

REVIEW

Grime Review: What can remote sensing do for plant ecology?

Inferring plant–plant interactions using remote sensing

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Abstract

1. Rapid technological advancements and increasing data availability have improved the capacity to monitor and evaluate Earth's ecology via remote sensing. However, remote sensing is notoriously 'blind' to fine-scale ecological processes such as interactions among plants, which encompass a central topic in ecology.
2. Here, we discuss how remote sensing technologies can help infer plant–plant interactions and their roles in shaping plant-based systems at individual, community and landscape levels. At each of these levels, we outline the key attributes of ecosystems that emerge as a product of plant–plant interactions and could possibly be detected by remote sensing data. We review the theoretical bases, approaches and prospects of how inference of plant–plant interactions can be assessed remotely.

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3. At the individual level, we illustrate how close-range remote sensing tools can help to infer plant–plant interactions, especially in experimental settings. At the community level, we use forests to illustrate how remotely sensed community structure can be used to infer dominant interactions as a fundamental force in shaping plant communities. At the landscape level, we highlight how remotely sensed attributes of vegetation states and spatial vegetation patterns can be used to assess the role of local plant–plant interactions in shaping landscape ecological systems.
4. *Synthesis.* Remote sensing extends the domain of plant ecology to broader and finer spatial scales, assisting to scale ecological patterns and search for generic rules. Robust remote sensing approaches are likely to extend our understanding of how plant–plant interactions shape ecological processes across scales—from individuals to landscapes. Combining these approaches with theories, models, experiments, data-driven approaches and data analysis algorithms will firmly embed remote sensing techniques into ecological context and open new pathways to better understand biotic interactions.

KEYWORDS

alternative stable states, community structure, competition, facilitation, non-invasive imaging, plant–plant interactions, remote sensing, self-organization, spatial pattern, transient dynamics

1 | INTRODUCTION

The use of remote sensing technologies to capture broad-scale ecological patterns is rapidly expanding. In plant ecology, the enhanced ability of remote sensing to collect biophysical and physiological data opens a wide range of opportunities to systematically characterise the development and performance of individual plants, the composition and structure of plant communities, and the functioning and dynamics of ecosystems in a fast, non-destructive way, at multiple spatiotemporal scales (Gamon et al., 2016; Magney et al., 2019; Zellweger et al., 2019). Despite the continuous developments, remote-sensing applications lack significant capacities, especially regarding the inference of key ecological processes. For example, it is notoriously challenging to remotely sense how plants interact with one another, which is a central question in plant ecology. Plant–plant interactions often act as key drivers of community assembly and functioning (Bilas et al., 2021) and determine evolutionary processes (Thorpe et al., 2011). They also play a central role in dictating primary productivity (Postma et al., 2021) and mediating climate change impacts on ecosystems (van Loon et al., 2014).

Inferring the direction and magnitude of plant–plant interactions has strongly relied on manipulative experiments that are labour-intensive and time-consuming and are therefore often restricted to small spatiotemporal scales (Schöb et al., 2012). Also, traditional approaches often interfere with the studied system, hampering result replication (Catchpole & Wheeler, 1992; Jimenez-Berni et al., 2018). These drawbacks typically fall into the domain where remote sensing technologies have clear advantages. However, the link between

plant–plant interactions and remote sensing indicators remains elusive.

Emerging research is beginning to overcome this major barrier. Clearly, interactions *per se* cannot be directly captured by sensors. However, many outcomes of key plant–plant interactions in shaping plant traits, community structure, ecosystem states, and landscape patterns can be reflected in remote sensing signals (e.g., Getzin et al., 2022; Xu, Holmgren, Van Nes, Maestre, et al., 2015). Therefore, many interaction attributes (e.g., direction and strength) can be indirectly inferred through remote sensing of interaction outcomes. Developing reliable remote sensing approaches to plant–plant interactions hinges on linking remote sensing signals with interaction attributes and interaction outcomes. Establishing these links necessarily requires the systematic integration of remote sensing tools with ecological theories, field observations, experiments and models. This paper reviews how remote sensing technologies can help infer plant–plant interactions and improve understanding of their roles in shaping ecological systems from individual to landscape levels (Figure 1). Our scope is focused on the following aspects:

- (i) Competition and facilitation—which are the key interactions in shaping plant communities (Holmgren et al., 1997).
- (ii) Three types of interaction inference:
 - mechanisms of pairwise plant–plant interactions (Inference I);
 - relative strengths of particular plant–plant interactions (Inference II);
 - emerging net outcomes of co-occurring plant–plant interactions (Inference III).

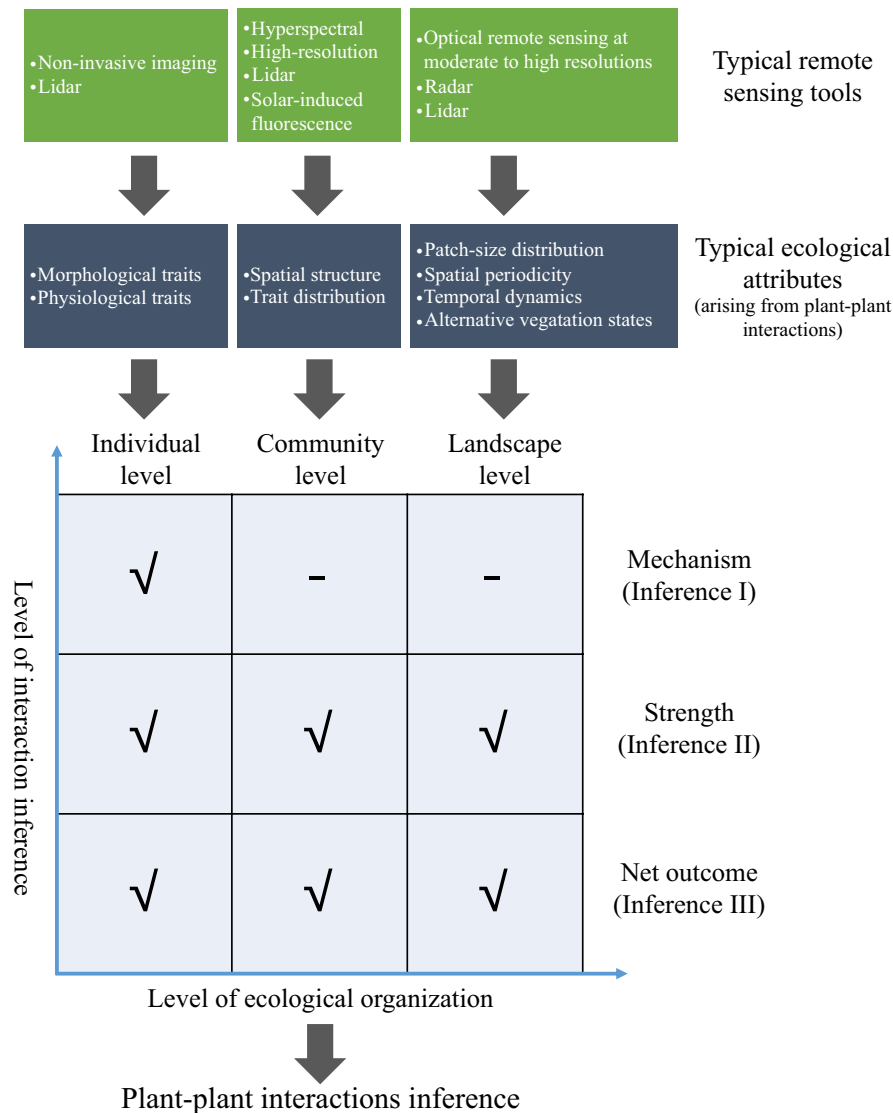


FIGURE 1 A general framework illustrating the use of remote sensing tools for inferring plant–plant interactions. Note that the listed items are not necessarily exclusive to each other for ‘remote sensing tools’ and ‘ecological attributes’.

(iii) Three levels of ecological organization:

- individual level (Section 2), at which interactions have typically been inferred by changes of morphological, physiological and functional traits of interacting plant individuals/species in the field or in experimental settings;
- community level (Section 3), at which interactions have typically been inferred by scrutinizing spatial and functional structures (e.g., over- or under-dispersion) of plant communities. While the term ‘community’ may be used for a wide range of spatial scales (Vellend, 2016), here the community level is restricted to a field plot scale, typically 10–100m².
- landscape level (Section 4), at which landscape patterns and states, in combination with theoretical models, can indicate interactions from snapshots or time series of remote sensing data.

At each level, we summarize the key plant–plant interaction outcomes captured by remote sensing data (Table 1) and review

the relevant theoretical bases and approaches of how plant–plant interactions can be inferred by remotely measuring these outcomes. This non-exhaustive review focuses on key ideas, transformative approaches, major challenges and future outlooks toward building rigorous links between remote sensing and ‘cryptic’ biotic interactions.

