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Review

UAVs as remote sensing platforms in plant ecology: review of applications and challenges

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Abstract

Aims Unmanned aerial vehicles (UAVs), i.e. drones, have recently emerged as cost-effective and flexible tools for acquiring remote sensing data with fine spatial and temporal resolution. It provides a new method and opportunity for plant ecologists to study issues from individual to regional scales. However, as a new method, UAVs remote sensing applications in plant ecology are still challenged. The needs of plant ecology research and the application development of UAVs remote sensing should be better integrated.

Methods This report provides a comprehensive review of UAV-based remote sensing applications in plant ecology to synthesize prospects of applying drones to advance plant ecology research.

Important Findings Of the 400 references, 59% were published in remote sensing journals rather than in plant ecology journals, reflecting a substantial gap between the interests of remote sensing experts and plant ecologists. Most of the studies focused on UAV remote sensing's technical aspects, such as data processing and remote sensing inversion, with little attention on answering ecological questions. There were 61% of studies involved community-scale research. RGB and multispectral cameras were the most used sensors (75%). More ecologically meaningful parameters can be extracted from UAV data to better understand the canopy surface irregularity and community heterogeneity, identify geometrical characteristics of canopy gaps and construct canopy chemical assemblies from living vegetation volumes. More cooperation between plant ecologists and remote sensing experts is needed to promote UAV remote sensing in advancing plant ecology research.

Keywords UAVs, drones, unmanned aircraft systems (UASs), plant ecology, species identification, community function

无人机遥感在植物生态学中的应用与挑战

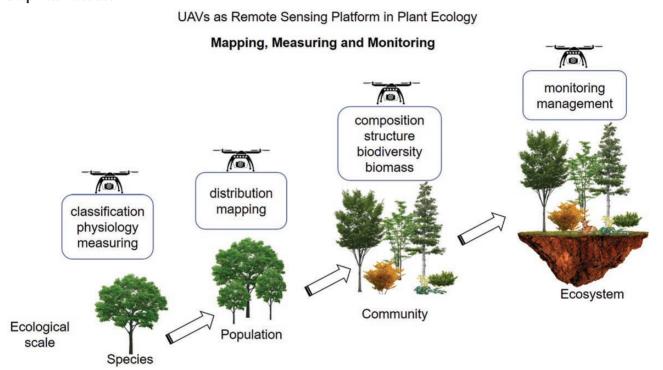
摘要:无人机为获取高时空分辨率的遥感数据提供了经济灵活的工具,为植物生态学家开展从个体到区域尺度的生态学研究提供了新的机遇和手段。但作为一种新兴的技术手段,当前无人机遥感在植物生态学中的应用仍充满了挑战,植物生态学的科研需求与无人机遥感的生态应用需要更为深入的融合。

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本文综述了无人机遥感技术在植物生态学中的应用,展望了无人机在植物生态学研究中的应用前景。在 所综述的400篇文献中,59%的文章发表于非植物生态学领域的遥感类期刊,遥感学者与生态学者的关 注点存在较大差异。当前的研究集中在无人机遥感的技术层面,如数据处理和遥感反演方法等,对生态 学问题本身的关注较少。综述的文献中,61%的研究案例集中在群落尺度,可见光(RGB)相机和多光谱 相机是最常用的传感器类型(75%)。无人机遥感数据中蕴藏着诸多待挖掘的、有重要意义的生态参数, 这些参数有助于我们识别林窗的几何特征,构建林冠的化学组合,更好地了解林冠表面的不规则性和 群落的异质性。无人机遥感技术在植物生态学研究中的深入应用,需要集植物生态学家和遥感专家之合 力共同推进。

关键词: 无人机, 植物生态学, 物种鉴定, 尺度, 功能性状

Graphical Abstract



INTRODUCTION

Plant ecologists study the relationships between plants and their environment from gene to global scales (Keddy 2007). Remote sensing from spaceborne, airborne and terrestrial platforms has provided abundant data and analytical tools for plant ecology studies at regional and global scales (Myneni and Ross 2012; Xie et al. 2008). As of early in 2018, 1738 satellites in Earth orbit were equipped with various types of remote sensors, such as multispectral cameras, hyperspectral cameras and light detection and ranging (LiDAR) sensors (Union of Concerned Scientists 2018). The satellites collect data with spatial resolutions ranging from kilometers (e.g. NOAA-AVHRR, 1100

m) to submeters (e.g. Worldview III, 0.31 m). The applications include the characterization of vegetation type, aboveground biomass, leaf area index (LAI), vegetation cover and canopy chemistry at regional and global scales (Gomez et al. 2019). Although these data have enabled researchers to assess ecological conditions in the context of global environmental change, satellite and airbornebased remote sensing systems often fail to meet the requirements of ecological and environmental research. Use of these systems by plant ecologists is limited by inadequate spatial, temporal and spectral resolution; lack of operational flexibility and noise caused by atmospheric conditions (Adam et al. 2010; Huylenbroeck et al. 2020). For groundbased remote sensing, with handheld devices or tower crane equipment, its measurements are often taken at limited points and the measurement process is time consuming. Accordingly, it is hard to apply the ground-based remote sensing to complex environments over larger areas.

In recent years, unmanned aerial vehicles (UAVs), also known as remotely piloted aircraft system, unmanned aircraft systems or drones, have been widely used in plant ecology. Such UAVs are easy to deploy and are economical and most importantly, technically capable of collecting imagery data at fine spatial, spectral and temporal resolutions. UAV data can complement ground observations and data collected from aircraft and satellite remote sensing platforms, and thereby provide a comprehensive remote sensing system for plant ecology studies ranging from individuals to ecosystems (Singh and Frazier 2018; Torresan et al. 2017; Valbuena et al. 2020).

There is an increasing number of studies on the applications of UAV remote sensing, and these studies span a broad array of topics including UAV platform classification and development (Colomina and Molina 2014; Floreano and Wood 2015; Hassanalian and Abdelkefi 2017; Watts et al. 2012), UAV applications in agriculture (Perich et al. 2020; Yang et al. 2018; Zhang and Kovacs 2012), resource management (Oliveira et al. 2020; Shahbazi et al. 2014), environmental studies (Pichon et al. 2019; Wang et al. 2018; Whitehead and Hugenholtz 2014; Whitehead et al. 2014) and biodiversity monitoring (Bagaram et al. 2018; Guo et al. 2016b). Some pioneering studies also discussed the potential use of UAV remote sensing in ecology (Anderson and Gaston 2013; Lian and Wich 2012; Valbuena et al. 2020). In this report, we review UAV remote sensing systems and their applications in plant ecology from a perspective that integrates the views of ecologists and remote sensing professionals. Our analyses are divided into five levels, i.e. individuals, populations, communities, ecosystems and landscape. conclude our review by discussing the challenges and prospects of UAV remote sensing in plant ecology research.

