horizontal resolution is dependent on the surveyed point density, range of 3D complexity at the study site, the scale of influence of the landscape for the process of interest, and the legacy scale of implemented modeled relationships. As a result, sensor, ecological considerations, and model origins must be accounted for when processing lidar data into DEMs.

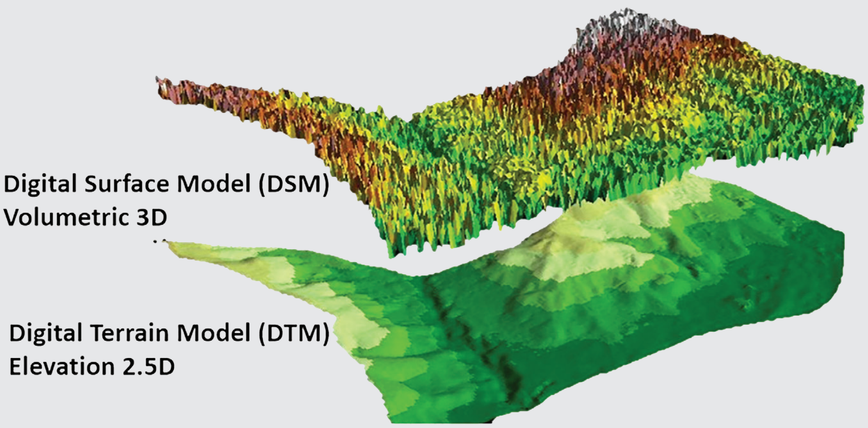

Figure 4. Example of a digital surface model versus a digital terrain model.

In addition to topographic information from bare earth DEMs, measures of forest canopy height provide estimates of canopy height, variance, and volume topographic variability with elevation trends removed. Lidar estimates of canopy height are generally based on differences between first return measures and bare earth estimates. Accuracy of canopy height estimates has typically been reported to be a function of sampling frequency (point density), land cover type, laser pulse intensity, flying height, and beam divergence (Andersen et al. 2006, Hopkinson 2007). Vertical canopy structure and morphology measures from lidar data are increasingly incorporated within ecological studies and often coupled with optical and other types of data to characterize forest and coral reef structure, classify land cover, and delineate habitat.

measurements of planimetric coordinates and elevation (3D coordinate tuple) can be visualized as voxels, a volumetric pixel, the 3D equivalent of a pixel (figure 5). In addition, voxels can be used to represent variability in the volumes' interior space, which cannot be done with conventional 2D polygons (Aijazi et al. 2013), thereby holding potential for modeling and visualizing the multidimensional structural properties of vegetation, buildings, and animal movement trajectories in time and space (Demšar et al. 2015, Chen and Xu 2016). Beyond the three spatial dimensions (x, y, z) and time, lidar also offers an additional dimension through the analysis of the intensity of laser returns, or backscatter, providing data on biophysical and chemical surface properties (Eitel et al. 2016). Furthermore, integrating passive optical imagery with