2 | INFERRING INDIVIDUAL-LEVEL INTERACTIONS WITH CLOSE-RANGE REMOTE SENSING

Remote sensing has been mostly applied to characterise large-scale systems. However, incorporating (high-precision) remote sensing tools at small spatial scales substantially enhances measurement efficiency for individual plants and can verify its reliability at larger scales (Lines et al., 2022). More importantly, this extended application of remote sensing tools, in combination with other innovative technologies,

TABLE 1 Summary of elements in inferring plant–plant interactions using remote sensing, including biotic/ecological attributes, typical remote sensing tools used for measuring these attributes, and inference of interactions that could be made correspondingly. Inference I: mechanisms/pathways of particular plant–plant interactions; Inference II: relative strengths of particular plant–plant interactions; Inference III: net outcomes of co-occurring plant–plant interactions

| Level | | Attributes measured | Typical remote sensing tools | Inference |
|--|---|--|---|-----------------------------|
| Individual | Whole plant | Volume, height, biomass | Non-invasive imaging, lidar | II & III |
| | | Leaf | Size (e.g., length, width, area, volume) | Non-invasive imaging, lidar |
| | | Posture (e.g., zenith, azimuth and dihedral angles) | Non-invasive imaging, lidar | I, II & III |
| | | Chemistry (e.g., chlorophyll, water, nutrients, structural and defence components) | Hyperspectral, multispectral, lidar | I & II |
| | | Temperature | Thermal imaging | II |
| | Branch | Size (e.g., length, diameter, volume) | Non-invasive imaging, lidar | II & III |
| | | Posture (e.g., zenith, azimuth, and dihedral angles) | | I & II |
| | | Spatial occupation within crown | | II & III |
| | Crown | Size (length, width, depth, volume, projected leaf area) | Non-invasive imaging, lidar | II & III |
| | | Openness, foliar density, branch density | | II & III |
| | | Foliar physical profile (area, volume) | | I & II |
| | | Foliar chemical profile (e.g., chlorophyll, element contents) | | I & II |
| | | Spatial occupation openness (e.g., foliar density, branch density) | | II & III |
| | Stem | Size (e.g., volume, diameter) | Non-invasive imaging, lidar | II & III |
| | | Height | | I, II & III |
| Reproduction | Flower (inflorescence volume) | Non-invasive imaging, lidar | II & III | |
| | Fruit (volume, shape) | | II & III | |
| Root | Single root (e.g., diameter, length, orientation, volume) | Tomographic technologies | I & II | |
| | Root system (e.g., distribution, biomass, density) | Tomographic technologies, ground-penetrating radar | I, II & III | |
| Community | Spatial attributes | Plant locations | Lidar | II & III |
| | | Plant density | | |
| | | Plant size (e.g., tree height, crown volume, diameter at breast height) | | |
| | | Canopy architecture (radiation regime, leaf orientation distribution) | | |
| | | Leaf area index | | |
| | Spectral attributes | Vegetation indices | Hyperspectral, multispectral, lidar, solar-induced fluorescence | II & III |
| Leaf mass area | | | | |
| Foliar chemistry (e.g., chlorophyll, water, nutrients) | | | | |
| Landscape | Landscape pattern | Patch-size distribution | Hyperspectral, multispectral, lidar | II & III |
| | | Spatial periodicity | | |
| | | Other spatial distribution features | | |
| | Vegetation state | Alternative stable states | Hyperspectral, multispectral, lidar | II |

provides opportunities for testing fundamental theories and generating new insights on plant–plant interactions. In this context, we refer to these tools as ‘close-range remote sensing’, which includes close-range photogrammetry, terrestrial lidar and other relevant imaging technologies that are not conventionally classified as remote sensing (such as ‘phenotyping’: Fiorani & Schurr, 2013; Sun et al., 2022).

Generally, it is straightforward to infer the net outcomes and strengths of plant–plant interactions (i.e., Inference II and III) at the individual level. For example, in well-controlled settings for paired/grouped plant individuals that compete for certain resources or facilitate one another, one can directly make these inferences by using close-range remote sensing tools to measure relative changes in

relevant plant traits (Figure 2a-e). By controlling the confounding factors and identifying the increase or decrease of a particular trait (for example, measured by the response ratio index), the resulting plant performance can be attributed to positive or negative interactions (Nash Suding et al., 2003). The most obvious example is the positive or negative density dependence of plant size. By contrast, it is often less straightforward to infer the mechanisms underlying particular plant–plant interactions (i.e., Inference I). One central reason is that plant–plant interactions include a range of diverse mechanisms, likely involving allelopathy (Wang et al., 2021), competition for light or water (Huber et al., 2021), plant–soil feedback (Crawford et al., 2019), and trophic cascades (Huang et al., 2019), to name a few. We cannot cover the numerous mechanisms, but use above- and below-ground examples to illustrate how remote sensing can boost interaction inference, especially where remote sensing tools play a game-changing role.

2.1 | Inferring above-ground interactions with close-range remote sensing of plant traits

Morphological, physiological and functional traits are tightly linked to resource-acquisition and stress-response efficiency of plants (Kunstler et al., 2016), driving the processes and reflecting the outcomes of plant–plant interactions (Butterfield & Callaway, 2013; Gross et al., 2009). Measuring plant traits is therefore essential to the inference of plant–plant interactions at the individual level. Non-invasive optical imaging techniques, which are the major components of current ‘plant phenotyping’ methods, have been widely used.

Competition for light is an example of inferring above-ground interaction mechanisms using non-invasive imaging. A classic hypothesis is that the red-to-far-red ratio (R:FR ratio, wavelengths of red and far red lights are around 660 and 730 nm, respectively)

