Scaling-up ecological understanding with remote sensing and causal inference

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Opinion

Scaling-up ecological understanding with remote sensing and causal inference

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Decades of empirical ecological research have focused on understanding ecological dynamics at local scales. Remote sensing products can help to scale-up ecological understanding to support management actions that need to be implemented across large spatial extents. This new avenue for remote sensing applications requires careful consideration of sources of potential bias that can lead to spurious causal relationships. We propose that causal inference techniques can help to mitigate biases arising from confounding variables and measurement errors that are inherent in remote sensing products. Adopting these statistical techniques will require interdisciplinary collaborations between local ecologists, remote sensing specialists, and experts in causal inference. The insights from integrating 'big' observational data from remote sensing with causal inference could be essential for bridging biodiversity science and conservation.

Highlights

Current biodiversity policy goals demand large-scale conservation and management actions.

Ecological relationships operating in fine-scale experiments and observational datasets do not necessarily apply at management-relevant spatial scales.

Remote sensing offers a solution for understanding ecological relationships at scale, but inferring causality from remotely sensed data presents various challenges.

Confounding variables and measurement errors, which are inevitable in large-scale observational datasets, can create bias and lead to spurious conclusions about causal relationships.

Remote sensing products can help to scale-up causal ecological relationships, but only if they are accompanied by careful analyses and inferences that address challenges posed by confounding variables and measurement errors.

Advances necessary to leverage remote sensing data to scale up ecological understanding and inform landscape-scale management

Maintaining, enhancing, and restoring the integrity, resilience, functioning, and services of ecosystems requires sustained, large-scale conservation and management [1]. Ambitious global and regional biodiversity targets demonstrate the current level of political commitment (e.g., the post-2020 Global Biodiversity Framework) [2]. However, management interventions will be more likely to succeed if they are informed by a causal understanding of ecological relationships and human–environment interactions. Thanks to decades of small-scale experimentation and observations, we have considerable understanding of the relationships between biodiversity and ecosystem processes, including ecosystem functions (e.g., [3]), multifunctionality (e.g., [4]), and ecosystem stability (e.g., [5]), at local scales and in experimental settings. However, these relationships do not necessarily hold across large spatial scales [6] – the scales most relevant to policy and management (Box 1) – or under natural and managed conditions [7,8]. Although small-scale empirical studies have provided useful information to guide decisions in biodiversity planning, landscape-scale studies offer unparalleled insight [9,10] and should be a high priority.

Remote sensing is key to solving this scaling challenge: it enables the collection of spatially contiguous data over larger **spatial extents** (see Glossary) at a variety of spatial resolutions [11,12]. Common applications of remote sensing are to map patterns of biological and environmental variation across large spatial and temporal domains (Table 1). Maps provide valuable information to guide conservation and restoration efforts, for example to prioritize and monitor areas for protection or restoration [13]. However, observing broad-scale patterns is not the same as either understanding the processes that generate or correctly anticipating the likely outcomes of management interventions. To advance this understanding, we believe that the future of remote sensing is to move beyond mapping patterns and begin to quantify large-scale causal relationships

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Box 1. Small-scale invasion research and theories do not always translate into effective landscape-scale management

Research on the relationship between species richness and invasibility provides an example of why processes revealed by small-scale experiments may not generalize to drive landscape patterns. In the late 1990s, experimental manipulations showed that invasive plant species were less likely to establish in species-rich communities (e.g., [70]). This empirical evidence supported the biotic resistance hypothesis which states that high diversity in native plant communities will decrease invasibility by ensuring that the available niches are filled [71]. However, results from observational studies, especially those conducted at broad spatial scales, were much less conclusive [72]. The resolution of these inconsistencies came with the insight that factors operating at larger scales that promote coexistence among native species can also affect the success of invasive species, regardless of species richness [73]. Small-scale experiments control for factors such as resource availability or disturbance, allowing the negative effect of species richness on invasibility to emerge. By contrast, in observational studies covering large spatial extents, these factors vary dramatically across the landscape, and impact on both native species richness and invasibility. They can therefore obscure the negative effect of species richness on invasibility [71,74].

This line of research shows that fighting invasions by managing for increased native species richness could work in theory, but the effect would likely be weak relative to other factors which promote invasions across the landscape. For example, sagebrush steppe bordering a heavily trafficked highway and experiencing high propagule pressure is likely to be invaded by cheatgrass (*Bromus tectorum*) – regardless of the native species richness (Figure I). Moreover, management to increase native biodiversity by, for example, increasing abiotic heterogeneity could also benefit invasive species by increasing the available niche space [75].

Similarly, promising management interventions identified using small-scale experiments sometimes lead to unexpected results when applied at the landscape level. For example, native plant recruitment may be lower, and reinvasion faster, in large treated management units than in small observational units, presumably because of different environmental conditions, edge-to-area ratios, disturbance histories, and limited native dispersal and seed availability in large invaded management units [19,76]. Designing effective invasive management would require better understanding the factors determining the success and failure of the invaders at the landscape scale.

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Figure I. Cheatgrass (*Bromus tectorum*) invasion in a sagebrush steppe in North America. Biotic resistance created by competition from native perennial grasses can be overwhelmed by heavy propagule pressure of cheatgrass (senesced grass in the picture) near busy roads or agricultural fields. Photo credit: Peter B. Adler.