REVIEW METHODS

We collected data from the ISI Web of Science Core Collection using the following search terms: TS = ('remotely piloted aircraft system') or ('unmanned aerial vehicles') or TS = ('unmanned aircraft systems') or TS = (drones) or TS = ('unmanned aerial systems) and LANGUAGE: (English). The

search results were then refined according to WEB OF SCIENCE CATEGORIES: (Remote Sensing or Ecology or Agriculture Multidisciplinary or Plant Sciences or Forestry). TIME SPAN was set at 2004–20 (August 2020), and INDEXES was set at SCI-EXPANDED. With the article type limited to 'research articles' and 'review articles', we found 1425 records in the ISI Web of Science. We screened the abstracts of references and removed those records that were not relevant to this review. In total, we identified 400 papers for detailed review, which included 354 research articles and 46 review papers (Appendix S1: Reviewed references list). Finally, our database included 354 reports of original research.

We designed a standardized template to review these articles (Appendix S1: Template of reviewed studies). The template included the following criteria: published year, the institution of the first author, location of the study site(s), study area, vegetation form, observation scale, UAV type, UAV producer, sensor type, flying altitude, processing method and research objectives in the context of plant ecology.

The review is presented in four parts. The first part is titled 'UAV Systems, UAV Data Processing and Analysis', which provides basic information about the UAV instrumentation, the data and the related processing and analytical methods. The second part is called, 'Applications of UAV Remote Sensing in Plant Ecology'. This part focuses on the relevance of UAV technology to ecology through broad applications of UAV remote sensing in plant ecology. This part organized according to well-acknowledged contributions of UAV to plant ecological studies and is also structured by considering three primary types of plant ecological studies: (i) Individual to population scales: individual detection, physiological assessment and species classification and distribution; (ii) Community scale: composition, structure, foliar functional traits, biodiversity and biomass and (iii) From ecosystem to landscape scale: monitoring and management. The third part discusses the challenges and prospects of UAV remote sensing in plant ecology. The main technical challenge is how to effectively fuse multisource remote sensed data including UAVs in the context of supporting plant ecology studies, while the primary application challenge is how to better integrate UAV obtained data to answer or solve basic scientific questions facing plant ecology. The prospects of UAV remote sensing in plant ecology are very promising, including automatic species identification, multiscaling spatial exploration of plant ecosystems, increased UAV applications from

describing ecological phenomenon to answering ecological questions, and the needs of more UAV-based novel methods to answer ecological questions. The last is the section of Conclusions.

UAV SYSTEMS, UAV DATA PROCESSING AND ANALYSIS

UAV systems

UAV remote sensing systems have at least five components, i.e. a platform system, a sensor system, a ground control and data transmission system, a data processing system and operators (Fig. 1). Previous reviews of UAV platforms and sensing payloads can be found in Watts *et al.* (2012) and Hassanalian and Abdelkefi (2017). In Table 1, we have summarized the advantages of UAV remote sensing systems by comparing them with traditional spaceborne and airborne remote sensing systems (Table 1). The first advantage is low cost (Xie *et al.* 2015; see a comparable cost analysis in Appendix S2). As a second advantage, UAV remote sensing provides high temporal and spatial resolutions. UAV systems

can acquire imagery with centimeter resolution at almost any time of the day and under most weather conditions. The very high-resolution imagery makes it possible for ecologists to study many canopy properties, including canopy structure and dynamics. Another advantage is that the operation of a UAV remote sensing system is flexible. In a complicated environment, small UAVs can take off and land on an operator's hands, which greatly increases the utility of UAV remote sensing in ecological studies. In addition, UAV remote sensing systems are relatively easy to use, such that operation requires only a short training period. As a final advantage, the ultra-low altitude flying of UAVs can reduce the effect of cloud on imagery and thereby improve the data quality.

Most of the 354 case studies of UAV application in plant ecology used a rotary wing (64%) or a fixed-wing UAV platform (26%). About 88% of these were off-the-shelf UAV platforms such as the DJI phantom series and the senseFly eBee series (Fig. 2a and b). Some parafoil wing and vertical take-off and landing fixed-wing UAVs were used, but the percentages were very low. In the 354 studies, the UAVs usually flew at altitudes of 10–120 m in order to obtain images with



Figure 1: The components of a UAV remote sensing system (adapted from Sun et al. 2017).

cloud influence Degree of Moderate Very low Flexibility Highest Lowest Low Very high Cost Low Short time Long With limitation No limitation Load demand for a landing point high-quality landing point
 Fable 1:
 Characteristics of spaceborne, airborne and UAV remote sensing systems
 automatically, nearly no Requires a pilot and a Remote control or fly Controllability 10-50 km 50-500 m 0.5-5 km Swath resolution Ш 0.5-10 cm 1-25 m Spatial 0.1 - 2Aerial remote Space remote UAV remote sensing sensing sensing System

ultra-high resolution and comply with UAV aviation regulations (Fig. 2c).

UAV data processing and analysis

Various types of sensors are available for the UAVbased platform, including RGB, multispectral, hyperspectral, thermal and LiDAR sensors. RGB cameras are most commonly used due to their low costs, lightweights and ease of use (Bagaram et al. 2018; Cunliffe et al. 2016; Pichon et al. 2019). Multispectral sensors (e.g. MicaSense RedEdge 3 camera, Micasense, WA, USA) provide more spectral bands (e.g. red-edge: 760 nm; near-infrared [NIR]: 810 nm) which can better evaluate plant health and stress status (Adam et al. 2010; Baluja et al. 2012; Wang et al. 2019b). Hyperspectral sensors (e.g. Cubert S185, Cubert, Ulm, Germany) provide continuous spectrum with narrow bandwidths (<10 nm) and thus offer useful means of detecting fine absorption features of plant biochemicals (Kwon et al. 2020; Pölönen et al. 2013; Saarinen et al. 2018). Thermal infrared sensors capture the thermal radiation from the plants which can be used to estimate the surface temperature of plants for monitoring plant water stress and forest fire (Calderón et al. 2013; Messina and Modica 2020; Smigaj et al. 2017). LiDAR sensors measure the distance to a target by travel time of the emitting laser light and can characterize canopy structural parameters such as tree height, crown width and canopy cover (de Almeida et al. 2020; Ganz et al. 2019).