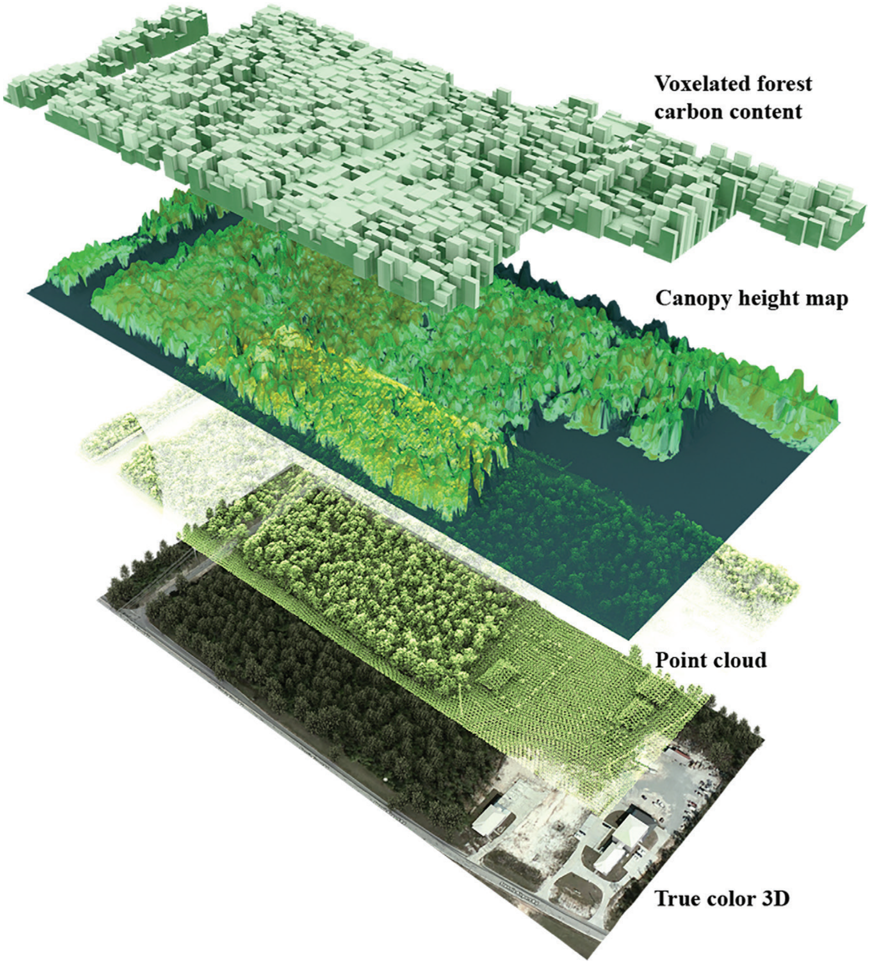

Figure 5. Illustration of how a 3D point cloud of a forest is represented and classified as a voxel. Multiple measures of surface elevation and canopy structure allows for characterization of ecosystem structural complexity and clouds of lidar elevation points representing measurements of planimetric coordinates and elevation. Landscape structure derived from a RIEGL VUX-1LR survey-grade waveform laser scanner flown by a long-range fixed wing UAV over forest www.carbomap.xyz Image: Iain H Woodhouse.

lidar can increase the explanatory power provided by 3D vertical structure. For example, fusion of imaging spectroscopy with lidar to map the canopy chemistry and biological diversity of terrestrial vegetation has revolutionized vegetation science (Asner et al. 2015). Such approaches then support 3D simulation modeling to create dynamic scenarios in virtual ecosystems that support monitoring of structural and chemical change (Shugart et al. 2015).

Case study: Mapping tropical forest biodiversity. Global biodiversity is greatest in tropical forests, which are rapidly being altered and destroyed by human activity, including land conversion, timber harvesting, and climate change, across broad spatial extents (Alroy 2017). Therefore, understanding how tropical forests are changing is one of the key challenges facing modern science and conservation. One of the most innovative uses of fused 2D and 3D imagery has focused on rapid high-resolution mapping, characterization, and monitoring of tropical forests. By combining hyperspectral and lidar observations, Féret and Asner (2014b) used microtopography of lowland Amazon forest canopy (Madre de Dios and Tambopata River landscapes, Peru) to predict plant species composition and diversity. Lidar data were first used to mask nonforest canopy pixels in the hyperspectral data and the portions of each tree crown that were shaded at the time of overflight. By taking this approach the hyperspectral data were made more comparable between tree crowns, and the confounding effects of varying canopy structure were minimized. The hyperspectral data were then used to directly classify and map the diversity (alpha and beta diversity) and spatial variability of the forest canopy using a spectral-species technique (Féret and Asner 2014a). Finally, the lidar data were used to develop a DEM of the land surface beneath the forest canopy. Using this DEM, Féret and Asner (2014b) partitioned the remotely sensed diversity from the hyperspectral data into landscape units for analysis, yielding new information on topoedaphic controls on the regional diversity of tropical forest canopies.