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Table 1. Remotely sensed maps: a non-exhaustive list of publicly available maps of environmental and ecological landscape characteristics derived from remote sensing imagery (and/or the code to achieve this) that can provide a basis for scaling up ecological understanding of ecosystem dynamics and human–environment interactions[a]

Example of openly available imagery	Remote sensing data source(s)	Spatial and temporal resolution	Refs and resources
Environmental characteristics			
Global topography: elevation and slope	PRISM on board the ALOS	30 m, 12.5 m	[83][i]
Global soil moisture	SMAP	9 km and 36 km, daily since 2015	[ii]
Global sea surface salinity	MIRAS on board SMOS	0.25° for daily and 9 day maps, and 1° for monthly maps, from 2011 to 2019	[84][iii]
Global sea ice thickness	MIRAS on board SMOS, and SIRAL on board CryoSat	25 km, weekly since 2010	Curated by the European Space Agency[iv]
Global night-time lights	VIIRS on board the S-NPP	500 m, daily since 2012	NASA Black Marble product suite [85]
Land cover			
Global land-cover map	Landsat thematic mapper (TM) and enhanced thematic mapper plus (ETM+) sensors	30 m, most recent map is for 2017	[86][v]
Pan-European CORINE (coordination of information on the environment) land-cover series	Landsat 5, 7, and 8, SPOT-4/5, IRS P6, REIS on board RapidEye, Sentinel-2	100 m, the most recent map is for 2018	Curated by the European Environment Agency[vi]
South African national land-cover dataset	Sentinel-2	20 m, the most recent map is for 2020	Created by the Department of Forestry, Fisheries, and the Environment, Republic of South Africa[vii]
Global forest-cover change	Landsat ETM+	30 m, difference between 2000 and 2012, and between 2000 and 2019	[68][viii]
Global impervious surface	Landsat 4, 5, 7, and 8	30 m, every 5 years 1985–2020	[87][ix]
Global bare-ground gain	Landsat 4, 5, 7 and 8	30 m, 2000–2012	[88]
Ecosystem properties and habitat quality			
Near-global vegetation structure: canopy cover and height	GEDI on board the ISS	25 m, monthly since 2019	[89][x]
Evapotranspiration, water-use efficiency and water stress between ~52°N and ~52°S	ECOSTRESS on board the ISS	70 m, every 1–5 days depending on latitude since 2018	[90][xi]
Rangeland productivity in continental USA: net primary productivity and biomass	Landsat	30 m, annual and 16-day predictions since 1986	Rangeland Analysis Platform [91,92][xii]
Functional traits for 19 sites of the National Ecological Observatory Network, USA	Airborne hyperspectral imaging spectrometer	1 m, summer 2016–2017	[93][xiii]

(continued on next page)

Glossary

Attenuation bias: random measurement errors in the treatment cause effects estimated from regression to be biased towards – or attenuate to – zero, thus underestimating the true effect.
Bias: the method (estimator) used to estimate the effect size will produce estimates that are different from the true value in magnitude or even sign.
Causal inference: the process of making evidence-based conclusions about the magnitude of a cause-and-effect relationship from an observed association.
Collider: a shared consequence of the treatment and outcome that creates bias when included in a regression analysis.
Confounding variable: a variable that influences both the treatment (e.g., invasion) and outcome (e.g., productivity).
Difference-in-differences: similar to 'before-after-control-impact' experimental designs; a statistical technique to estimate the effect of a treatment by comparing control and treated units over time. It accounts for time-invariant unobserved confounding variables (e.g., soil type) by exploiting longitudinal data.
Directed acyclic graph (DAG): a graphical representation of all presumed causal relationships between variables (Box 2).
External validity: the extent to which causal effects can be generalized or transferred to other contexts, for example to other species, ecosystems, biomes, locations, or time-periods.
Heterogeneous treatment effect: variation in a treatment effect across units based on additional characteristics, often estimated via conditional average treatment effects.
Instrumental variable (IV): a regression approach that leverages variation in a variable (an 'instrument') that is correlated with the treatment but does not directly affect the outcome. IVs can eliminate bias from measurement error, reverse causality, and confounding when their assumptions are met.
Matching: a preregression technique that creates pairs of treated and control observations that have similar values of confounding variables.
Measurement error: the difference between an observed value and the true value. Measurement error can arise from

Table 1. (continued)

Example of openly available imagery	Remote sensing data source(s)	Spatial and temporal resolution	Refs and resources
Invasion in South Africa for selected catchments in strategic water-source areas: Berg-Breede, uMngeni, Tugela, uMzimvubu, Sabie-Crocodile, and Luvuvhu catchments	Sentinel-2 and data fusion (Sentinel-1, ALOS)	10–20 m, maps created for 2019–2023	MAPWAPS project [94,95][xiv,xv]
Global assessment of coral reefs: benthic map, reef bleaching, and water turbidity	PlanetScope satellite constellation	3125 m, daily	[96][xvi]
Beetle infestation along the Colorado River	Airborne multispectral sensor	20 cm, based on difference between 2009 and 2013	[97][xvii]
Leaf area index	MODIS on board Aqua and Terra	500 m, every 8 days since 2000	[98][xviii]
Disturbance			
Global fire data: near-real time locations of active fires, and timing and spatial extent of historical fires	MODIS on board Aqua and Terra	1 km (active fires), 500 m (historical fires), daily	Fire Information for Resource Management System[xix]
	VIIRS on board S-NPP and NOAA-20	250 m, twice per day	MODIS burned area product [99][xx]
	Landsat 8 and 9	30 m, every eight days	
Burn severity in the USA	Landsat	30 m, 1984 to present	Monitoring Trends in Burn Severity program [100][xxi]
Forest disturbance in primary humid tropical forests	Sentinel-1	10 m, every 6 to 12 days	Radar for detecting deforestation [101][xxii]