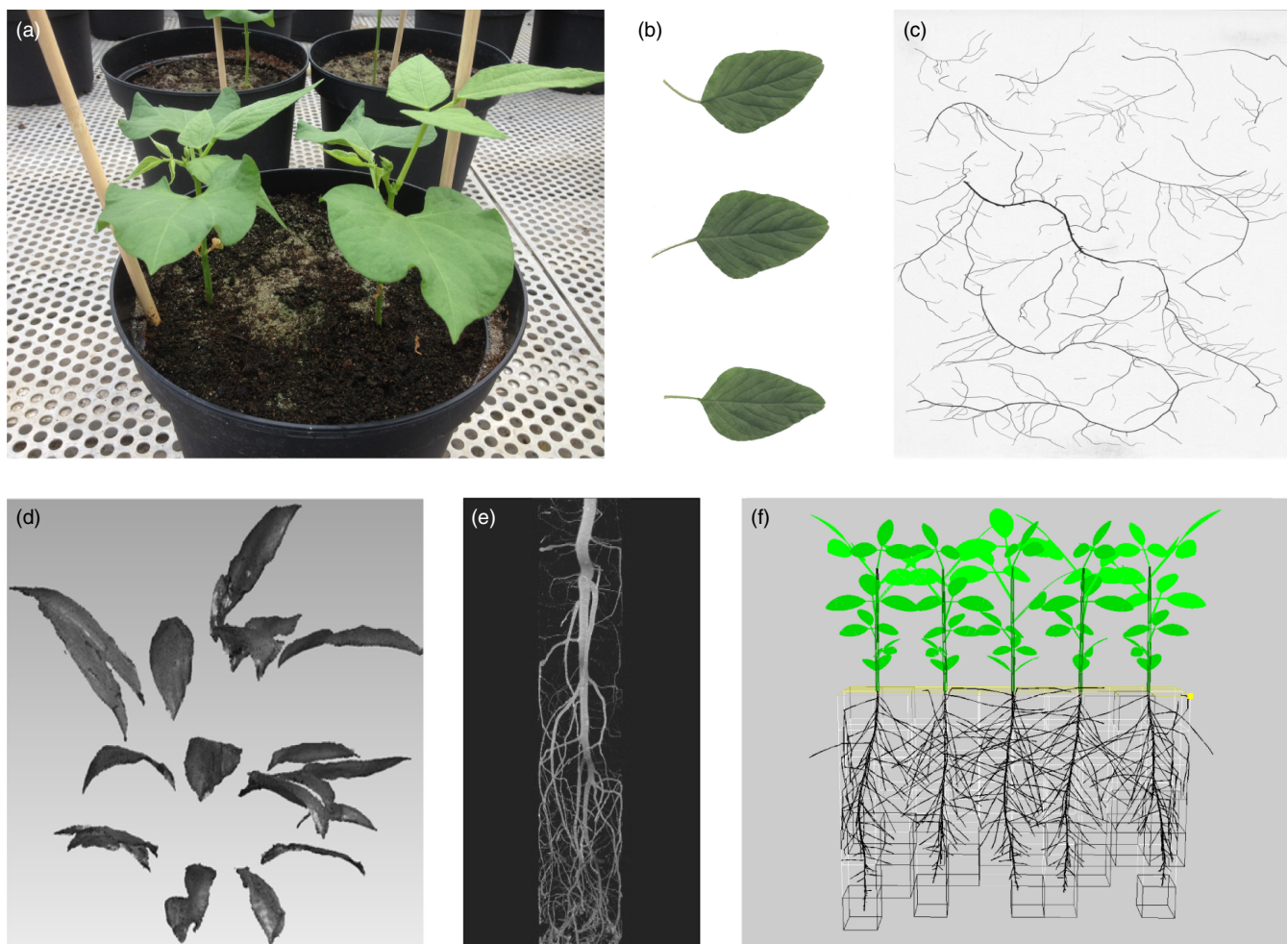


FIGURE 2 Illustrations of close-range remote sensing data in studies of plant–plant interactions at the individual level. (a) A typical laboratory setting where plants are grown in the vicinity of neighbours. Conventional hand-based methods of measuring (b) above- and (c) below-ground plant traits are often time-consuming. Non-invasive imaging as a close-range remote sensing tool can measure plant traits with high precision and efficiency. For example, (d) point cloud data from lidar can be used to reconstruct single leaves and spatial distribution of leaves, which can be used to retrieve the leaf size and posturing of plants. (e) Structure and distribution of root systems can be non-invasively measured and routinely tracked by MRI. Remotely sensed traits can be used to validate functional-structural plant models. (f) The well-validated models in turn can help to validate remote sensing inferences and to better predict the outcome of plant–plant interactions. The figure of an MRI-scanned root system in (e) is provided by IBG-2: plant sciences, Forschungszentrum Jülich.

serves as a cue for light competition between neighbouring plants (the ratio is circa 1.2 for direct sunlight, but becomes much lower than 1 for light that is intercepted or reflected by leaves) (Fernández-Milmanda & Ballaré, 2021; Huber et al., 2021). To test this hypothesis, a typical experimental design is to treat focal plants with fixed light availability but with higher fractions of far-red radiation, which mimic the changes of R:FR ratio induced by neighbouring plants (e.g., Chitwood et al., 2015; de Wit et al., 2016; Vandenbussche et al., 2005), while precluding potential confounding factors invoked by the 'true' presence of neighbours (such as lower light availability) (Morgan & Smith, 1976). In these experiments, plant traits, for example, height, leaf angle and tillering, are compared between the treatments and the references to isolate the competition effect induced by the R:FR ratio (e.g., Casal et al., 1987; Gruntman et al., 2017; Rajcan et al., 2004). Shade-intolerant plants use declines in the R:FR ratio to infer the presence of competitors and respond with the 'shade avoidance syndrome,' for example, by increased elongation of petioles and stems, upward movement of leaves, and reduced branching or tillering (Huber et al., 2021) to maximize light capture (Vermeulen et al., 2008).

In light competition experiments, conventional hand-based measurements of plant traits are highly time-consuming and, more importantly, cause significant bias through disturbances. Even non-destructive plant handling can activate thigmomorphogenic pathways that may alter plant phenotypes (Braam & Davis, 1990). A range of non-invasive imaging technologies can solve these challenges by retrieving the 3-D structure of plant organs or the whole plant with high precision. These techniques may include passive methods such as 'stereoscopic imaging' (Biskup et al., 2007), 'structure-from-motion imaging' (Zhang, Teng, et al., 2016), and 'light field imaging' (Apelt et al., 2015), and active techniques such as 'time-of-flight camera imaging' (Klose et al., 2009), 'laser triangulation' (Kjaer & Ottosen, 2015), and 'light detection and ranging (lidar)' (Omasa et al., 2007). Notably, application of these techniques is still challenging; for example, resolving small branches and individual leaves under windy conditions (Disney, 2019) or measuring very fine traits *per se* (e.g., leaf thickness, Dupuis et al., 2017).

Another example of inferring above-ground interactions via non-invasive imaging comes from the studies of 'induced defence'. Plant individuals under herbivore attack or other stress may release chemicals as 'early warning cues' that can be recognized by other individuals (Karban et al., 2006). This interaction produces a facilitative effect by helping the neighbouring plants prepare for the upcoming adverse impacts, for example, through amplified expression of genes resistant to insect herbivory (Markovic et al., 2018). Do Prado Ribeiro et al. (2018) used time-series hyperspectral imaging to show that changes in the concentration and composition of leaf chemicals can be captured by changes in the spectrum of leaf reflectance. They observed different spectral reflectance between the insect-infected and non-infected solitarily grown plants. However, such differences vanished when the non-infected plants shared air or soil with the infected plants, suggesting that above- and below-ground

communications with the infected plants cause non-infected plants to defend themselves. This hyperspectral remote sensing approach enables non-invasive identification of defence responses in high temporal detail, which has been impossible using traditional lab approaches. In this sense, close-range remote sensing provides a transformative approach for inferring the existence of induced defence, which may also be applied to other interactions.

2.2 | Seeing the hidden half: new insights into below-ground interactions with remote sensing

Below-ground plant–plant interactions are notoriously difficult to infer. Optical imaging techniques based on rhizobox (e.g., Ljubotina & Cahill, 2019) and transparent potting media (e.g., Fang et al., 2013) have been used to measure root interactions non-destructively in 2-D and 3-D, respectively. Penetrable imaging techniques such as X-ray computed tomography (Gregory et al., 2003), magnetic resonance imaging (MRI, Pflugfelder et al., 2022), photoacoustic tomography (Proto et al., 2020) and ground penetrating radar (Liu et al., 2018) can be used to measure the distribution and development of root systems in real soils and their response to below-ground interactions with neighbours.

Moreover, these close-range remote sensing tools need to be supplemented with other technologies to improve inference of interaction mechanisms. For example, Faget et al. (2013) used a rhizobox setup equipped with the planar optode technique to study inter-specific root interactions between maize and bean plants. As a real-time 2-D luminescent imaging method, the planar optode technique can capture fluorescence from specific-light-excited analyte-specific indicators, thereby measuring the concentrations of soil substances such as H^+ (pH), O_2 , CO_2 , NH_4^+ and NO_3^- (Li et al., 2019; Pedersen et al., 2015). By repeatedly imaging rhizospheric soil pH over time under single-individual and paired-individual treatments, Faget et al. (2013) demonstrated that root secretions of beans can acidify soils in the inter-specific root intermingle zones, increasing phosphorus availability for maize (Zhang, Zhang, et al., 2016). This inferred facilitative effect explains the elevated production in maize-bean intercrops (Li et al., 2003) even when roots strongly overlap, which is often interpreted as a sign of intensified inter-specific root competition (Chen et al., 2020). To date, the application of planar optode imaging remains scarce in below-ground interaction studies, but show a great potential in combination with close-range remote sensing of roots.

For plants that have complex root systems, it is difficult to directly differentiate between the roots of individual plants. The fluorescent protein technique can overcome this obstacle in combination with root imaging (e.g., Weidlich et al., 2018). The roots of a focal plant that has genetically been transformed to express fluorescent protein can be distinguished from root crowds when excited by light with a specific wavelength and then imaged with a light-filtered camera (Faget et al., 2009). Using this technique, Geisler-Lee et al. (2017) tracked the development of a 3-D root system of a green-fluorescent-protein labelled *Arabidopsis thaliana* in response

to intraspecific neighbour density in transparent gels. Interestingly, in contrast to the widely accepted hypothesis that the direction of root horizontal extension of plants should preferentially go towards unoccupied spaces, they found a periodic spiral-like hot-spot pattern of root growth regardless of the density or locations of neighbours. Clearly, the potential of fluorescent protein techniques are far beyond illustrating root distributions. By coupling the expressions of the fluorescent protein gene with other specific genes in plant roots (Rellán-Álvarez et al., 2015), it is possible to investigate mechanisms of belowground interactions in detail.