3D structural complexity in shallow benthic marine ecosystems

Remote sensing of seafloor bathymetry is also revolutionizing our ability to characterize, investigate, and monitor the links between structure, function, and change in benthic seascapes at a range of spatial scales. Recently, a shift to 3D mapping of the seafloor has focused on quantifying and characterizing complex terrain morphology to better understand coastal geomorphic processes and investigate important ecological drivers of biotic patterns. In the present article, we focus on shallow-water coastal seascapes, where the majority of landscape ecology has been applied (Boström et al. 2011).

Marine ecology has until recently been limited to using 2D planar models, such as categorical benthic habitat maps depicting discrete patch mosaics for studying the biophysical structure of the seascapes, but growing recognition of the ecological importance of terrain structure has resulted in the advancement of marine geomorphometry (Wedding and Friedlander 2008, Pittman et al. 2009, Bouchet et al. 2015, Lecours et al. 2016). Although methodologies developed for terrestrial remote sensing have been modified for marine

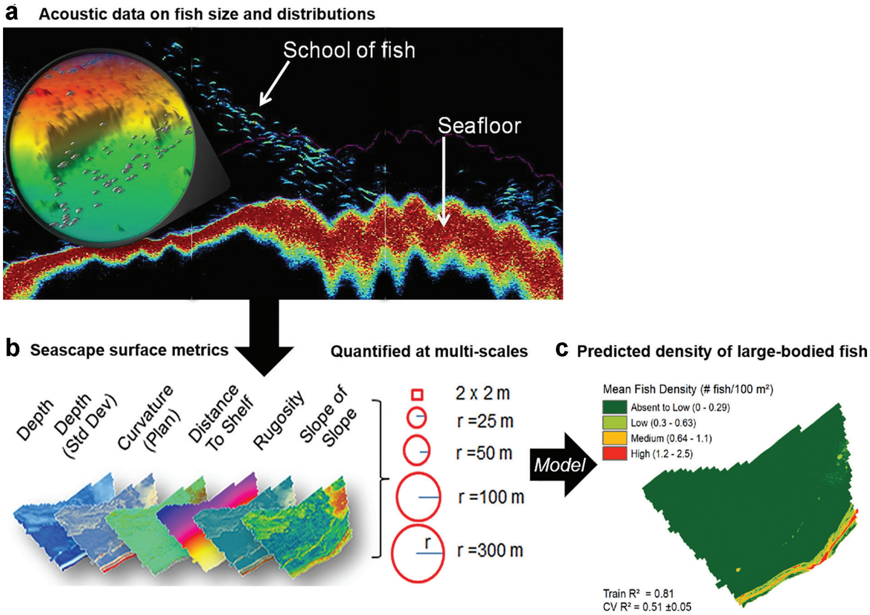

Figure 6. Turning marine acoustic data into fish distribution maps. (a) Split-beam sonar maps fish size and position, whereas multibeam sonar maps the seafloor surface. (b) Morphometrics applied at multiple spatial scales to a digital elevation model of the seafloor provides spatial predictors to explain fish distributions. (c) Boosted regression trees created predictive maps of suitable habitat for fish showing an edge effect through locations of shelf edge spawning aggregations. Source: Adapted from Costa and colleagues (2014).

environments, mapping seafloor terrains has been achieved primarily with acoustic techniques, such as side-scan and multibeam sonar (Brown et al. 2011). However, although ship-based acoustic sensors are the most widely used tools to map 3D seafloor terrains across a wide range of water depths, they are limited in the biological detail that can be resolved when not used in conjunction with optical imaging.

In the coastal zone, however, seamless land-sea digital terrains (topobathymetric surfaces) are being created using airborne lidar and multispectral satellite data to allow spatial continuity in visualizations across the land–sea interface and for numerical modeling of land–sea processes (Collin et al. 2012, Brock et al. 2016, Collin et al. 2018). Airborne—and now space-borne (ICESat-2)—lidar has been used to map seafloor bathymetry in water shallower than 40 m, with rare exceptions of deeper seafloor mapping in very clear waters (Forfinski-Sarkozi and Parrish 2019). Where finer detail is required, terrains are increasingly being modeled using SfM photogrammetry applied to images captured by drones and underwater diver surveys (Burns et al. 2015, Casella et al. 2017, Young et al. 2017). For instance, SfM applied to aerial drone images of saltmarshes in Canada captured considerably finer spatial resolution (1–2.9 centimeters [cm]) topography than airborne lidar (0.5–1 meters [m]; Kalacska et al. 2017). SfM enables accurate measurements of coral volume, surface area, architectural complexity, and topographic complexity at very high resolution (centimeters) over hundreds of square meters with great potential for new metrics that could increase our understanding of ecological relationships (Burns et al. 2015, Duvall et al. 2019). Although SfM is a computationally demanding technique, advances in software and technology have enabled the low-cost production of accurate, high-resolution digital 3D models for a diverse array of aquatic environments (D'Urban Jackson et al. 2020). Drones equipped with green lidar and hyperspectral sensors show great promise as tools for enabling the application of landscape ecology to the sea.