(i) LiDAR (light detection and ranging) technology is typically used for measuring surface and structural features. Example sensor in the table: global ecosystem dynamics investigation (GEDI) on board the International Space Shuttle (ISS).
(ii) Optical remote sensing provides vegetation properties linked to productivity, biochemistry, and phenology through light reflected in the visible to shortwave IR. Example sensors and satellite (constellations) in the table: panchromatic remote-sensing instrument for stereo mapping (PRISM) on board the Advanced Land Observing Satellite (ALOS), Land Remote Sensing Satellite (Landsat), moderate resolution imaging spectroradiometer (MODIS) on board Aqua and Terra, PlanetScope, Satellite Pour l'Observation de la Terre (SPOT), Indian Remote Sensing (IRS), RapidEye earth imaging system (REIS), visible IR imaging radiometer suite (VIIRS) on board the Suomi National Polar-orbiting Partnership (S-NPP) and National Oceanic and Atmospheric Administration (NOAA)-20 and Sentinel-2.
(iii) At longer wavelengths, thermal imaging provides land-surface temperature measurements that reveal insights into water stress and water use. Example sensors in the table: ecosystem spaceborne thermal radiometer experiment on space station (ECOSTRESS) on board the ISS, microwave imaging radiometer using aperture synthesis (MIRAS) on board Soil Moisture and Ocean Salinity (SMOS).
(iv) Radar (radio detection and ranging) instruments can penetrate vegetation canopies into the upper layers of the soil to give information on soil moisture or freeze/thaw status. They can also penetrate through clouds, enabling change detection in areas that are commonly clouded (e.g., to detect illegal logging in tropical areas). Example sensors and satellite (constellations) in the table: Soil Moisture Active Passive (SMAP), synthetic aperture radar (SAR) interferometric radar altimeter (SIRAL) on board CryoSat and Sentinel-1.
[a]Earth surface properties can be remotely and consistently measured from towers, drones, aircraft, and from space by using different components of the electromagnetic spectrum.

between biodiversity, ecosystem processes, environmental conditions, and human interventions. Such understanding is needed for evaluating and designing effective management interventions at the landscape level. Realizing the full potential of remotely sensed data for causal understanding will hence require the adoption of statistical techniques that can cope with the complexities of observational data – techniques that are new to many ecologists and remote sensing scientists.

different sources (e.g., cloud cover in satellite data, image misregistration, inadequate error-correction methods, biases in calibration and validation datasets). When the measured variable with error is included in a regression analysis either as a treatment or outcome, bias is introduced.
Mediator: a variable on the causal path from the treatment to the outcome which represents a process through which a causal effect arises.
Moderator: a variable that influences the direction and/or strength of the relationship between the treatment and the outcome.
Multiple imputation: a method to correct the effect size of a relationship based on the measurement error structure of the data. For remotely sensed data, this structure can be estimated by comparing the data with (a typically smaller set of) ground-truth data.
Outcome: response or dependent variable of interest that is causally influenced by a treatment. An outcome can be binary (e.g., decision to deforest) or continuous (e.g., productivity).
Overcontrol bias: controlling for mediators will artificially reduce the treatment effect size by absorbing some of the variation due to the total treatment effect.
Quasi-experimental technique: a research design to establish cause-and-effect relationships from observations without randomized treatments.
Random assignment: randomizing a treatment means that, on average, treated and control units have equal background characteristics or, in other words, that treatment assignment is uncorrelated with confounding variables.
Regression discontinuity: a statistical technique that compares observations on both sides of a naturally occurring discontinuity in treatment assignment, for example via boundaries created by wildfire, or a policy change in space or time, so that confounding variables are uniform on either side of the discontinuity.
Spatial extent: the total area over which observations are collected.
Spatial grain: the size of the observational units. In ecological data, grain often corresponds to the size of a plot; in remotely sensed datasets, this corresponds to the pixel size or the spatial resolution of an image.
Treatment: the independent or causal variable of interest. A treatment can be

Causal inference frameworks will help to harness the large and high-dimension data provided by remote sensing to scale up causal understanding of relationships between biodiversity and ecosystem processes. Contrary to the popular belief in ecology that causality can only be deduced from experiments, advances in other disciplines (e.g., economics, computer science, public health) have led to a variety of techniques to infer causal relationships from observational data (we refer ecologists to [14,15] for review). However, causal inferences in remote sensing data are difficult because (i) at large spatial extents and over long temporal dimensions, the number of variables that confound the relationship between biodiversity and ecosystem processes increases – as does the range over which they vary, and (ii) the translation of raw, remotely sensed data into meaningful ecological and environmental maps creates **measurement error**. Both create statistical **bias**. We discuss how causal inference methods address these two potential sources of statistical bias, and can thereby lead to an improved understanding of large-scale ecological relationships. This perspective brings two emerging trends together: the call for more rigorous approaches to causal inference in ecology (e.g., [15–17]), and a more explicit focus on big data and large-scale biodiversity patterns to inform conservation planning (e.g., [1,18]). We present a forward-looking approach for using remotely sensed data to test ecological hypotheses at scale to inform landscape-scale management, and call for new collaborations between researchers in ecology, statistics, and remote sensing.