In general, the data preprocessing of optical sensors (RGB, multispectral, hyperspectral and thermal sensors) includes geometric correction and radiometric correction. Geometric correction is generally performed based on the GPS and inertial measurement unit data. Ground control points are often used to improve the accuracy of geometric Recently, new photogrammetry techniques such as structure from motion (SfM) have been used to generate orthophoto mosaic based on matching feature across overlapped images (Gil-Docampo et al. 2020; Wallace et al. 2016). Software such as Agisoft Photoscan (now Metashape, Agisoft LLC, St. Petersburg, Russia) and Pix4d mapper (Pix4D SA, Lausanne, Switzerland) have integrated these algorithms into software and support automatic image preprocessing, which include image matching, mosaic, geometric correction, brightness and contrast adjustment (Forsmoo et al. 2019).

Radiometric correction converts the digital numbers of images to reflectance. RGB

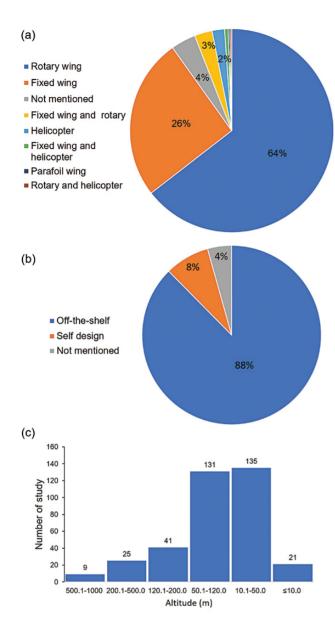


Figure 2: Characteristics of UAVs used in plant ecology studies (**a** and **b**), including their flying altitudes (**c**).

thermal cameras are generally hard to calibrate due to the nonlinear gamma correction effect. As a result, they are often used for image classification or temperature measurement which does not highly rely on radiometric calibration. Multiple spectral sensors have different ways to perform radiometric correction. One way is to have a sensor onboard to measure the downwelling radiance and calculate in-time reflectance. Another way is to place one or more ground targets with standard known reflectance during the flight and then to perform an empirical line correction (Aasen *et al.* 2018). It should be mentioned that the empirical line correction method requires a stable sunny

sky condition, i.e., the solar illumination does not change much during the flight. For long distance flights, a concurrent radiance measurement of ground targets using field spectrometers is often suggested (Aasen *et al.* 2018). These techniques of radiometric corrections also apply to hyperspectral sensors.

Data processing and analysis include imagery-based methods (for RGB data), point clouds methods (for RGB and LiDAR data), statistical models (for multispectral and hyperspectral data) and physical models (for multispectral and hyperspectral data). RGB images can be used to detect trees using object-based image analysis such as eCognition software or deep learning methods (Mu *et al.* 2018; Petrich *et al.* 2020). The RGB images can also be used to observe forest phenology and crop lodging (Berra *et al.* 2019; Zhang *et al.* 2020).

Individual tree segmentation can be achieved from LiDAR and RGB mosaic data (Wallace et al. 2016). LiDAR and RGB point clouds are generated in different ways. LiDAR point clouds can be obtained during the laser scanning, but RGB point clouds need to be constructed through the SfM algorithm. After the point cloud generation, LiDAR and RGB data can be further processed using the same methods. The point clouds are first interpolated to create digital surface model (DSM) and digital terrain model (DTM) by using techniques such as Delaunay Triangulation and triangulated irregular networks. The height calculation is done with the canopy height model (CHM) by subtracting DTM from DSM. Tree detection can then be conducted from CHM or DSM using variable-sized window and watershed delineation (Yin and Wang 2019), or directly from point clouds using point cloud segmentation and layer stacking (Wallace et al. 2016). Tree height, crown width and canopy cover can be derived from CHM or point clouds (Guerra-Hernandez et al. 2016; Solvin et al. 2020). RGB data usually require more interpolations to build DSM and DTM, because the point clouds obtained through the SfM algorithm are much sparser than those from LiDAR data. Therefore, the structural attributes extracted from the LiDAR point clouds are usually more accurate than those extracted from the RGB point clouds.

Statistical models are developed for classification and regression. Machine learning algorithms such as random forest, support vector machine and convolutional neural networks have been developed to perform automatic (unsupervised) or semiautomatic (supervised) classification of UAV remote sensing data (Nguyen et al. 2019). Recently, deep learning algorithms based on neural network have emerged as an effective tool for species classification (Lopez-Jimenez et al. 2019; Plesoianu et al. 2020; Zou et al. 2019). For regression, the relationship between a parameter of interest (e.g. leaf chlorophyll or nitrogen) and the spectral data is established. Statistical approaches include vegetation indices, linear regression approaches such stepwise linear regression and partial least squares regression, nonlinear regression approaches such as random forest, support vector machine and artificial neural network (Padua et al. 2017). Physical models describe the interaction and transfer of solar radiation based on physical laws and provide the advantage of transferability over statistical models. Physical model was rarely used in previous studies and was found to map the reflectance anisotropy of a potato canopy (Roosjen et al. 2017).

APPLICATIONS OF UAV REMOTE SENSING IN PLANT ECOLOGY

General characteristics of UAV remote sensing applications in plant ecology

The 354 case studies in our database were carried out in 43 countries, mostly in North America, East Asia and West Europe; the two leading countries were the USA and China (Fig. 3). The earliest study in our database was carried out in 2005 in the USA; after that, the number of studies increased rapidly over time, especially during 2016–2019 (Appendix S2; Supplementary Fig. S1). There were 215 case studies published in remote sensing journals, while 139 in plant science and ecology journals.

Among the 46 review papers, 21 were published in remote sensing journals and 25 were published in plant science and ecology journals. The reviews in remote sensing journals mainly focused on the challenges and applications of UAV systems in environmental monitoring. Reviews in plant science and ecology journals primarily focused on precision agriculture and forest management. The previous reviews were conducted from the perspective of remote sensing experts, i.e. they focused on mapping, measuring and monitoring plant properties rather than on answering questions in biology or ecology. There is an obvious gap between the concerns of remote sensing scientists and ecologists. Of the 354 case studies, most of them used RGB or

multispectral cameras, focused on the community to ecosystem scale and applied on forests and crops (see a detailed tabulation in Appendix S1). Therefore, a comprehensive assessment of UAV applications in plant ecology is needed, especially for different ecological scales such as the individual, population, community, ecosystem and landscape scale.