Case study: Mapping coral reef biodiversity. Coral reef ecosystems are the most biologically diverse and threatened marine ecosystems on Earth, with millions of people reliant on them for food and livelihoods, especially through fisheries. Large-bodied Caribbean reef fishes have declined markedly in abundance over the past few decades (Stallings 2009). Understanding the association between fish distributions and seascape structure, including fish positions in the water column, is a high priority for fisheries management and the efficacy of marine protected areas. To address this priority, Costa and colleagues (2014) used two ship-based acoustic sonar techniques (split-beam and multibeam echosounders) to simultaneously map the 3D location of fish together with the surface morphology of the underlying seafloor terrain (figure 6a). Specifically, acoustic data were collected over shelf-edge coral reef ecosystems (22 to 100 meters [m] depth) in the US Virgin Islands, in proximity to known fish spawning aggregation sites. Terrain morphometrics and spatial predictive modeling using machine learning algorithms were then applied to link fish body size distributions to seafloor morphology. Six terrain surfaces (depth, standard deviation of depth, plan curvature, rugosity, slope of slope, and distance to the shelf edge) with a 2 × 2 m spatial resolution (i.e., grain) were computed at four spatial extents (i.e., mean values within a radius of 25, 50,100, and 300 m) to consider scale effects on fish distributions (figure 6b). Of these terrain surfaces, water depth and standard deviation of depth (quantified at both the 100 m and 300 m spatial extents) were the most influential predictors, explaining 32% of the variance of large-bodied fish distributions. The information was then used to create predictive maps of habitat suitable for large-bodied fishes in other regions to support site prioritization in fisheries management (figure 6c).

Fusion of hyperspectral imagery

Data fusion, such as between active and passive sensors, is now commonplace and provides a far greater depth of understanding of landscape or seascape. For instance, as the tropical forest case studies notes, the fusion of lidar with data sets from different sensors offers additional unique observations for extracting and visualizing remotely sensed imagery, allowing for a richer and novel understanding of ecological processes than individual sensor data alone. Imaging spectroscopy has emerged as one of the most powerful synergistic data streams with lidar for quantifying ecologically relevant land cover characteristics, particularly vegetation (Asner et al. 2007). Spectroscopy measurements collected in the visible to shortwave infrared portions of the electromagnetic spectrum (380 to 2500 nanometers) provide a suite of biological and biochemical information that inform functional traits of vegetation, and complement the 3D structural information provided by lidar. The power of fusing imaging spectroscopy and lidar data for analyzing biodiversity and ecosystem health has been demonstrated primarily through the pioneering work of the Global Airborne Observatory (formerly the Carnegie Airborne Observatory, http://asnerlab.org), resulting in improved tools for conservation management (Asner et al. 2017).

In the terrestrial environment recent studies have demonstrated the enhanced structural and ecological information gained from fusing 2D and 3D imagery (Asner et al. 2012). For example, detection and mapping of forest canopy chemicals is greatly enhanced by filtering 2D hyperspectral data with 3D lidar data (Asner and Martin 2009). Specifically, the lidar data are used to select top-of-canopy locations under similar tree crown-to-crown illumination conditions, thereby selecting comparable 2D spectral pixels for subsequent chemical analyses (Asner and Martin 2008, Asner et al. 2015).