Dimensions of spatial scaling

There is a mismatch between the scale at which most experimental studies are conducted (Box 1) and the scale at which biodiversity losses, increases, and management take place [19,20]. Therefore, scaling up relationships between biodiversity and ecosystem processes is now a major research goal [10]. Two dimensions of spatial scale need to be considered: spatial extent and **spatial grain** (Figure 1).

The first scaling need is to increase spatial extent by studying ecological relationships over larger areas. This addresses questions about the **external validity** (or generality) of evidence from experiments and locally established knowledge [21]. For example, a key question when designing large-scale management is whether relationships and outcomes found for a given set of samples and locations can be generalized to larger or different locations. Thanks to the myriad standardized data-collection protocols and open-data policies, this scaling challenge is being addressed by combining plot-level field observations across sites, regions, or even continents (e.g., [8,22]). Remotely sensed data could accelerate these advances further by providing data in undersampled regions [23] and by ensuring more continuous and complete coverage across environmental gradients, while respecting data sovereignty and CARE (collective benefit, authority to control, responsibility, ethics) and FAIR (findable, accessible, interoperable, reusable) principles [24].

The second dimension of scale is the size of observational units, or the spatial 'grain', of a dataset. Grain size is an important consideration when aiming to translate scientific findings into management recommendations because interventions can be applied at different spatial resolutions (e.g., forestry clearcuts) [19,25]. Different mechanisms underlying observed ecological patterns may operate at these different resolutions (Figure 1). For instance, local ecosystem functioning depends on alpha-diversity through resource-complementarity effects, whereas in larger units, beta-diversity may drive function through positive spatial insurance effects when species respond asynchronously to environmental variation [6,26]. Theoretical simulations that vary the spatial grain of analysis show a non-linear scale-dependence of the biodiversity–ecosystem functioning relationship which can depend on habitat fragmentation [10] and compositional turnover [6]. This theoretical scale-dependence has important implications for how species loss or management

binary (e.g., whether a site is invaded or not), nominal (e.g., different chemical treatments for invader eradication), or continuous (e.g., different chemical concentrations). A treatment can be a human intervention or naturally occurring changes in an ecosystem (e.g., biodiversity change).

Weighting: a technique whereby the full set of observations are weighted in a regression analysis based on their likelihood to be treated, conditional on observed confounding variables.

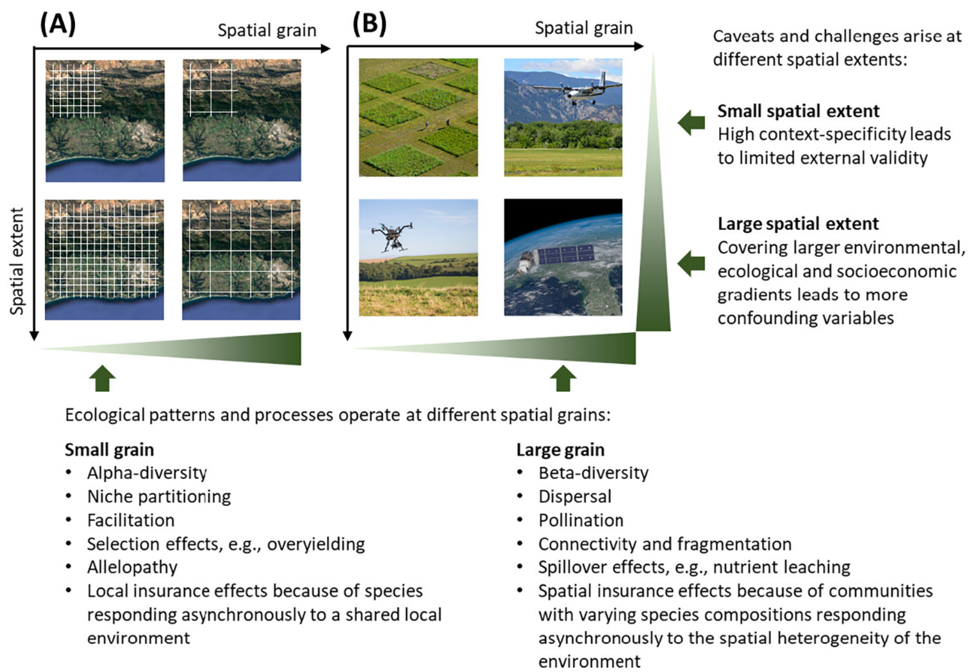

Figure 1. Scaling aspects of space. Spatial scale is defined by two dimensions: spatial extent, namely the scope or area over which a set of observations is collected, and spatial grain, namely the size of the units of observation. (A) shows RGB imagery of a part of the Garden Route in South Africa which is characterized by a gradient in elevation from the coast (South) to the mountains (North). When scaling up biodiversity–ecosystem function relationships along those dimensions, different caveats, challenges, ecological patterns, and processes will be involved. (B) Remote sensing technology offers opportunities to scale up information and hypothesis testing along the two scale dimensions. Note that all platforms depicted in (B) can scale up along both scale dimensions, but are visualized as examples in the category that best reflect their unique strengths – for example, drones can cover relatively large terrains with fine spatial resolution. Picture credits: images reproduced, with permission, from the following sources: field plots at Cedar Creek, USA: Jacob Miller; drone: National Trust Images/James Dobson; aircraft: National Ecological Observatory Network (NEON); satellite: NASA.

interventions targeting biodiversity impact on ecosystem functions across scales – meriting empirical tests of this theory.