Individual to population scales: individual detection, physiological assessment and species classification and distribution

UAV remote sensing data have been widely used to measure crown characteristics of individual plants. Surovy et al. (2018) built a point cloud to estimate the height and position of individual trees. Mu et al. (2018) measured the crown width and crown projection area of individual peach trees. Stress and other physiological changes in plants can be tracked by variations in the visible and NIR wavelengths. Stressed plants often exhibit a higher reflectance in the visible and lower reflectance in the NIR than nonstressed plants. Indicators of plant stress and growth such as leaf chlorophyll and LAI can also be estimated from the spectra. When plants experience drought stress, the leaf stomata close, resulting in a higher leaf temperature, which can be monitored using thermal imagery (Leinonen et al. 2006). For instance, Berni et al. (2009) used thermal imagery to assess the water-stressed status of peach trees and to guide precision irrigation (Berni et al. 2009). Spectral indices, such as the normalized difference vegetation index (NDVI = $(R_{800} - R_{670})/(R_{800} + R_{670})$, Rouse etal. 1974), the renormalized different vegetation index $(RDVI = (R_{800} - R_{670}) / \sqrt{(R_{800} + R_{670})}, Rougean and$ Breon 1995), the modified triangular vegetation index 1

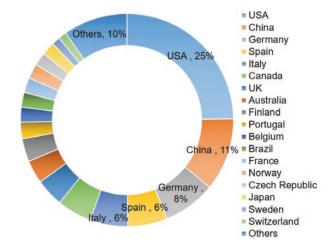


Figure 3: The percent of case studies in our database conducted in the indicated countries.

 $(MTVI1 = 1.2 \times [1.2 \times (R_{800} - R_{550}) - 2.5 \times (R_{670} - R_{550})],$ Haboudane et al. 2004), the triangular vegetation index $(TVI = 0.5 \times [120 \times (R_{750} - R_{550}) - 200 \times (R_{670} - R_{550})],$ Haboudane et al. 2004), the ratio transformed chlorophyll absorption ratio index $(TCARI = 3 \times [(R_{700} - R_{670}) - 0.2 \times (R_{700} - R_{550}) \times (R_{700}/R_{670})],$ al. Haboudane et 2002) and the optimized soil-adjusted vegetation index $(OSAVI = (1 + 0.16) \times (R_{800} - R_{670})/(R_{800} + R_{670} + 0.16),$ Haboudane et al. 2002), have been used to assess the water stress of orange and mandarin trees (Zarco-Tejada et al. 2012) and grapevines (Baluja et al. 2012; Romero et al. 2018). Hyperspectral and thermal imageries have also been used to quantify the effect of a disease (Verticillium wilt) on the stomatal conductance of olive leaves (Calderón et al. 2013). Species classification is the most common use of UAV remote sensing at the individual scale. Satellite remote sensing has been widely used to generate global or national land cover maps on which the vegetation is classified as forests, grasslands, deserts and wetlands (He et al. 2009). The image processing and classification procedures have been detailed by Laliberte et al. (2011). Because of the coarse spatial resolution of satellite imagery, however, plant species are difficult to be distinguished unless the target species have unique growth forms or phenology (Bradley 2014; Huang and Asner 2009). In contrast, UAVs can obtain ultra-high spatial and spectral resolution imagery, satisfying the requirements of vegetation classification at the species level. In a lake ecosystem, e.g., 49 lacustrine plant species/ vegetation classes were identified by using highresolution optical imagery with an accuracy of 95.1% (Husson et al. 2013). By incorporating tree heights with spectral features, image textural features and hyperspectral vegetation indicators, UAV accuracy in identifying mangrove species can be as high as 88% (Cao et al. 2018). Understory herbs can potentially be identified to species in sparse forests with optical and multispectral imagery (Leduc and Knudby 2018; Sanders 2017).

The accuracy of species identification depends on four factors: spatial resolution, spectral resolution, habitat complexity and classification algorithms. Spatial resolution is the primary determinant of identification accuracy (Ashraf *et al.* 2010). A 5-cm resolution was not sufficient to identify some herbs at the species level (Dunford *et al.* 2009). In contrast, images with 1-cm resolution could identify herbaceous plant species in a wetland with an accuracy of 93% (Ishihama *et al.* 2012). At a scale

of 1/50 unit, populations of *Phragmites australis, Typha domingensis* and *Miscanthus sacchariflorus* were clearly discriminated in a river estuary (Kaneko and Nohara 2014). Therefore, ultra-high resolution images obtained with cameras on UAVs flying at a low altitude will greatly improve plant identification at the species level (Cao *et al.* 2018; Li *et al.* 2017; Yang *et al.* 2016; Zarco-Tejada *et al.* 2012). However, the high cost of hyperspectral UAVs (Manfreda *et al.* 2018; Whitehead and Hugenholtz 2014) limits their applications in plant ecology (Adão *et al.* 2017).

Accurately identifying species in complicated habitats is challenging, especially when the target species are small and similar to each other. A case study in the Arctic Tundra indicated that VIS-NIR high-resolution imagery could identify the main vegetation groups but could not distinguish between species (Mora et al. 2015). In rain forests and subtropical forests, tree properties (e.g. crown size, crown status, crown contour, crown architecture, foliage cover, foliage texture and foliage color) must be integrated in order to identify the dominant species in the canopy layer, but the number of species that can be accurately identified is still limited (Trichon 2001; Yang et al. 2016). In summary, UAV remote sensing for species identification has mostly been applied in relatively simple habitats, such as rangelands (Karl et al. 2020; Laliberte et al. 2011; Rango et al. 2006, 2009), wetlands (Chabot and Bird 2013; Doughty and Cavanaugh 2019; Husson et al. 2014; Ishihama et al. 2012; Zweig et al. 2015), plateau shrub swamps (Fletcher and Erskine 2012) and riparian forests (Husson et al. 2013). There are a few studies carried out in urban areas although the habitats are relatively simple. Flying drones in cities often requires strict approval procedures, which limits their use in urban environments.

Image processing methods are required for the use of UAV remote sensing in plant ecology. In addition to popular pixel-based and object-based image analysis, a 'feature learning' approach based on machine learning represents a novel and effective method for species identification (Hung *et al.* 2014; Lary *et al.* 2016; Plesoianu *et al.* 2020). The fusion of multisource data, such as hyperspectral, RGB and LiDAR data, can also improve the accuracy of species classification (Cao *et al.* 2018; Yin and Wang 2019).