Airborne lidar is now commonly flown with multispectral and hyperspectral imagers for survey of shallow marine environments in which fusion of bathymetric lidar and data from passive optical sensors is increasingly used to map coral reef environments (Wozencraft and Park 2013, Thompson et al. 2017). Typically, the lidar data are used to help interpret the spectral seafloor reflectance images derived from hyperspectral imagery and can be used in segmentation to map coral reef zonation, biotopes, and 3D habitat complexity. With the help of machine learning classifiers, the accuracy of the resulting seafloor classification map is typically greater than classifications generated using either the lidar or the hyperspectral images alone (Zhang 2019).

3D tools for quantifying structure and pattern

In concert with the movement of landscape and seascape ecology to 3D sciences has been the development of new metrics and tools for quantifying structure and patterns. For instance, most geographic information systems (GIS) now include metrics for quantifying structure in continuous terrains (ArcGIS's Spatial Analyst Toolbox, Evans et al. 2014; DEM Surface Toolbox, www.jennessent.com/arcgis/surface_area.htm; QGIS Raster tools, www.qgis.org; Landserf, www.landserf.org; SAGA-GIS and R software, e.g., http://sourceforge.net/apps/trac/saga-gis/wiki/Terrain Analysis—Morphometry module library, Hesselbarth et al. 2019). Likewise, the classic landscape metric program FRAGSTATS now includes a suite of surface metrics, including morphometrics for quantifying structure from 3D elevation models (www.umass.edu/landeco/research/fragstats/fragstats.html). In the context of marine environments, the Benthic Terrain Modeler extension for ArcGIS, developed by NOAA (the US National Oceanic and Atmospheric Administration) and Oregon State University, has been used to quantify surface patterns from bathymetry (e.g., rugosity, slope, bathymetric position index; Walbridge et al. 2018). Finally, many novel mathematical transforms have been applied to multidirectional and multiscale surface characterization, such as ridgelet, curvelet, and contourlet transforms (Li et al. 2015).

Although a number of new metrics have been developed for 3D analyses, ecologists have not yet explored their behavior and meaning. Therefore, it remains for ecologists to demonstrate the utility of these metrics, or to develop new surface metrics better suited for landscape ecological questions (McGarigal 2013). In addition, many morphometrics have high multicollinearity, leading Lecours and colleagues (2016) to identify seven specific terrain attributes that capture most of the topographic variability, similar to earlier work that evaluated collinearity in landscape metrics (e.g., Riitters et al. 1995). As such, determination of an ecologically relevant and informative set of metrics remains a work in progress.

The availability of automated tools and free elevation data sets allow an unprecedented number of users, from novice to expert, to experiment with and develop products. Although product development is easily achieved, appropriate scientific analysis and conclusions typically require knowledge of the data source and sensor characteristics in addition to domain expertise. Artifacts that manifest similarly to valid environmental phenomena can be mistakenly produced if appropriate collections and processing protocols are not strictly adhered to. For example, if raw lidar flight lines contain spatial alignment issues between lines, this can be represented as artificial drainage pathways in surface hydrology models. Users must also be aware of how uncertainty in data sources can adversely affect the quality of derived products, which, in turn, can produce artifacts that mimic physical phenomena. Users should be aware of these issues and consult experts in the field before conducting in-depth analysis for a particular area of interest. To aid users in adopting high-resolution topography derived from lidar, several organizations provide resources to aid with analysis. For example, NEON (the US National Ecological Observatory Network) provides a series of self-paced tutorials, teaching modules, and videos at their resources page (www.neonscience.org/resources) and Open Topography provide a "Resources for Educators" page (https://opentopography.org/learn/resources-educators).

The fluidity and volumetric nature of ocean systems also means marine environments (and therefore marine biota distributions) are more spatiotemporally dynamic than terrestrial (Wright 2007). Recent developments in 3D modeling and visualization have produced a number of tools for analyzing multidimensional marine data sets, such as voxel models (Hademenos et al. 2019). Voxel models can assess multiple physical features (such as lithological layers) as voxel layers in 3D cubes that can be viewed as isosurfaces, sections, or volumes (Hademenos et al. 2019). Such information is valuable for ecological understanding of marine biota distributions and biodiversity hotspots, as well as global climate regulation (Sahlin et al. 2012). An established application of 3D visualization in marine environments is networks of ecological marine units (EMUs), which are a way to objectively classify global marine environments through 3D volumetric information on oceanic properties and statistical clustering. EMUs consequently have a wide number of potential uses from ecosystem accounting to marine disturbance assessments, although would benefit from finer spatial and temporal resolutions for detailed ecological applications (Sayre et al. 2017).