Grain size could be increased by simply aggregating small-scale observations into coarser observational units (e.g., [10,27,28]). However, the potential to do this scaling using traditional field observations is limited – if not impossible. For instance, the degree to which observational units can be aggregated to coarser observational units depends on the sampling design (e.g., the nestedness and number of observations); sampling large field plots spread across large spatial extents is logistically challenging and expensive. Remote sensing offers opportunities to explore the impact of spatial grain on causal relationships between biodiversity, ecosystem processes, and human interventions (e.g., [29]). It is important to note, however, that the optimal grain size will depend on the outcome or intervention of interest because meaningful variation may also be lost when aggregating to larger grains [30].

The challenge of confounding variables

Remote sensing offers unprecedented opportunities to investigate ecological relationships at scale, but, to advance understanding, researchers need to consider the potential pitfalls and solutions for inferring causality from big observational datasets [31,32]. By contrast, randomized controlled experiments enable causal inference by randomizing a **treatment** – which is used synonymously for the independent or causal variable of interest (e.g., invasion, management intervention). **Random assignment** of a treatment ensures that treated and control units have similar background characteristics on average (e.g., elevation, soil type, climate, land-use history), thus eliminating these variables as a source of confounding variation. However, in observational datasets, such as many remotely sensed datasets, a treatment is not assigned randomly, and instead may be influenced by the characteristics of a location. When these background characteristics also influence the treatment's **outcome** or dependent variable of interest (e.g., ecosystem functions), they are **confounding variables** that can lead to spurious correlations between the treatment and outcome. For example, higher rainfall may increase productivity by relieving water limitation, and increase the likelihood of invasion because fast-growing invaders are highly competitive [33]. Do we then find higher productivity in highly invaded areas because invasion promotes productivity or because both variables are influenced by rainfall? Confounding variables can also manifest themselves in temporal dimensions (e.g., climate change, management changes) [8]. Problems with confounding variables are often summarized under the statement that correlation does not imply causation. As a result, conventional methods for estimating effect sizes, such as linear correlations or differences-in-means tests, will be biased and lead to incorrect inferences [15].

Disciplines with a longer tradition of analyzing large, observational datasets, such as econometrics, computer science, and public health, have well-established approaches to eliminate bias from confounding variables [34]. These advances are slowly being adopted in ecology (e.g., [8,16,35,36]), but have a longer history of use in research investigating the impacts of protected areas and conservation programs (e.g., [37–39]). Despite their potential, these techniques remain underused by researchers working at the intersection of biodiversity science and remote sensing (*cf [*35,40,41]) and provide additional solutions beyond the methods currently being used to deal with confounding variables (e.g., by using stratified sampling designs [9]). Thus, we briefly highlight commonly used methods from other disciplines and provide references to more technical literature (ecologists are referred to [14,15,42,43]). All these modern causal inference techniques focus on careful consideration of and transparency around assumptions, which are described in more detail in the provided references.

When predicting large-scale patterns from remotely sensed data, a common approach is to include a large set of explanatory variables and then perform a model reduction or selection approach to find the most parsimonious model (e.g., [44]). However, this approach for model selection can be problematic when the purpose is to identify and quantify causal relationships among variables [42,43]. When the goal of a study is to infer causality, great care is needed when deciding which covariates to include and exclude. Causal diagrams or **directed acyclic graphs (DAGs)** [45] are a useful tool to help to decide which variables should be accounted for (Box 2). Creating a fully articulated DAG requires *a priori* knowledge, emphasizing the need for collaboration between local knowledge holders of the study system and technical experts. Especially in complex social-ecological systems, causal relationships among variables can differ in different contexts and across broad spatial extents, necessitating the construction of different DAGs that fit different local contexts. For example, management intensity may confound the relationship between diversity and ecosystem functioning in managed areas, whereas climate variables may be more important confounders in natural areas with no management. Importantly, DAGs transparently share researcher assumptions about the causal structure of an ecosystem.

Once confounding, colliding, and moderating variables have been identified, their effects can be accounted for (Box 2). Including confounding variables as covariates in a regression model is a common approach, but this approach makes strong assumptions about the functional form of links between confounding variables and the outcome, and can lead to highly complex models. Instead, a first set of techniques – **matching** [46] and **weighting** [47] – explicitly take confounding variables into account without these limitations to create a balance in the distribution of confounding variables to mimic randomized treatment assignments. For example, positive effects of invasive animal control on native canopy cover were not always detected without weighting sites based on confounding variables [16]. Matching and weighting techniques can be easily used with remotely sensed data; thanks to recent sensor and computational developments, remote sensing now enables mapping of a wide variety of potential confounding variables ranging from environmental and ecological variables to information about land use and disturbance history (Table 1). For causal interpretation of estimates, these techniques, however, still rely on the strong assumption that all confounding variables are known and can be measured with minimal error (on top of other assumptions; reviewed in [15]). Therefore, it is important to perform sensitivity tests to assess the potential impact of unobserved or unmeasured confounding variables [48].