Mapping the spatial distribution of plant species at the population scale is a popular application of UAV remote sensing. For instance, Flynn and Chapra (2014) used UAV remote sensing to map the

distribution of a green alga (*Cladophora glomerata*) in rivers. Kalacska *et al.* (2013) used UAV remote sensing to map the spatial distribution of *Eriophorum vaginatum* and to evaluate its contribution to CH₄-C flux in an ombrotrophic bog in Canada. Other researchers have used UAV remote sensing to detect and map species and thereby to help manage populations of weeds and invasive plants (Abeysinghe *et al.* 2019; Alvarez-Taboada *et al.* 2017; Hill *et al.* 2017; Peña *et al.* 2013; Tamouridou *et al.* 2017).

Community scale: composition, structure, foliar functional traits, biodiversity and biomass

Species composition (13 species) of a wetland area in Hong Kong was mapped with a UAV-based hyperspectral image and DSM derived from photogrammetric point clouds (Li *et al.* 2017). Banerjee *et al.* (2017) identified and mapped five plant species in a complex upland swamp community using a UAV-hyperspectral system, and the overall accuracy of classification was 88.9%. In a study by Chisholmryan *et al.* (2013), the use of a UAV LiDAR system (flown 1.5 m above the ground) to obtain DBH data for trees provided a new way to conduct below-canopy forest surveys.

The horizontal as well as the vertical structure of plant communities can be investigated through UAV remote sensing (Campos-Vargas et al. 2020; Schneider et al. 2019). Using a UAV-optical camera, Getzin et al. (2012) characterized the horizontal patterns of small gaps (<5 m²) in 10 temperate forests and found that these small gaps, which could hardly be detected by conventional aerial or satellite images, made up the majority of gaps in the canopies. The canopy height, aboveground biomass and canopy complexity measured by UAV LiDAR and an optical camera were used to estimate frugivorous bird abundance and forest recovery (Zahawi et al. 2015). In areas with relatively low canopy closure, the SfM point clouds obtained with a UAV-optical camera provided abundant information on forest structure (Jensen and Mathews 2016; Wallace et al. 2016). LAI and vegetation coverage can be estimated with UAV remote sensing to evaluate community structure (Tian et al. 2017; Wang et al. 2019a). UAV remote sensing has also become increasingly important in forest phenology studies (Mariano et al. 2016). The spatial and temporal changes of a forest were studied at the community scale by using a UAV-optical camera (Klosterman et al. 2018).

Foliar functional traits refer to a range of biochemical and physiognomic characteristics of plants, such as macronutrients (N, P, K, Ca, Mg, S), trace minerals (B, Cu, Fe, Mn, Zn) and Al, cellulose, lignin, sugars and starches, have been widely estimated using manned aircraft remote sensing (Asner *et al.* 2014; Schneider *et al.* 2017; Wang *et al.* 2018, 2020). With higher security and flexibility, UAV remote sensing has the potential to collect foliar functional traits with higher spatial and temporal resolutions. A number of studies have been conducted in croplands and grasslands (Table 2).

The diversity of the dominant species in the upper canopy layer of a subtropical or mangrove forest were quantified using UAV-optical or hyperspectral cameras (Cao et al. 2018; Yang et al. 2016). Theoretically, the biodiversity of a canopy layer can be easily calculated based on the information of tree canopies. However, UAV remote sensing has rarely been used to directly measure biodiversity (Guo et al. 2016b). Saarinen et al. (2018) used UAV-based photogrammetric point clouds and hyperspectral imaging to monitor dead wood quantity and species richness in a boreal forest. Getzin et al. (2012) used UAV to calculate eight different gap metrics and to determine whether those metrics were correlated with floristic biodiversity of the forest understory at a landscape scale.

Plant biomass can be estimated through UAV remote sensing in two ways (Man et al. 2014). For the first approach, a relationship between the remote sensing data and biomass is first established; biomass can then be estimated by *K* nearest neighbor classification, multiple regression analysis, neural network methods or statistical ensemble methods. For example, vegetation indices derived from UAVmultispectral or hyperspectral images have been widely used to estimate aboveground biomass, productivity or yield (Geipel et al. 2014; Getzin et al. 2012; Gonzalez-Jaramillo et al. 2019; Pölönen et al. 2013). On the other hand, tree height, DBH or crown volume are extracted from UAV remote sensing images and then used to calculate biomass with allometric equations (Bendig et al. 2014; Cunliffe et al. 2016). In general, UAV LiDAR can generate more accurate results than the optical image-based point cloud (Ganz et al. 2019).

From ecosystem to landscape scale: monitoring and management

UAV remote sensing has been used to detect, monitor and fight forest fires (Pastor *et al.* 2011). Equipped with visual, infrared and thermal cameras, UAVs can effectively track fires, predict their expansion and provide real-time information to firefighters

 Table 2:
 Ecological concerns, UAV data requirements and current studies using UAV remote sensing at different ecological scales

Ecological scale	Ecological concerns	UAV data requirement	Previous studies using UAV remote sensing
Individual	The relationship between an individual organism and its environmental factors, including the relationship between individual growth, environmental conditions and biological adaptability to the environment.	Sensors: RGB, multispectral, hyperspectral, LiDAR, thermal Temporal-spatial resolution: day to year; millimeter to decimeter	Individual detection [90, 143, 191, 217, 313, 251, 385, 399]; location [64, 82, 249]; number [69, 99]; growth [201, 250, 400]; crown structure [201, 249]; crown width [64, 249]; crown volume [365]; crown projection area [143]; height [64, 82, 249, 251, 384, 400]; stem diameter [55]; phenology [400]
Population	The variation of population size or quantity in time or space and its regulatory mechanisms.	Sensors: RGB, multispectral, hyperspectral Temporal-spatial resolution: month to year; centimeter to decimeter	Population size [163, 194, 262]; spatial distribution mapping [165, 167, 193, 196, 210, 231, 238, 360]; spatial and temporal variability [130, 164, 181, 275, 351]; seedling emergence [38, 95, 279, 309, 341]; phenological traits [239, 248]
Community	The relationship between community and environment. It mainly studies the structure, function, formation and development of plant community as well as the interrelationship with the environment.	Sensors: RGB, multispectral, hyperspectral, LiDAR, thermal Temporal-spatial resolution: month to year; centimeter to decimeter	Interspecific relationship [3, 37]; functional traits [4, 17, 36, 39, 43, 49, 61, 77, 78, 106, 180, 190, 247, 316]; canopy structure [16, 20, 81, 86, 91, 110, 184, 202, 219, 307, 394]; community structure [31, 65, 70, 75, 87, 94, 105, 111, 126, 282, 377, 379]; phenology [22, 27, 100, 256, 314, 392]; aboveground biomass [23, 57, 63, 131, 135, 138, 148, 152, 170, 182, 188, 218, 220, 258]; communities classification [32, 127, 224, 298, 327]; relationship between canopy variables and biodiversity patterns [40]; community recovery monitoring [42, 237]; community composition [47, 205, 225, 226, 263, 264, 356];