2.3 | Integrating remote sensing with functional-structural plant models

Plant models can help to validate remote sensing inferences and to predict the outcome of plant–plant interactions (Figure 2f). Functional-structural plant (FSP) models simulate plant growth and development in 3-D as a function of the availability of resources such as light, water and nutrients (Louarn & Song, 2020). Competitive interaction between plants is therefore an emergent property of such models. Using these models, plant- and field-level traits, such as height, leaf area index and root length density can be predicted by considering the interaction between plants. Such models typically contain many parameters defining plant traits related to growth, development and architecture. Considerable amounts of data at the whole plant and population levels are needed to parameterise these models properly and evaluate the predictive performance of FSP models in terms of whole plant and canopy growth (Evers et al., 2018). Ideally, such data are collected over time, allowing temporal dynamics to be captured. Non-invasive and non-destructive quantification of these traits is therefore preferred, and this is where remote-sensing techniques can play an important role (O'Sullivan et al., 2021). For example, Perez et al. (2022) suggested that integrating lidar-derived shoot architectural parameters of oil palm with an FSP model can help quantify shoot allometry in relation to neighbourhood competition intensity. By calibrating and validating an FSP model of root systems using the MRI data of root development and associated soil-water movement of pot-grown *Lupinus albus*, Koch et al. (2019) assessed the relationships between root architecture dynamics and water uptake. These relationships—obtained by integrating FSP models and remote sensing—provide an important basis for inferring plant–plant interactions. If the assumed interactions in FSP models yield good fits with observed plant growth, then the interactions could be considered realistic.

3 | INFERRING INTERACTIONS FROM REMOTELY SENSED COMMUNITY STRUCTURE

Dominant plant–plant interactions often play essential roles in shaping the composition and structure of ecological communities. At

the community level, ecologists are often interested in inferring the dominant interaction types and strengths (Interference II and III) that emerge across all species to shape the community (Gross et al., 2009; Liancourt & Dolezal, 2021). We discuss how these interaction inferences can be made based on community structure in terms of spatial (Section 3.1) or trait distributions (Section 3.2). Our examples are mostly from forest communities, but similar approaches can also be applied to other (more open) ecosystem types, such as shrublands (Chacón-Labela et al., 2016) and savannas (Xu et al., 2011).

3.1 | Linking interactions to remotely sensed spatial community structure

Many aspects of community structure have causal relationships with plant–plant interactions. Plant density as a measure of crowdedness might be the simplest structural metric relevant to interaction inference. For example, several studies have used density-based indices as proxies of competition intensity within forest communities, where higher crowdedness is interpreted as stronger competition (Van Mantgem et al., 2009; Zhang et al., 2015).

Point pattern analysis based on spatial locations of plant individuals obtained from high-resolution optical images or lidar data have been extensively used for inferring plant–plant interactions (Inference III; Atkinson et al., 2007; Garzon-Lopez et al., 2014; Moustakas et al., 2008). Local facilitation tends to lead to higher frequencies of co-occurrence of the interacting plants. As a result, community structure is expected to face spatial under-dispersion compared with spatial randomness. At the same time, competition is expected to lead to over-dispersed patterns. Therefore, over- and under-dispersion in space, detected for example by the multi-scale pair correlation $g(r)$ function, may reflect the signals of competition and facilitation between plants, respectively (Wiegand & Moloney, 2014). However, there are important caveats when inferring specific plant–plant interactions from point pattern information, primarily because similar spatial patterns may arise from completely different processes. For instance, both facilitation and dispersal limitations can lead to under-dispersion (Wiegand & Moloney, 2014).

Spatial structural information on plant performance has been used to infer the strengths of facilitation and competition (Inference II). In studies of biodiversity-ecosystem functioning (BEF) relationships, the growth performance of focal plants has been linked to species diversity in the neighbourhood (Fichtner et al., 2017; Fichtner et al., 2018). A positive association between focal plant growth performance and neighbour species richness has led to the conclusion that local facilitation may contribute to the positive BEF relationship (Inference III; Fichtner et al., 2018).

Remotely sensed canopy architecture may help to infer the intensity of light competition between plants. For example, the extent of crown overlap (Figures 3 and 4) is a straightforward indicator for assessing the difference in available light resources between individual plants (or functional groups), thus helping to infer competition for light. Refined indicators can be generated by further in-depth analyses

quantifying the effective leaf area index (LAI), distinguishing between sunlit and shaded leaves, or characterising the detailed radiation regime in three dimensions across the entire community. More detailed and precise competition inference may be achieved by using radiative transfer models that incorporate physiological processes (e.g., photosynthesis and respiration), which are driven by structural and spectral remote sensing metrics (Kattenborn et al., 2017; Ligot et al., 2014). The above-mentioned approaches typically use information on plant identity, spatial location, growth performance, or canopy structure. Hyperspectral, high-resolution optical and lidar remote sensing tools are especially powerful for obtaining such information.

A central challenge is to accurately identify/segment individual plants from the community (Lines et al., 2022). In relatively open ecosystems (e.g., savannas), this goal can be achieved by using many types of remotely sensed data (e.g., high-resolution optical images and lidar data: Chen et al., 2006; Jing et al., 2012; Mishra & Crews, 2014). However, significant methodological hurdles remain for closed

ecosystems such as dense forests, where automatic segmentation algorithms of trees are often inaccurate, even for very-high-resolution data such as terrestrial laser scanning (TLS; Lines et al., 2022). This is especially relevant in mixed forest stands with heavily overlapping tree crowns or low crown base height, which prevent the identification of tree stem locations as seed points of a TLS-based algorithm to segment tree crowns. Moreover, separating the points in the crown-overlapping regions is the most challenging part of automatic segmentation algorithms. This problem may be solved by using comprehensive point cloud data to combine both terrestrial and aerial laser scanning systems with the support of advanced algorithms (Lines et al., 2022).

3.2 | Inferring interactions from trait distributions

Distributions of plant functional traits across the community can provide vital information for inferring plant-plant interactions (Inference II

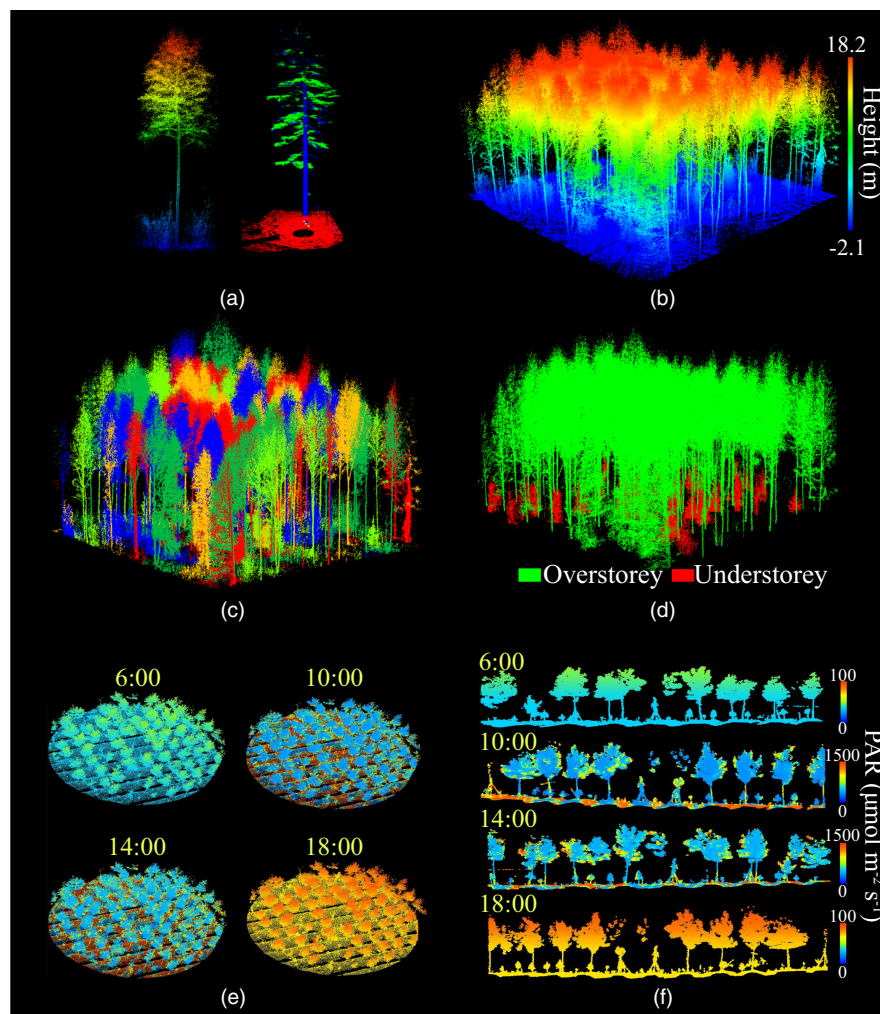


FIGURE 3 Illustrations of terrestrial laser scanning (TLS) data for characterizing tree and forest structures. (a) TLS point cloud data for individual trees with colours representing height (left) and different parts including photosynthetic (leaves) and non-photosynthetic (stems and branches) components. (b) TLS point cloud data for a forest stand with colours representing height. (c) Identification of individual trees from the TLS data based on an automatic segmentation algorithm; (d) Differentiation of overstorey vs. understorey tree individuals from the TLS data based on an automatic segmentation algorithm; (e) A 3-D and (f) 2-D view of the spatial distribution of hourly photosynthetic active radiation (PAR) calculated using TLS data and a radiative transfer model.