What if you do not know or have not measured all of the confounding variables, or do not have the 'true DAG' of the system to inform which covariates to measure and control for? Other **quasi-experimental techniques**, such as **difference-in-differences** [49,50], **instrumental**

Box 2. An example of combining remote sensing with tools from the structural causal model to address causal questions

The primary tool of the structural causal model is a directed acyclic graph (DAG) which is used to visualize the causal structure of a system and its data-generating process. To consider using remote sensing combined with tools from the structural causal model, we discuss a case study of the Greater Cape Floristic Region in South Africa. Fynbos vegetation covers only 4% of the South African land surface, but hosts 67% of the threatened plant taxa of the country [77]. However, it faces serious threats from invasive alien species. Alien trees are particularly problematic because they can have major impacts on ecosystem function. For example, they generally use more water than native species in South Africa, thus reducing runoff and groundwater recharge in an already water-scarce nation [78] and amplifying the effects of anthropogenic climate change [79].

In this case, a causal question is: does invasion by alien trees increase biomass in the Fynbos biome (Figure I)? This question is especially relevant at large spatial scales given the increased risk of high intensity fires with higher biomass. In this system, as in many, numerous confounding variables affect both the probability of alien invasion and biomass (e.g., rainfall) (Figure II). To isolate the effect of alien invasion on biomass, DAGs reveal rainfall and other confounding variables, including fire occurrence history and topography, that need to be accounted for.

Note that the treatment effect of invasion on biomass may differ based on contextual features. One way to address this challenge is to allow for heterogeneous treatment effects where different subareas have a different outcome conditional on covariates. For example, we would expect the effect of *Pinus* spp. – an invasive alien tree from Europe/America – on biomass to be higher in mountainous areas compared to some lowlands because the latter ecosystems have high biomass already. In other words, the type of Fynbos ecosystem is a **moderator**.

DAGs also help to identify variables that can lead to bias when included in a model. For instance, fire severity is a **collider** because it is caused by both productivity (through the buildup of fuel) and invasion (e.g., through changes in flammability or the vertical structure of vegetation) [80] (Figure I). In a scenario where there is no association between invasion and productivity, controlling for fire severity will introduce a non-causal correlation between them [42,76]. In the scenario where invasion does affect productivity, controlling for fire severity may even flip the sign of the causal effect in the opposite direction [42,76].

DAGs can be used to illustrate variables that fall on the causal path between invasion and productivity – or that mediate processes which explain how or why a causal effect occurs. For instance, invasion may partly impact on productivity through changes in the functional composition of a community [81]; therefore, functional composition is a **mediator** (Figure I). Mediating variables can be the focus of a research question when one is interested in identifying and quantifying the strength of the mechanisms underlying the causal relationship between a treatment and outcome (e.g., [82]). Otherwise, controlling for mediators leads to **overcontrol bias**. In this example, the effect of invasion on productivity would be reduced to near-zero if functional composition is a strong mediator.

In summary, controlling for covariates only makes sense if they are confounding variables. Other types of covariates, such as colliders and mediators, should not be controlled for because they actually lead to spurious estimates of causal effects. For more details on use of DAGs we refer the reader to in-depth reviews for ecologists [42,43].

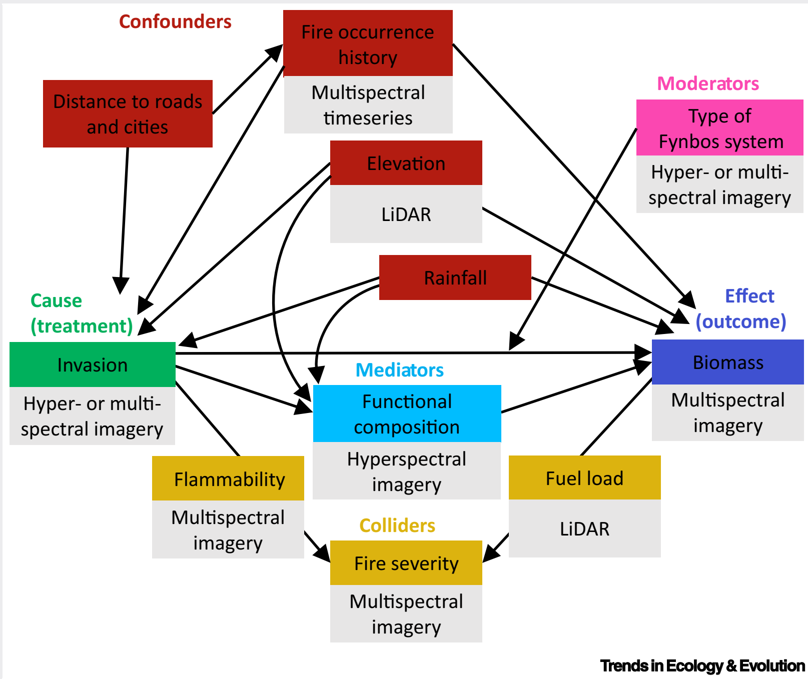

Figure I. A directed acyclic graph showing relationships between tree invasion, productivity, and other covariates in the Fynbos biome in South Africa. Variables are color-coded according to their role in the causal diagram: cause (green), effect or outcome (dark blue), confounders (red), moderators (pink), mediators (light blue), and colliders (yellow). The gray boxes contain suggestions of remote sensing data sources to derive information for each variable (Table 1).