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Ecological scale	Ecological concerns	UAV data requirement	Previous studies using UAV remote sensing
			community disturbances [54, 141, 192]; community health [28, 72, 159, 236, 278, 369, 350]; spatial and temporal variability [74, 204, 207, 223, 355, 358, 368]; biodiversity [102, 333]; effect of canopy structure on light interception [376]
Ecosystem	The ecosystem processes, structures, functions, management, material cycles and energy flows.	Sensors: RGB, multispectral, hyperspectral, LiDAR, thermal Temporal-spatial resolution: month to decades; centimeter to decimeter	Plant diseases and insect pests [156, 227, 270, 273, 287, 293, 335, 342, 390]; productivity [35, 62, 83, 84, 96, 139, 145, 153, 166, 288, 391, 397]; biological invasion [183, 268, 340, 345]; ecosystem management [185, 265, 269, 276, 318, 397]; ecosystem monitoring [45, 260, 277, 297]; habitat monitoring [68, 80, 132, 304]; disturbance feedbacks [155]; environmental monitoring [234]; relationship between vegetation structure and the thermal environment [147]; influences of human disturbance [370]
Landscape	The spatial structures, interactions, coordination functions and dynamics of the entirety of many different ecosystems.	Sensors: RGB, multispectral, hyperspectral, LiDAR, thermal Temporal-spatial resolution: month to decades; centimeter to meter	Habitat fragmentation [48]; land cover classification [108, 154, 169, 187, 1299, 344]; vegetation type classification [109, 136, 198, 200]; farming landscape management [142, 176]; ecosystem phenology [206]

Note: The references can be found in Appendix S1: Reviewed references list.

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(Bradley and Taylor 2015; Merino et al. 2012). A fire management system on a UAV remote sensing platform was demonstrated in Yuan et al. (2015). In addition to fire management, the visual, thermal, multispectral, hyperspectral and LiDAR data acquired from UAV remote sensing can reveal the biotic and abiotic variations of an ecosystem (Valbuena et al. 2020). Such data are effective for long-term ecosystem monitoring and management. Mancini et al. (2013), for instance, used an SfM image-based approach to generate a DSM of a beach dune system in Italy; the essential features and complexity of the beach dune habitat were shown in the DSM, which provided basic data for future ecosystem management. In addition, the estimation of LAI, nitrogen content, pigment content and water stress via UAV remote sensing can provide a foundation for precise irrigation and fertilization in agriculture (Mathews and Jensen 2013). UAV remote sensing also serves as a cost-effective and flexible tool for monitoring ecological succession (de Almeida et al. 2020), restoration (Knoth et al. 2013; Zahawi et al. 2015) and natural resource management (Inoue et al. 2014; Shahbazi et al. 2014; Zhang et al. 2016).

At landscape scale, UAV remote sensing was mainly used to monitor habitat fragmentation (Yi 2016), land cover change (Cruz et al. 2017) and vegetation change (Nguyen et al. 2019). Fixed-wing UAV played a more important role in landscape scale studies due to its longer flight time. However, for land cover or vegetation monitoring, imagery with centimeter-level accuracy was helpful but not required and satellite data were sufficient for most landscape studies (Komarek 2020). Considering the distance of remote control (about 5 km), security and difficulty of data processing, UAV is not ideal for ecological studies on landscape scale. Thus, only a limited number of ecological studies using UAV remote sensing were carried out at landscape scale.

CHALLENGES AND PROSPECTS

UAV remote sensing in plant ecology faces a number of challenges.

Challenges in the use of UAV remote sensing systems

Regulatory constrains are major barriers for the use of UAV remote sensing in ecological studies (Allan *et al.* 2015; Rango *et al.* 2009; Werden *et al.* 2015). Stöcker *et al.* (2017) reviewed the current state of UAV regulations worldwide and reported that the

regulations were still preliminary and varied by region due to the rapid emergence of civil UAVs. In some regions, there are no government agencies established in charge of UAV regulation and management, and it is therefore difficult or time consuming to obtain permission to operate a UAV remote sensing system (Vincent *et al.* 2015).

Both the hardware and software of UAV remote sensing systems require improvement. Although more lightweight and smaller sensor systems have become available, they are still expensive. For instance, the Cubert S185 hyperspectral camera (Cubert GmbH, Germany) weighs only 490 g but costs about 88 000 US\$. A UAV LiDAR system generally costs about 120 000-170 000 US\$. It is worth mentioning that prices are dropping. Recently, a new UAV LiDAR system (DJI L1) that integrates a Livox LiDAR module and a mapping camera, has been officially on sale with a price about 12 000 US\$. Although its accuracy has yet to be verified, this low cost system will significantly improve its acceptance and promote the applications of LiDAR in plant ecology. In addition, the integration between UAV platforms and sensors requires improvement. Except for RGB imager, most of the multispectral, hyperspectral and thermal imager are built independent of UAV platform and need an extra GPS module (such as Cubert S185 hyperspectral imager, TC640 thermal imager). Only to UAV with fully integrated sensors, can sensors be triggered through the flight control system. The majority of UAVs, such as DJI M600 PRO do not allow an external device to share GPS information. Therefore, it is still challenging to link the GPS information of UAVs with the collected hyperspectral images, which complicates the data analysis for ecologists (Sha et al. 2018).