Synthesis and future directions

Scientific research in imagery and 3D data fusion and integration has grown in the last decade, and landscape and seascape ecologists can now critically frame 3D ecological questions that, until recently, have been challenging to answer at broad spatial scales. For terrestrial applications, understanding geomorphology from a 3D perspective offers great potential to advance our knowledge of the functional links between geomorphic and anthropogenic structures (e.g., buildings) and ecological processes in the environment. In the case of marine environments, although they present dynamic, spatially complex, multidimensional systems, we do have the geospatial tools and methods to capture the 3D complexity in them, even though the temporal component (the fourth dimension) remains challenging (Wedding et al. 2016). Future research applications in the marine environment should focus on addressing the challenges associated with integrating the dynamic oceanographic data sets available through remote sensing (e.g., sea surface temperature, chlorophyll α) into products capable of capturing the spatial and temporal variability in the environment, at the scales relevant to pelagic predators and their prey.

Beyond the biophysical realm, the next steps involve a socioecological systems approach that also incorporates the 3D patterns of human use and the effects of human activities that alter the 3D landscape structure. Human activities have long been considered on terrestrial landscapes (i.e., cultural landscapes) in Europe (Naveh 1995) and increasingly so in other regions of the world. As a result, 3D visualization of human dominated landscape and seascape structure can advance our understanding of how humans use the 3D environment in both space and time and support advances in management of complex socioecological systems. Furthermore, the integration of this 3D approach in natural resource management may support the development of conservation and management plans and shift the way that policymakers evaluate current and future regulations in a dynamic environment.

Related to socioecological systems, another area within which integration of approaches would be of great benefit is urban ecology and the design, management, and policy decisions that affect cities. Specifically, the integration of data could provide important information for designing and planning urban green spaces (parks, roofs, etc.), which is critically needed for addressing contemporary urban biodiversity questions (Aronson et al. 2017, Lepczyk et al. 2017). For instance, 3D data on rooftop height from the ground may be important for green roof networks. Using a 3D perspective could also provide needed insight into advancing urban gradient studies that have traditionally focused only on two dimensions. Cities have abundant sensing technologies embedded in them already and much of the data are publicly accessible. Remote sensing data could be fused with lidar and other imagery to develop a more complete picture of the ecological characteristics in cities.

The shift toward a 3D theoretical and applied framework in landscape ecology is changing the way scientists study and interpret the world and, as a result, can now inspire a significant shift toward managing human use and activities in three dimensions. As landscape and seascape ecology looks toward the future, there should be a continued progression toward a 3D science that will shift the way we view and conceptualize the spatial patterns and processes. The disciplines of landscape and seascape ecology are at the point of being revolutionized through the advancement of a new generation of spatial technologies that yield extremely voluminous and complex data sets (i.e., big data) together with advanced processing and informatics suitable to work with big data. The integration of large and disparate data types presents new challenges in how ecologists analyze and synthesize big data and the amount of information available offers unprecedented opportunities for understanding both the landscape and seascape in a way that informs management decisions at multiple scales. Future emerging lidar technology and data fusion streams from other satellite-based sensors will increasingly allow for analysis of big data, offering unprecedented opportunities to study and understand ecosystem dynamics and swiftly inform management decisions. However, the true utility of harnessing the power of big data lies in the distillation of the data into knowledge in a way that can effectively provide the best available science to inform management and policy. We anticipate that a focus on establishing, developing, and maintaining stronger communication channels between the remote sensing community, conservation biologists, natural resource managers, and policymakers will become increasingly important in collaborative work and fundamental for the development of a coordinated, effective research agenda (Pettorelli et al. 2014). As a result, the distillation and communication of 3D-based scientific findings will be an important consideration to ensure the successful uptake of information and timely responses from resource managers and policymakers.

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