Figure II. Invasion of 'escaped' pine trees from a pine plantation into the biodiverse Fynbos shrublands in the Southern Cape of South Africa. Invasive alien trees in South Africa often have high numbers of propagules which are dispersed from plantations by wind, water, or animals. Because plantations tend to be established in areas that receive enough rainfall, and rainfall also drives productivity, rainfall can potentially confound the causal effect of invasion (the treatment) on the productivity of the native Fynbos (the outcome). Photo credit: Johan Baard.

variable (IV) [51], and **regression discontinuity** [52] methods, relax the strong assumption that a researcher knows and has controlled for all confounding variables. These techniques can control for unobserved or unmeasured confounding variables. To illustrate, positive effects of post-fire seeding on sagebrush recovery have been found when applying difference-in-differences [36]. By contrast, these effects were not observed using traditional regression analyses with adjustments for covariates or matching, neither of which accounts for unobserved confounding variables. Integrating these quasi-experimental techniques with remote sensing (e.g., [40]) could dramatically improve our understanding of diversity effects on ecosystem functioning at large scales, especially now that several satellite sensors have been in orbit for multiple decades (e.g., Landsat 1-9), leading to rich time-series. These approaches can also be used to estimate **heterogeneous treatment effects** to elucidate when and where effects are present, absent, stronger, or weaker, based on contextual factors or subgroups [53], or to consider why and how effects occur through mediation analysis (reviewed in [54,55]).

Although these quasi-experimental techniques can also improve analyses of traditional, plot-level datasets, they are exceptionally relevant for large-scale analyses owing to the increased number and range of confounding variables. In fact, we now have an opportunity to establish best practices for causal inference before the use of remotely sensed products to study large-scale causal relationships becomes common. Now is the crucial moment for interdisciplinary collaborations between landscape ecologists, biodiversity scientists, remote sensing specialists, and specialists in causal inference to establish the state of the art.

The challenge of measurement error in remotely sensed data

Even if confounding variables are controlled for statistically, measurement error adds additional complexity to causal inference and poses another source of statistical bias that is being increasingly recognized in the literature using remotely sensed data (e.g., [56–59]). Although the goal of mapmaking is to represent reality as accurately as possible, prediction uncertainties are unavoidable. The translation of raw, remotely sensed data into meaningful ecological and environmental patterns involves many assumptions and decisions – many which are relatively technical and require specific expertise. Thus, understanding all the sources of bias and uncertainty that may contribute to measurement error is particularly challenging for those interested in causal inferences. When working with derived remote sensing products, grasping these potential sources of error can be even harder. End-users of coarse and spatially aggregated maps are often unaware of under- or overestimation of measurement errors owing to poor assumptions related to the aggregation process [60]. Ignoring measurement error can lead to statistical bias in downstream analyses and to incorrect conclusions and policy recommendations [58,61,62]. We highlight two practices that could minimize these impacts.

First, understanding and reporting the nature of uncertainties in remote sensing data is important, especially for inference. Measurement errors are not unique to remotely sensed maps, and should also be considered in studies working with other types of data (e.g., by correcting for inter-observer reliability). However, structured or systematic – instead of random – measurement errors tend to be common in remote sensing data, making this a particularly important source of bias. Whereas random errors or noise in measurements causes **attenuation bias** towards zero effect sizes, structured or systematic measurement errors are more nefarious because the direction of the bias is not consistent and therefore more problematic [58]. Measurement errors might be systematically related to landscape or ecological variables owing to flaws in sensors, geolocation errors, or downstream methodological aspects (e.g., biases in the calibration and validation datasets). For example, canopy height derived from the space-borne LiDAR (light detection and ranging) global ecosystem dynamics investigation (GEDI) system is systematically less accurate on steep terrains [63], estimates of tree cover may be less accurate in dryland biomes that have sparse tree cover [64], and the misclassifications of a land-cover map may be larger for some types of land cover, such as tropical biomes that have more cloud cover and thus less imagery available for classification [57]. This latter example showcases one of the reasons why different land-cover maps may over- or underestimate deforestation depending on the product used (e.g., [57,65]). As a result, conclusions about the efficacy of forest conservation programs or about the impact of forest-cover changes on ecosystem services can vary greatly [57]. More generally, results from previous papers using regression analyses and remotely sensed measurements without correction have been called into question [58].

Fortunately, current research is developing solutions to deal with measurement errors in remotely sensed imagery; for instance, a solution to limit bias from misclassification in binary outcomes (e.g., deforested or not, burnt or not, infected or not) has been proposed [57]. Further, **multiple imputation** [58] and IV [66] methods can be used to reduce bias from measurement error (and IVs also to reduce confounding bias). For instance, it was demonstrated that naive regression estimates of the relationship between road length – quantified via remote sensing – and population density are biased because predictions of road lengths are systematically too low for long roads [58]. To deal with these systematic measurement errors and the resulting bias, a small set of ground-truth data were used to adjust road length values and generate unbiased effect sizes via multiple imputation [58].