Challenges in image processing and analysis

Apart from data collection, data processing and analysis represents a main bottleneck of the ecological applications of UAV remote sensing. Compared with conventional aircraft aerial photography, UAV aerial photography is manifested by the low altitude of the flight platform and the small and nonspecialized camera (Whitehead and Hugenholtz 2014). The quality of data acquired by UAV depends on types of UAVs and cameras, which is often characterized by small image amplitude, RGB true color and high spatial resolutions. The attitude angle and heading of UAV often produce deviation and result in unstable photo swing angle and overlap due to the influence of air flow and wind direction. In addition, UAVs are

generally equipped with nonmeasurement cameras that requires high-cost processing. The nonlinear optical distortion (such as barrel or pillow distortion) on the image edge brings challenges for image mosaic and analysis (Hardin and Jensen 2011). The processing of UAV data is quite different from that of satellite data, which produces a new demand on data processing software. Due to the small coverage area of a single UAV image, the mosaic workload of orthographic images is significantly higher than that of satellite remote sensing images, which takes up the majority of processing time. For example, the mosaic of 2000 RGB images (each with 8256×5504 pixels) captured by Nikon D850 poses a great challenge for both software and hardware. Even with a highperformance computer, the image mosaic may need 15-20 h.

Image processing software such as Metashape and Pix4d mapper can perform automatic mosaic for high-resolution RGB images. However, it is still challenging to mosaic multispectral or hyperspectral images with low spatial resolutions, small spatial coverages and few image textures if no concurrent GPS data is available. Advanced algorithms such as scale invariant feature transform have been utilized to select matched points between multispectral images and mosaic images. This method was found to be less affected by image scaling and rotation, illumination change and 3D camera view (Lowe 2004; Ren et al. 2017). Also, with the increase of spatial and spectral resolutions, image processing becomes quite time consuming. As a result, more efficient algorithms need to be developed.

For data analysis, one challenge is the generality of the models used to estimate plant ecological parameters from UAV remote sensing data. Current studies on remote sensing of plant ecology are data dependent and case specific. The prediction models proposed in these studies are usually not generalizable due to the uncertainties in data collection and processing (especially radiometric correction), and the differences in sampled study areas, acquisition dates or plant species. The physically based method, to some extent, can solve the model transferability issue. This is because the physically based method can simulate the radiative transfer process within plant leaves and canopies under different circumstances (e.g. different leaf biochemical content, canopy structure and viewing geometry). Machine learning approaches have the potential to capture the nonlinear relationship between remote sensing data and vegetation parameters. By combining machine learning approaches and physically based models, prediction models with both flexibility and transferability could be developed.

There are also many challenges in fusing multisource remote sensing data. One is the coregistration of multisource data, which aims to geometrically align multisource images. In practice, images derived from multisensors tend to have various spatial resolutions (e.g. 30-cm vs. 2-m resolutions), georeference accuracies (e.g. 5-cm vs. 1-m geometric errors), spectral characteristics (e.g. RGB vs. NIR bands), acquisition dates (e.g. early vs. late growing seasons) and viewing geometries (e.g. back vs. forward scattering angles). All these factors greatly affect the searching for tie points among multisource images. This process in turn determines the coregistration accuracy. When it comes to the UAV-based remote sensing with large amounts of images, an automatic coregistration workflow is often needed. Recently, some progress has been made in this area. For instance, Scheffler et al. (2017) developed an open-source Python package 'AROSICS' (Automated and Robust Open-Source Image Co-Registration Software), which enables the automatic coregistration of multisensor satellite images. However, the applicability of this package to UAV-based images that usually have a higher spatial resolution still needs testing.

Another challenge is how to integrate the information derived from multisource remote sensing data. As mentioned above, multisource remote sensing data provide different information on ground objects. For instance, multispectral data can be used to infer the biophysical parameters of plants (e.g. LAI, percent vegetation cover), hyperspectral data to infer the biochemical or physiological parameters of plants (e.g. leaf chlorophyll and nitrogen contents) and LiDAR data to infer the structure parameters of plants (e.g. plant heights, gap fraction). Although most studies have shown the benefits of adding more information into analysis, there is no consensus on the framework of fusing multisource information. Some recent work indicates that machine learning algorithms (e.g. deep convolution neural networks) have the capability of integrating multisource information at different levels (Yao et al. 2019).

Automatic species identification

Species classification provides a foundation for assessing many plant community properties, such as community composition, structure and biodiversity. At present, most species classifications via UAV remote sensing require human participation and

interpretation. The accuracy relies on many factors including sensor type, the integration between the UAV platform and the sensor, image resolution, habitat complexity, operator experience and the coordination between ecologists and technologists. With 'big data analytics' and machine learning especially coevolutionary technology, network algorithms for image processing (Brodrick et al. 2019), automatic species identification through UAV remote sensing is becoming increasingly feasible (Jin et al. 2018; Sandino et al. 2018). If the dataset used for training is 'big' enough, computer learning should theoretically generate a satisfactory classification outcome. Crowdsourcing, i.e. the outsourcing of tasks or data collection among a large group of nonprofessionals, has been demonstrated to be an effective approach for big database construction (Minet et al. 2017).

The ground-UAV-airplane/satellite multiscale monitoring system

UAV remote sensing bridges the gaps between ground observations and manned aircraft and satellite remote sensing. This bridge makes it possible to answer basic ecological questions across multiple scales. For instance, D'Oleireoltmanns *et al.* (2012) used UAV to acquire the visual images of a soil erosion area in Morocco at 70 and 400 m height and analyzed the distribution, volume and temporal dynamics of gullies at a local scale. Then the authors assessed the mechanism of soil erosion at the sampled

sites and across the entire region by combining UAV remote sensing with satellite images. The multiscale sampling method can also be used to monitor the biodiversity changes at different scales (Gonzalez et al. 2020; Guo et al. 2016a) and help to detect the form and drivers of biodiversity-ecosystem function relationships across space and time (Williams et al. 2021). Under this premise, the research of spatial scaling of ecological stability might also benefit from ground-UAV-satellite monitoring system (Wang et al. 2017). Similar applications of a ground-UAV-satellite framework have been reported for precision agriculture (Matese et al. 2015; Zecha et al. 2013) and land management (Browning et al. 2016). Most of the satellite images are available for public research access. A number of platforms, such as Google Earth Engine (GEE), EarthServer, Docker and the Coupled Model Intercomparison Project (CMIP), have been increasingly used in ecological and environmental studies due to the cloud-based geospatial processing capability and the access to a large collection of geospatial datasets such as Landsat and MODIS without requiring downloading and local handling of the images (Baumann et al. 2015; Gorelick et al. 2017; Liang et al. 2020). The higher resolution images from UAVs can serve as 'ground truth data' to train and validate the processing of in-cloud images in these platforms, thereby facilitating the construction of a ground-UAV-airplane/satellite multiscale ecological monitoring system.