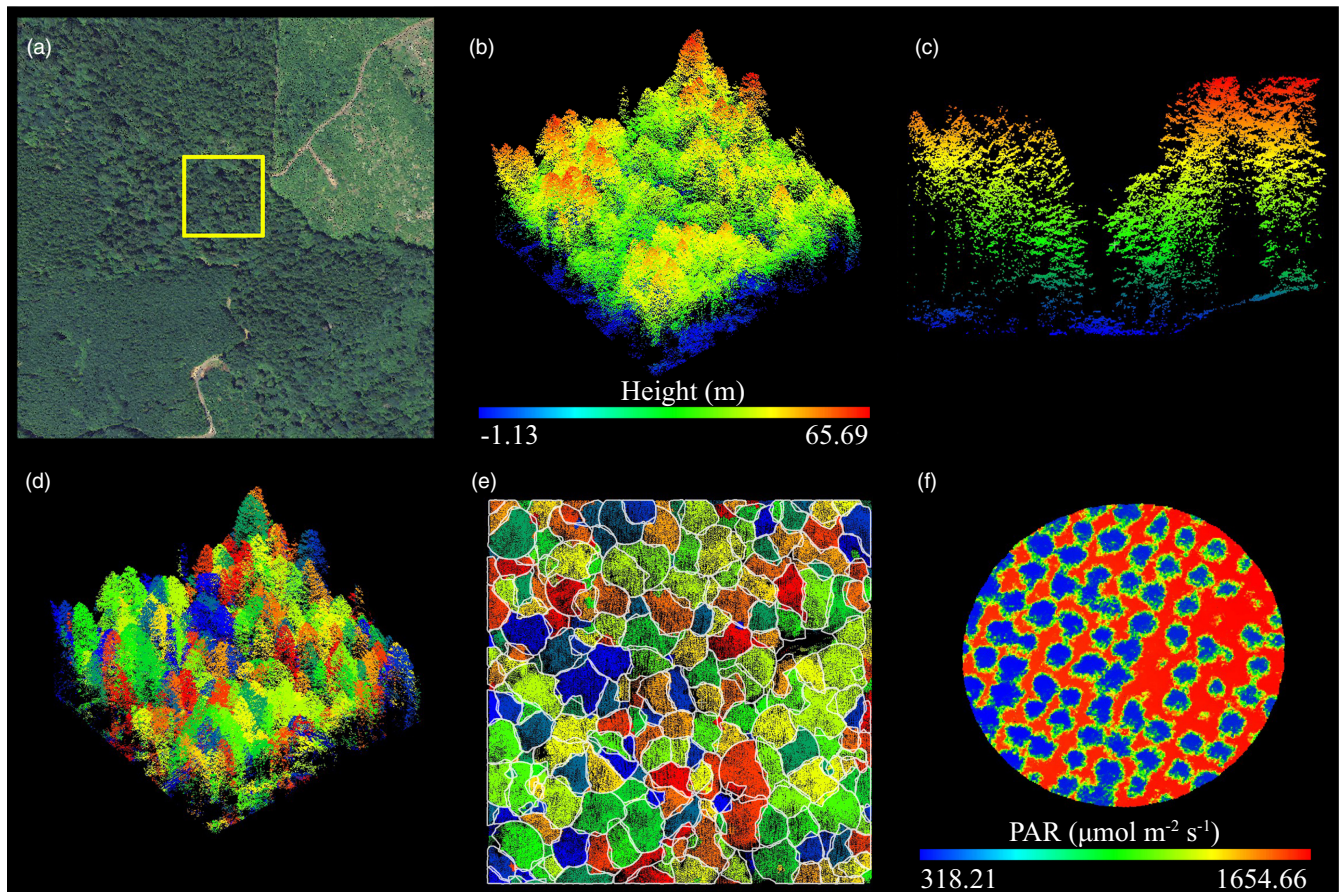


FIGURE 4 Illustrations of airborne laser scanning (ALS) data for characterizing forest structures. (a) High-resolution image of the example forest site for the ALS data; (b) ALS point cloud data of the forest stand with colours representing height; (c) ALS point cloud data of neighbouring individual trees with colours representing height; (d) Identification of individual trees and (e) Crown areas from the ALS data based on an automatic segmentation algorithm. (f) Spatial distribution of daily photosynthetic active radiation (PAR) calculated using TLS data and a radiative transfer model.

and III). In addition, trait similarity has been used as an indirect indicator of facilitation and competition. For communities in transient dynamics such as long-term succession, trait similarity observed in a particular phase may be a proxy for niche overlap. For instance, species with highly similar traits are more likely to compete with one another due to strong niche overlap, whereas species with different traits are more likely to facilitate one another due to potential niche complementarity (Lohbeck et al., 2014; Purschke et al., 2013). Trait similarity thus may indicate interaction type and intensity in the subsequent time period (Inference II & III). For communities in equilibria, trait divergence (over-dispersion) has been interpreted as an indicator of strong long-term competition (Cornwell & Ackerly, 2009) since species with similar traits may have experienced competitive exclusion. However, these indirect approaches have notable caveats. For example, species with similar traits do not always face stronger competition, and trait differentiation can be driven by other factors (D'Andrea & Ostling, 2016; Kunstler et al., 2012). Combining information on trait distribution (divergence and convergence) and spatial distribution (e.g., species co-occurrence) may help to deal with confounding factors, such as abiotic effects, allowing for improved inference of plant–plant interactions (Gross et al., 2009; Gross et al., 2013). Remote sensing techniques, such as airborne lidar and

hyperspectral imaging at high resolutions, can measure a range of plant functional traits, providing an important tool to assess community-level trait distributions at large spatial scales (Shi et al., 2018).

Using repeated TLS data to trace crown development of individual trees in response to neighbourhood interactions provides valuable information for inferring competition within the community. For example, Martin-Ducup et al. (2016) characterised 3-D crown structures (e.g., length, width, volume, surface, density, sinuosity, openness and shade of crowns) of sugar maple trees using TLS. They found that maple trees grown in mixed stands produced crowns with larger volumes, greater extents of openness and sinuosity, and also a higher ratio between crown length and tree height compared to pure stands, suggesting stronger intra- than inter-specific competition. Similar experimental designs may help to generalize the relative importance of intra- vs. inter-specific competition at the community level.

3.3 | Integration of multiple remote sensing data as transformative tools

Recent studies have shown exciting advancements of multi-sourced information fusion that may further boost interaction

inferences at the community level. It is now possible to integrate 2-D physiological and 3-D morphological data, which were simultaneously obtained by different remote sensing tools. For instance, ortho-geolocation of the hyperspectrally imaged 2-D canopy chemistry data, based on 3-D lidar data, enabled high-resolution estimates of vertical profiles of various foliar chemical traits, such as photosynthetic pigments, macro- and micro-nutrients, leaf structure and defensive compounds (Asner et al., 2015; Kamoske et al., 2021; Marconi et al., 2021). Similarly, the laser return intensity from single, multiple and hyperspectral lidar systems, combined with the 3-D structural information traditionally provided by this laser-based technology, makes it possible to capture structural, biophysical, and/or functional information simultaneously (Eitel et al., 2016). It has been suggested that TLS concurrently provides information on LAI and foliar chlorophyll concentration (Eitel et al., 2011), as well as foliar nitrogen concentration (Eitel et al., 2011; Sun et al., 2017), leaf water content (Elsherif et al., 2018; Gaulton et al., 2013), and photosynthetic performance (Magney et al., 2014). These integrated remote sensing data can simultaneously quantify spatial and functional structure across relatively large scales. Such novel applications have allowed us to develop comprehensive procedures that improve the inference of community level plant–plant interactions.

3.4 | Integrating remote sensing with individual-based models

Community structural metrics derived from remote sensing data can verify predictions derived from mechanistic models, assuming that plant–plant interactions encompass important drivers. For example, lidar data can map 2-D or 3-D forest gaps at high resolution (Du et al., 2021), allowing quantification of a range of key summary statistics such as gap size distribution and gap geometry (Ma et al., 2018). Jucker (2022) proposed an integrated approach using these lidar-derived forest gap structures and individual-based models to elucidate the mechanisms underlying the spatial structure of forest gaps. This can be achieved by comparing remotely-sensed gap structure and outputs of individual-based models that explicitly account for particular mechanisms. While this approach has not been applied to the inference of plant–plant interactions, the concept can be generalized for integrating mechanistic modelling with remote sensing of community structure.

4 | LINKING PLANT INTERACTIONS TO REMOTELY SENSED LANDSCAPE PATTERNS AND STATES

Plant–plant interactions may have consistent signs and strengths across the landscape, enabling scaling from local interactions to landscape patterns (Teng et al., 2020). Thus, (vegetation) patterning provides important signals that enable detection and prediction of

plant–plant interactions, using remote sensing and theoretical models (Inference II and III).