Second, we emphasize the importance of sound ecological knowledge to inform analyses (Box 2) and to identify the sources of measurement error that are relevant for a particular study context and question. For example, interpreting fire severity indices is complex because they can reflect not only fire behavior but also vegetation height [67]. Alternatively, researchers may have too much confidence in freely distributed maps that incorrectly represent local conditions. Global datasets are often poorly calibrated for the Global South. For example, some global maps represent woody plantations of alien trees as 'forests' in the Greater Cape Floristic Region of South Africa [68], leading to restoration programs being misclassified as 'logging'. Local ecological knowledge is essential to avoid major consequences of resultant poor decision making or policy formation [69]. These examples also highlight the importance of collaboration among people generating and using remote sensing-derived maps to ensure an appropriate understanding of measurement error.

Concluding remarks

Harnessing the big data revolution in ecology to advance understanding and inform management will require integration of remote sensing and causal inference. The ability to account for confounding variables and measurement errors in remotely sensed data will improve the understanding of large-scale processes (see Outstanding questions). That understanding will increase the effectiveness of the large-scale conservation and restoration interventions that will be necessary to build resilience in the face of environmental change. A greater appreciation of the potential to untangle complex, applied ecological questions at scale could also guide the development of future satellite missions and land-surface models (see Outstanding questions). More interdisciplinary collaboration and training of ecology researchers in the technically demanding topics of remote sensing and causal inference will enable a more robust understanding of biodiversity dynamics at the scale at which management decisions are made.

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Outstanding questions

What is the magnitude of the causal effect of biodiversity on ecosystem functioning at large spatial scales, and how large is it relative to other drivers? How much does the effect of biodiversity on ecosystem function at landscape scales operate through spatial insurance effects?

How does non-linear scaling influence multiscale causality? Is there a spatial grain threshold at which the slope of the relationship between biodiversity and ecosystem function stabilizes, and is this influenced by landscape characteristics?

How can researchers best account for measurement error of remote sensing products in causal inference approaches? How incorrect are the effect sizes estimated in studies that ignore systematic measurement error, and how large an error is acceptable for meaningful causal inference? Does accounting for measurement error change policy recommendations?

How do satellite mission requirements limit or enable causal inference studies? Satellite sensors exhibit trade-offs in spectral, spatial, and temporal resolution, as well as in signal-to-noise ratios. What is the consequence of these trade-offs for inferring causality at larger spatial scales?

How can causal relationships established at large spatial scales using remote sensing data be incorporated into next-generation numerical land-surface models?

What are the consequences of using covariates as a predictive variable of the outcome for causal inference? For example, in combination with the normalized difference vegetation index (NDVI), weather can be used as a predictor of biomass. Can we subsequently make causal inferences about the impact of weather on biomass, or is it a circular argument?

How can we build collaborations among remote sensing scientists, ecologists, and experts in causal inference to better address biases arising from the use of remote sensing products, and thereby advance ecological understanding and management impact evaluation at scale? What type of training and training models can enable applied researchers to collaborate across these technical areas and keep up with the exponentially increasing changes in technology and techniques?

Declaration of interests

The authors declare no competing interests.

Resources

[i]https://developers.google.com/earth-engine/datasets/catalog/JAXA_ALOS_AW3D30_V3_2#description

[ii]https://smap.jpl.nasa.gov/data/

[iii]https://bec.icm.csic.es/ocean-datasets/

[iv]https://earth.esa.int/eogateway/catalog/smos-cryosat-l4-sea-ice-thickness

[v]http://data.starcloud.pcl.ac.cn/

[vi]https://land.copernicus.eu/pan-european/corine-land-cover

[vii]https://egis.environment.gov.za/sa_national_land_cover_datasets

[viii]https://earthenginepartners.appspot.com/science-2013-global-forest/download_v1.7.html

[ix]https://zenodo.org/records/5220816

[x]https://gedi.umd.edu/data/download/

[xi]https://ecostress.jpl.nasa.gov/data

[xii]https://rangelands.app/

[xiii]https://tinyurl.com/neontraits1

[xiv]https://drive.google.com/file/d/1dM7dAnYCUsB3ia8yJT5Ph2iO374_azqI/view

[xv]https://drive.google.com/file/d/1NerUPUdprYvXFcCZKwo1y6FdPBdiHlml/view

[xvi]https://allencoralatlas.org/#1/0/0

[xvii]https://www.sciencebase.gov/catalog/item/5a144ec0e4b09fc93dcfcffa

[xviii]https://modis.gsfc.nasa.gov/data/dataprod/mod15.php

[xix]https://firms.modaps.eosdis.nasa.gov/

[xx]https://lpdaac.usgs.gov/products/mcd64a1v061/

[xxi]https://www.mtbs.gov/

[xxii]https://www.wur.nl/en/research-results/chair-groups/environmental-sciences/laboratory-of-geo-information-science-and-remote-sensing/research/sensing-measuring/radd-forest-disturbance-alert.htm

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