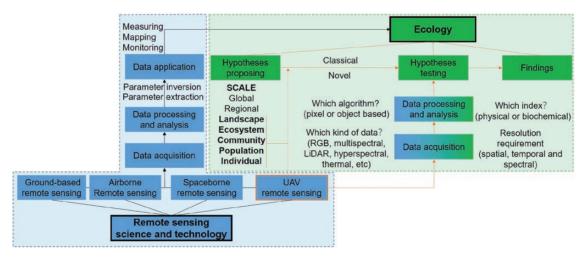


Figure 4: The connection between UAV remote sensing and ecology. The contents in blue boxes belong to remote sensing science and technology and those in green boxes belong to ecology. The boxes with half blue and half green represent the interdisciplinary parts. UAV remote sensing is suitable for answering ecological questions derived at individual, population, community, ecosystem and landscape scales. In addition to classical ecological questions, there are some novel questions need to be answered, for instance, the relationship between tree crown structure and species competition; the relationship between canopy biochemical feature and environmental change.

From describing ecological phenomenon to answering ecological questions

The majority of the reviewed studies were published on journals in the field of remote sensing with emphasis on remote sensing technology rather than on ecological issues. Only a few papers focused on answering some basic ecological questions, i.e. the relationship between organisms and the relationship between organism and environment (Rissanen et al. 2019; Waite et al. 2019; Zhang et al. 2016; Zhao et al. 2020). Most of previous studies have focused on ecological phenomenon descriptions, i.e. retrieving ecological parameters through UAV remote sensing. Furthermore, these studies rarely examined these parameters to answer ecological questions. There is now a strong call to join technological developments with scientific challenges to answer basic scientific questions (Santos et al. 2018).

UAV remote sensing opens new possibilities in plant ecology by addressing classical ecological questions at different ecological scales. Ecologists and remote sensing experts should collaborate to determine how data can be collected and analyzed by UAV remote sensing systems to understand ecological processes, such as photosynthesis, nutrient cycling, interspecific relationships and succession (Fig. 4). At the individual scale, crown maps can be linked with environmental variables to explore the adaptive evolution of species and interspecific relationship, such as the relationship between crown shape, environmental factors and interspecies competition. At the community scale, traditional measurements limited to subcanopy/understory can be combined with parameters of overstory captured by UAV to study community composition and structure, including but not limited to canopy structure, plant functional traits and diversity. At the ecosystem scale, maps or parameters derived from UAV remote sensing can be linked with flux tower measurements to investigate ecosystem process and function, especially ecosystem disturbances (Table 2).

Novel methods are needed to fully exploit the use of UAV data

A number of tools or products developed by remote sensors have played a great role in promoting ecological research. These tools or products originate from spaceborne and airborne remote sensing data and generally focus on solving issues on landscape, regional and global scales. With the development of UAV remote sensing, data and products with ultra-high spatial resolutions have been available for ecological studies at scales from individual to ecosystem. From species identification to community's biophysical and biochemical structure detection, the new research direction has presented new challenges to the development of remote sensing tools or products.

UAVs bring a 'bird's view' of ecosystems to ecologists, and the view is unprecedentedly clear. However, the value of these data is not fully exploited if they are simply used to retrieve the traditional parameters that can be collected on the ground, such as height, DBH or species diversity. UAV remote sensing data include the color, shadow, density and three-dimensional properties of the canopy, but the quantification and analysis of such data with the goal of answering ecological questions remains a challenge. Previous studies have tried to construct canopy chemical assemblies from living vegetation volumes, and geometrical characteristics of canopy gaps in order to better use UAV remote sensing data (Asner et al. 2014; Getzin et al. 2014). More ecologically meaningful parameters need to be extracted from those data to better understand the canopy surface irregularity and community heterogeneity. In addition to traditional species biodiversity, new metrics need to be developed to include color, biochemical and canopy structure diversity for biodiversity assessment. Furthermore, many interesting ecological phenomena on canopy and community scale such as the crown shape under different species competition intensity can be further understood by ecologists using UAV remote sensing. Data collection and processing of UAV remote sensing is new and complicated for most ecologists, strengthened collaboration between ecologists and remote sensing professionals is needed to promote the application of UAVs in plant ecology and to answer both old and new ecological questions.

CONCLUSIONS

UAV remote sensing bridges the gaps in both scale and resolution between ground observations, conventional manned aircrafts and satellite remote sensing. The maturity of civilian UAV technology is the origin of ecological application of UAVs, and the emergence of SfM photogrammetry promotes the ecological applications of UAV. Mapping, measuring and monitoring of vegetation are three major applications of UAV remote sensing in plant ecology.

From the species to population scale, physiological assessment, species identification and population mapping are the most reported uses of UAV in the literature. Physiological assessment through UAV remote sensing provides a basis for precision ecosystem management. Nevertheless, the ecological applications need to further integrate remote sensing data and ecological process. Species identification and population mapping are the foundation of studies on biodiversity and many ecological processes. The accuracy of species identification in complex habitats could be improved by the integration of big data technology with a machine learning approach. At the community scale, community structure, diversity and biomass are the major concerns of ecologists, but the application of UAVs in these areas are still in early stages. At the ecosystem scale, ecosystem monitoring and management are the primary research fields of interest for UAV application. UAV remote sensing has played an essential role in fighting forest fires, monitoring ecosystem restoration and providing precision crop management. Future applications of UAV remote sensing in plant ecology should deploy the ground-UAV-airplane/satellite multiscale remote sensing system. Most of the ecological applications of UAV remote sensing have been driven by improving the technology rather than answering ecological scientific questions. Close collaboration between ecologists and remote sensing experts is now needed to improve the use UAV remote sensing for resolving ecological questions.

Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Appendix S1: Reviewed references list and template of reviewed studies.

Appendix S2: A comparative cost analysis of airborne, spaceborne and drone-based remote sensing system and a detailed description of main characteristics of UAV remote sensing case studies in plant ecology.

Figure S1: Number of UAV studies classified by (a) publication year, (b) sensor type, (c) study scale and (d) processing method.

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Authors' Contributions

Z. Sun and Y. Xie conceived the study; Z. Sun and X. Wang acquired the data; Z. Sun, L. Yang and Y. Huang analyzed the data; Z. Sun wrote the first draft; Z. Wang contributed to the revision of the text. All authors provided input to the final draft.

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