Many remote sensing data (especially those at coarse or moderate spatial resolutions) may not be able to capture species/individual traits or fine-scale community structures at the landscape level. However, most can distinguish between vegetated vs. non-vegetated areas or different vegetation types (e.g., forest, shrubland, savanna, grassland). Patchy vegetation landscapes, characterised by spatially mixed patches with different vegetated states, are widespread in nature. Depending on the system of interest, useful remote sensing data for characterising patchy vegetation patterns may range from very high to moderate spatial resolutions, from visible-infrared to microwave bands, and from satellite- to air-borne data. In the following sections, we discuss how remotely sensed landscape patterns of patchy vegetation can be used to infer plant–plant interactions from patch-size distributions (Section 4.1), spatial self-organization (Section 4.2), transient landscape dynamics (Section 4.3) and alternative vegetation states (Section 4.4).

4.1 | Vegetation patch-size distribution as general indicators

The majority of vegetation patterns are irregular (in terms of the shape of patches) and non-periodical in space. For this class of vegetation patterns, patch-size distribution (i.e., the number of vegetation patches as a function of patch size) has been frequently used for quantifying their spatial signatures. Previous theoretical and empirical works have suggested that patch-size distribution type and key parameters could serve as useful indicators for inferring plant–plant interactions (e.g., von Hardenberg et al., 2010; Xu, Holmgren, Van Nes, Maestre, et al., 2015). Specific examples are elaborated below.

Positive plant–plant interactions are prevalent in stressful environments such as drylands and coastal tidal flats. Extensive studies have suggested that such local positive interactions can give rise to power laws (or scale-free properties) in patch size distributions at the landscape level (Berdugo et al., 2017; Berdugo et al., 2019; Kéfi, Rietkerk, Alados, et al., 2007; Scanlon et al., 2007; von Hardenberg et al., 2010; Zhao et al., 2019). That is, when plotted on a logarithmic scale, the number of vegetation patches and their size are negatively and linearly correlated (Figure 5a). The causal link between positive interactions and power-law distributions can be intuitively understood. Under stressful conditions, positive interactions between plants are important in sustaining vegetation cover and biomass. For example, in dryland ecosystems, established plants can facilitate understory seedlings and juveniles by alleviating water stress, increasing nutrient availability, and protecting against herbivory (Brooker et al., 2008). Plant–plant facilitation also exists in coastal vegetation that suffers from strong salt and wave stress in the tidal front areas. Established individual plants, such as cordgrass (*Spartina*), can act as important ecosystem engineers that facilitate plant colonization and expansion (Bertness & Ellison, 1987). These local positive effects can form self-reinforcing feedback for vegetation, driving

the establishment of plant clusters and sustaining large vegetation patches. In line with this intuitive reasoning, it has been demonstrated that the power-law distributions can arise due to plant–plant facilitation, generating patches larger than expected by randomness (Kéfi et al., 2011). Therefore, the presence of power-law-like patch-size distribution in vegetation patterns in stressful environments hints to positive interactions.

However, positive interactions are neither sufficient nor necessary conditions for power-law distributions. First, power-law distributions can result from non-facilitation processes such as disturbances or trophic interactions (Kéfi et al., 2011). Staver et al. (2019) used airborne lidar to reveal universal power-law patch size distributions of African savanna trees but presented an almost invariant power exponent across relatively broad environmental

gradients (e.g., moisture). However, existing models incorporating plant–plant interactions tend to yield distributions with varying exponents under different environmental conditions such as precipitation (Scanlon et al., 2007). This inconsistency implies that there may be an overlooked essential mechanism (beyond pure plant–plant facilitation) underpinning savanna landscape patterning and that plant–plant facilitation may not be confidently inferred from power-law distributions alone (Staver et al., 2019).

Second, non-power-law distributions can also arise from positive interactions. Xu, Holmgren, Van Nes, Maestre, et al. (2015) analysed high-resolution remotely sensed images to show that hump-shaped (log-normal like) patch-size distributions with heavy right tails are widespread in global drylands (Figure 5b), and the skewness of such humped distributions can signal the strengths of positive plant–plant

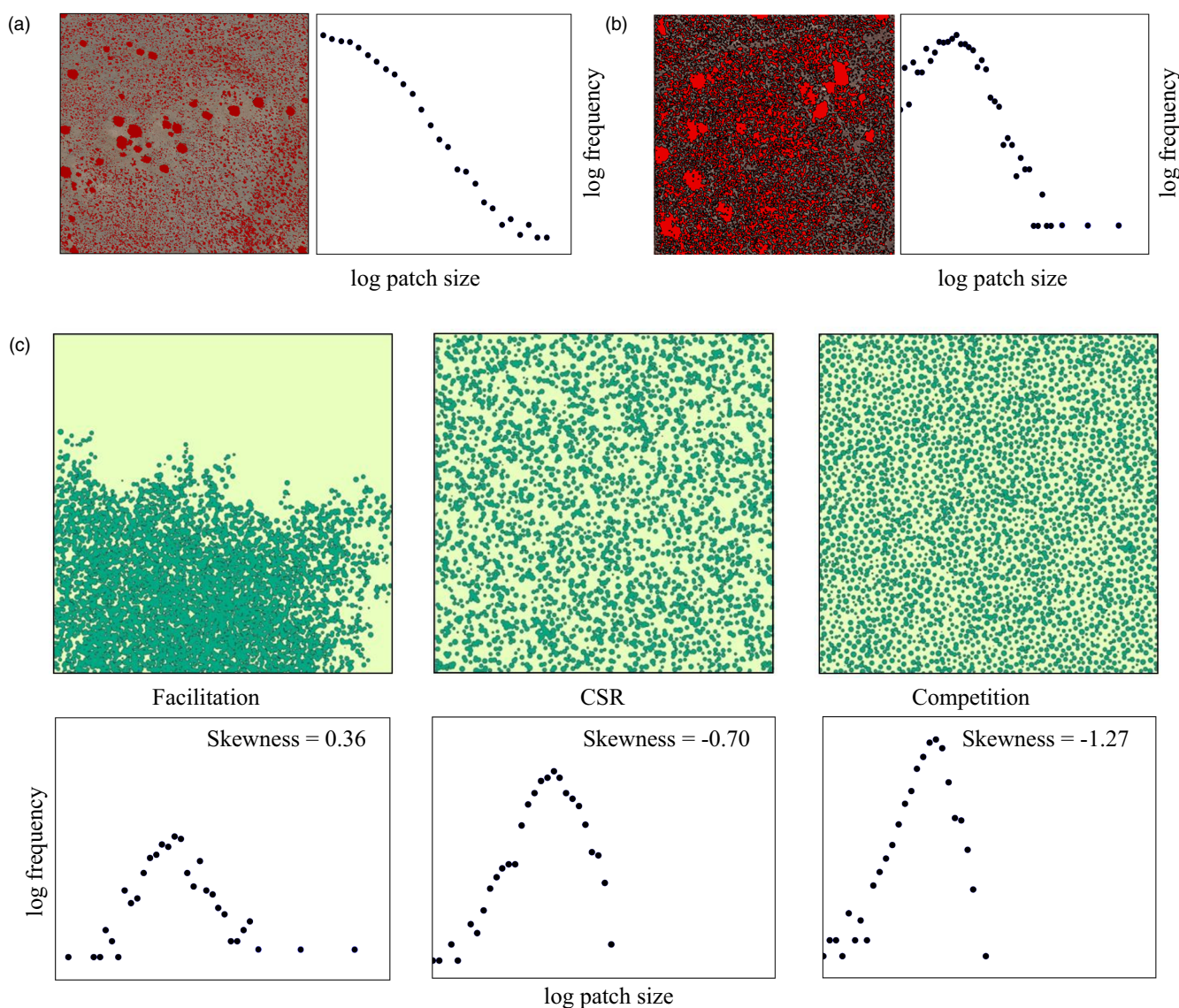


FIGURE 5 Illustrations of remotely sensed patch-size distributions of dryland vegetation as useful indicators for inferring plant–plant interactions. Dryland vegetation showing (a) a power-law-like patch-size distribution, and (b) a patch-size distribution characterized by a hump and a heavy right-tail. Dark red in the left panels represents vegetation patches. (c) A null model suggests that the deviation of skewness of patch-size distribution from complete spatial randomness (CSR) may serve as an indicator of facilitation or competition (Xu, Holmgren, Van Nes, Hirota, et al., 2015).

interactions. Specifically, plant clusters predominantly formed by plant–plant facilitation (rather than disturbances or environmental heterogeneity), demonstrate patch-size distribution skewed to the right (i.e., toward larger patches). In contrast, when negative interactions such as competition are the dominant force, neighbouring plants tend to ‘reject’ each other, making it more difficult to form larger plant clusters. Stronger negative interactions would thus lead to more left-skewed distribution (towards smaller patches). A well-tailored null model may serve as a baseline generating neutral patch-size distributions; deviations can provide quantitative (signed) indications of plant–plant interactions in stressful environments (Figure 5c) (Xu, Holmgren, Van Nes, Maestre, et al., 2015).

4.2 | Spatial self-organization as specific indicators

An interesting class of vegetation patterns pertains to ‘spatial self-organization’ (Klausmeier, 1999; Meron, 2015; Rietkerk et al., 2004). Governed by the self-organization principles involving particular plant–plant interactions (see below for more details), this class is characterised by patterns periodically extended in space, such as rings, stripes, spots, gaps or labyrinths (see Figure 6 for some examples).

A common mechanism underlying the spontaneous formation of spatially periodic vegetation patterns is ‘scale-dependent feedback’, characterised by short-range positive feedback together with long-range negative feedback (also referred to as ‘Turing instability’ or finite wave instability) (Meron, 2015; Rietkerk & Van de Koppel, 2008). Typical scale-dependent feedbacks have been commonly found in dryland vegetation. Plant–plant facilitation, such as the ‘nurse plant effect’, is widespread in arid conditions, eventually enhancing the survival and growth of neighbouring plants (see also Section 4.1). Such local facilitation creates positive feedback operating at short ranges. In the meantime, plants in disjointed vegetation patches may compete for soil-water with lateral roots in inter-patch areas or by accumulating surface runoff along slopes. In either case, the competition creates negative feedback, affecting longer ranges than the local facilitation. These facilitative and competitive effects operate at different spatial scales, thus creating scale-dependent feedbacks, which act as ‘activators’ for plant growth within the patch areas and ‘inhibitors’ in the inter-patch areas, giving rise to periodically extended vegetated vs. bare areas across dryland landscapes (Getzin et al., 2016; Rietkerk et al., 2004). Such ‘Turing patterns’ (named after Alan Turing who originally proposed the ‘activator-inhibitor’ mechanism underpinning pattern formation; Turing, 1952) provide a unique spatial signature for inferring not only the existence but also the operating scales of plant–plant interactions.

4.3 | Transient dynamics may provide useful signals

Early studies have focused on persistent states (equilibrium) when analysing pattern formation. However, recent studies have

suggested the use of transient dynamics. For example, during the early colonization of coastal saltmarsh vegetation, regular, ring-like spatial patterns of cordgrass form and expand (a ‘slow-fast process’ in a theoretical term), plausibly driven by non-Turing mechanisms where strong competition for nutrients between plants plays a critical role (Zhao et al., 2021). Time-series of remotely sensed images could help to unravel the transient pattern formation and to understand the role of plant–plant interactions therein.

Plants may face behaviour-driven dynamics as reflected in spatiotemporal patterns (Pereira et al., 2017; Reijers et al., 2019). For example, Reijers et al. (2019) revealed that landscape-building beach grass experience heavy-tailed random walks in their spatial expansion trajectories. This Lévy-like strategy can also lead to large vegetation patches through self-promoting feedback, where local facilitation may act. The trajectories of vegetation’s spatial expansion have been observed in the field but also can be successfully captured by time-series of high-resolution optical images (e.g., drone images) and lidar data (e.g., Zhao et al., 2021).

Plant–plant interactions may also exist at cross-ecosystem levels, for example, vegetation zonation in coastal landscapes. The traditional approach is that coastal zonation is determined mainly by physical stressors, such as soil and water salinity. However, it has been increasingly demonstrated that biotic interactions, including inter-specific competition and facilitation between plants, operating at short or long distances, give rise to clear zonation features at landscape scales (van de Koppel et al., 2015). Using time-series Landsat data in combination with field data of elevation, sediments, and salinity, as well as theoretical modelling, Wang et al. (2022) analysed the transient dynamics of a coastal landscape and revealed that invasive cordgrass at low elevations might produce a cross-ecosystem, with a long-distance facilitative effect on a native reed at high elevations.

4.4 | Linking positive interactions and alternative (or multi-stability) vegetation states

Plant–plant interactions have been linked to the existence of alternative stable states (D’Odorico et al., 2007; Kéfi, Rietkerk, Van Baalen, et al., 2007; Rietkerk et al., 2004, 2021; Xu, Van Nes, et al., 2015; Zelnik et al., 2013). Positive interactions between plants may generate positive feedbacks, which are necessary but insufficient conditions for alternative vegetation/ecosystem states (Kéfi et al., 2016). Conversely, the presence of alternative (or multi-stability) vegetation states hints that strong positive plant–plant interactions may act as a potential mechanism.

Again, taking drylands as an example, plant–plant facilitation (see also Sections 4.1 and 4.2) can form positive feedbacks that force the system into distinct, often discontinuous, states (e.g., high vs. low vegetation biomass) (Aguiar & Sala, 1999). This issue has been well investigated by a range of studies (Kéfi, Rietkerk, Van Baalen, & Loreau, 2007; Rietkerk & Van de Koppel, 2008; Xu, Van Nes, et al., 2015), pointing to a strong link between positive

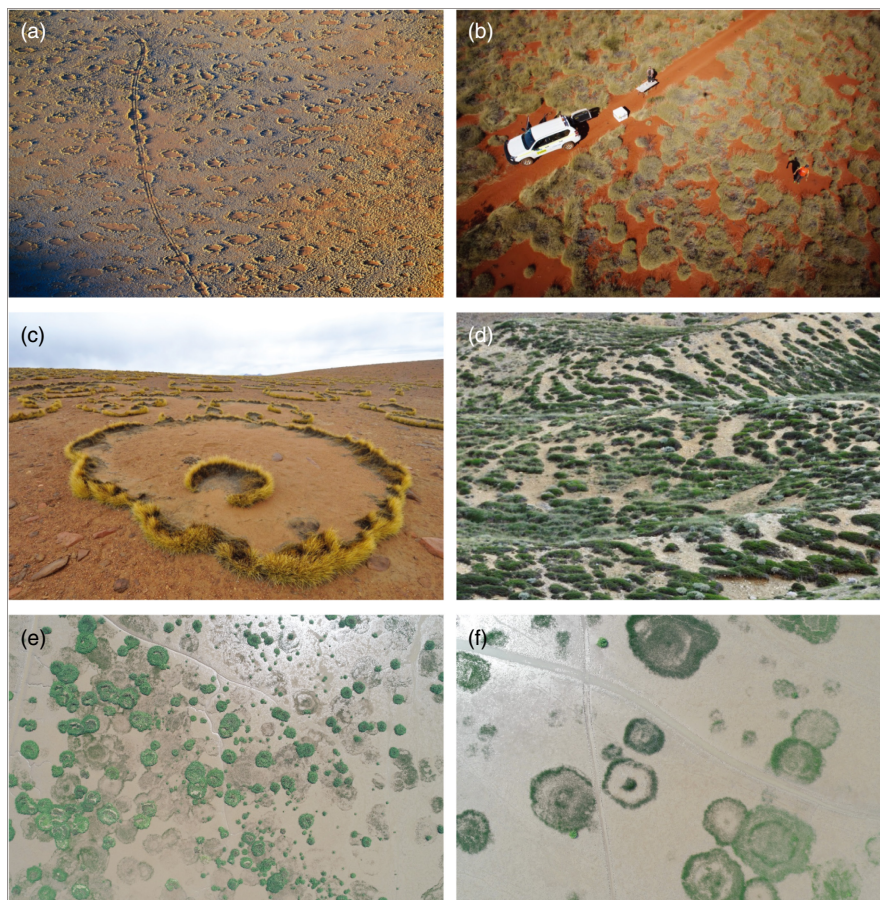


FIGURE 6 Self-organized vegetation patterns. (a) Fairy circles which are periodic gap patterns in the Namib Rand Nature Reserve in Namibia (average annual precipitation is 75 mm/year; 24.9652S, 15.8845E). The picture was taken from a balloon. (b) Small gaps and labyrinth-like pattern of *Triodia basedowii*, also known as Spinifex grass, near Newman in Pilbara region in Western Australia (360 mm/year; see Getzin et al., 2022; 23.4413S, 119.8379E). (c) Large rings of Paja brava grass (*Festuca orthophylla*) showing clonal growth in the high and remote Altiplano in Bolivia (100 mm/year; 4900 m above sea level; 21.8952S, 66.8640W). (d) Example of vegetation pattern in Ladakh, India (32.8900N, 77.5300E) at an altitude of 4500 m a.s.l. The mean annual precipitation in this area is less than 200 mm/year. The vegetation patterns show a mix of bands and spots developed on hillslopes. (e, f) Drone photos of ring-like transient vegetation patterns in the coastal saltmarsh in Shanghai, China (30.9975 N, 121.4426E; Zhao et al., 2021).

plant–plant interactions and the existence of alternative states in green–desert transitions.

The underlying positive feedback may not be related to direct plant interactions (as detailed above) but rather to indirect interactions. For example, tropical fire-adapted savanna grasses can invoke recurrent fires that largely preclude tree recruitment (Murphy & Bowman, 2012). This fire-mediated positive feedback of tree cover has been attributed to the alternative stable states of forest and savanna across the global tropics (Hirota et al., 2011; Staal et al., 2016; Staver et al., 2011). While plant–plant interaction studies often do not consider this kind of effect, the indirect negative tree–grass interactions resemble ‘apparent competition’ mediated by fire (Holt & Bonsall, 2017).

Multiple remote sensing datasets have been used to detect alternative vegetation states, including MODIS- and Landsat-derived products of tree cover and NDVI (Hirota et al., 2011; Staver et al., 2011; Xu, Holmgren, Van Nes, Hirota, et al., 2015), and satellite-borne lidar-derived canopy height products (Scheffer

et al., 2018; Xu et al., 2016). Notably, remotely sensed vegetation states, for example, of tree cover or canopy height, that present multi-modalities in their frequency distributions under similar environmental conditions, may indicate alternative vegetation states. This notion has been used to reconstruct the systems’ ‘potential landscapes’, directly from the (remote sensing) data, a powerful data-driven approach for detecting and visualizing alternative attractors. Based on these approaches, remotely sensed tree cover and canopy height have been used to differentiate alternative stable vegetation states from unstable ones at the biome scale (Hirota et al., 2011; Scheffer, Hirota, et al., 2012; Xu et al., 2016). Available time-series data of remotely sensed vegetation states could help detect alternative vegetation states, such as sudden jumps or signs of critical slowing down (Scheffer, Carpenter, et al., 2012). Theoretical and methodological details of alternative stable state inference, as well as the important caveats, can be found in the literature (e.g., Dakos et al., 2015; Scheffer et al., 2015; Scheffer & Carpenter, 2003).

4.5 | Opportunities and challenges for inferring interactions across large spatial scales

The rapid development of remote sensing products of ecosystem attributes largely amplifies the ability to quantify landscape patterns and states. For instance, alternative vegetation states in the tropics were revealed by studying global-scale tree cover and canopy height products (Hirota et al., 2011; Staver et al., 2011; Xu et al., 2016). These advancements bridge the knowledge gaps of ground-sourced studies (Sankaran et al., 2005). The increasing availability of high-resolution images (e.g., drone images) makes it possible to detect self-organization patterns in equilibrium and transient dynamics with spatial and temporal details (Getzin et al., 2021; Zhao et al., 2021). These remote sensing tools provide exceptional opportunities for inferring large-scale plant–plant interactions, which were not available two decades ago.

Linking spatial patterns and processes is a long-standing but challenging task in ecology. Many factors may prevent using spatio-temporal vegetation patterns as ‘symptoms’ to ‘diagnose’ the nature of plant–plant interactions. Although we cannot enumerate all confounders, we will elaborate on three general issues.

A central confounding issue is that different processes could give rise to similar patterns, causing a caveat for inferring interactions from vegetation patterns. For instance, the co-occurrence of plants observed in the field may be attributed to limited dispersal or other factors rather than facilitation (Morales-Castilla et al., 2015). The lack of robust correspondence between vegetation pattern signature and plant–plant interactions applies to the so-far most elucidated periodic vegetation patterns. For example, both scale-dependent feedbacks invoking facilitation and competition and other mechanisms that do not invoke plant–plant interactions can explain the formation of almost identical, common vegetation patterns (Ge & Liu, 2022).

The difficulty to distinguish between ‘equilibrium’ and long ‘transient’ patterns is another noteworthy but largely overlooked confounder responsible for the elusive causal link between vegetation patterns and plant interactions. While observed spatial patterns have often been assumed to approach equilibrium of the system states, they could merely be part of long transient dynamics in slow systems (Hastings et al., 2018). The inference of interactions may reach substantially different conclusions from existing approaches and theoretical models under the equilibrium vs. transient assumptions. Remote sensing could effectively track system changes over time. Long-term time series remote sensing data thus may help to overcome this challenge, revealing whether the system is in ‘equilibrium’ or in ‘transient’ state, and infer the causality.

In addition, it is often difficult to accurately fit particular distributions to real data when assessing inferences. It has been suggested that inappropriate methods can lead to inaccurate identification of power-law distributions from empirical data across a wide range of real-world systems (Clauset et al., 2009). Also, the noisy nature of real data may further obscure the distinction between different types of distributions.

5 | OUTLOOK

Robust sensors and equipment platforms, as well as comprehensive datasets and computational platforms, have increasingly become available to the public in recent years. Notably, the expanding Earth-observing missions (e.g., GEDI, BIOMASS, NISAR) provide promising tools to systematically measure ecosystem attributes globally, and open more opportunities to study plant–plant interactions at lower costs and with higher accuracies. Increasingly available ecological ‘big data’ are expected to amplify the strength of remote sensing further. For instance, long-term and in-situ data generated by field surveys, automatic electronic devices, and manipulative experiments from National Ecological Observatory Network (NEON), Treenet (Zweifel et al., 2021), and other large-scale research networks allow for cross-validating and scaling remotely-sensed plant–plant interactions. Also, the development of data processing algorithms (e.g., lidar-based automatic plant segmentation algorithms) and platforms (e.g., the Google Earth Engine and the Multi-Mission Algorithm and Analysis Platform, MAAP) can vastly enhance the efficiency of harnessing a tremendous amount of data.

Inferring plant–plant interactions from remote sensing data is expected to help address a wide range of fundamental theories, key hypotheses, and new questions at large scales (e.g., the stress gradient hypothesis, species range expansion, and novel ecosystems), thereby advancing many fields, including macroecology, global change biology and conservation biology. Moreover, improved inference of plant–plant interactions using remote sensing may spark new ideas and new links between established fields. For example, remotely-sensed time-series of 3-D plant community structure may help to depict how local-scale plant–plant interactions scale up from organs (e.g., leaves, branches, and canopy) to the individual and community levels, which may be better understood in a new framework of cross-scale, multi-dimensional self-organization (Franklin et al., 2020). Looking at the big picture, biotic interactions are ubiquitous, occurring locally to globally (Bertness, 2020) and profoundly shaping the planet Earth. Yet, understanding biotic interactions at large spatial scales (especially landscape and regional scales) remains limited. Integrating remote sensing tools could pave the way toward filling this key gap (Gross et al., 2009; Maestre et al., 2021; Xu, Holmgren, Van Nes, Maestre, et al., 2015), making remotely-sensed biotic interactions a promising direction.

6 | SYNTHESIS

It would be naïve to expect remote sensing to replace ground-sourced assessments of plant–plant interactions. However, given the efficiency of remote sensing data collection and the opportunity to scale remotely sensed information across different spatial scales, identifying remote sensing indicators of plant–plant interactions presents an exciting avenue for enhancing existing approaches to understanding fundamental ecology. Plant–plant interactions and a considerable portion of research topics in

community ecology were traditionally studied at small spatiotemporal scales. Remote sensing extends these topics' domains to broader and finer scales, aiding the scaling of ecological patterns and the search for generic rules. Combining theories, experiments, models, data-driven approaches, and data analysis algorithms is crucial to embedding remote sensing into ecological contexts. Developing robust remote sensing approaches for inferring plant-plant interactions paves an important road towards achieving this challenging goal.

AUTHOR CONTRIBUTIONS

Bin J. W. Chen, Shuqing N. Teng, Guang Zheng, Lijuan Cui, Shao-peng Li, Jan U. H. Eitel, Thomas W. Crowther, Jian Zhang, Qiang He, Hezi Yizhaq, Kechang Niu, Quan-Xing Liu and Chi Xu conceived the idea; Bin J. W. Chen, Shuqing N. Teng, Guang Zheng, Shao-peng Li, Arie Staal, Jan U. H. Eitel, Thomas W. Crowther, Miguel Berdugo, Lidong Mo, Haozhi Ma, Lalasia Bialic-Murphy, Constantin M. Zohner, Daniel S. Maynard, Colin Averill, Jian Zhang, Qiang He, Jochem B. Evers, Niels P. R. Anten, Hezi Yizhaq, Ilan Stavi, Eli Argaman, Uri Basson, Quan-Xing Liu, and Chi Xu wrote the original draft of the manuscript; all authors revised the manuscript; all authors participated actively in execution of the study, and gave final approval for publication.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

No data were generated or analysed in this work.

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