The Spatial and Temporal Domains of Modern Ecology

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Abstract

In order to properly understand ecological phenomena, it is necessary to quantify their behavior over the range of spatial and temporal scales at which they manifest. Ecology has been concerned with this need for decades, and the ability to collect ecological observations across multiple scales has grown rapidly since then. Characterizing the spatial and temporal domains (the distribution of observations within one or more scale spectra) of modern ecological observations can therefore provide important insight into the field's progress towards a more comprehensive understanding of ecosystem behaviour. To characterize these domains, we conducted a meta-analysis of recent (2004-2014) ecological studies, in which we quantified

four primary dimensions of their reported observations: plot resolution, sampling interval, effective duration (time between start and end of temporal replicates), and effective extent (area enclosed by spatial replicates). We also estimated the *actual* extent and duration, which respectively represent the summed area and time covered by spatial and temporal replicates. Replace this text with more specific summary of observed scales: Here we show that ecology remains a largely field-based discipline that makes observations within generally narrow spatial and temporal domains, despite the well-established literature on the importance of scale (*1–3*).

The scales at which ecosystems are observed plays a critical role in shaping our understanding of their structure and function (*1–3*). Ecological patterns emerge from temporal and spatial domains that may be coarser or finer than the processes that shape them, which means that investigation across multiple scales is essential for understanding ecological phenomena (*1*). This awareness has grown rapidly since the 1980s, accelerated by the need to understand how changes in the global climate, ocean, and land systems are affecting everything from individual populations (*4*) to entire biomes (*5*), while technological advances in areas such as remote sensing and genetics are making it ever-easier to quantify ecological features across a broad and increasing range of scales (*2, 6*).

Given the growing awareness of scale, expanding data gathering capabilities, and the fact that the most comprehensive (and arguably best-known) analysis of ecological research scales was published in 1989 (*7*), it is both timely and important to assess the scales of contemporary ecological investigation. To address this need, we quantified the spatial and temporal domains of empirical observations that were reported within recently (2004-2014) published ecological studies (here domain means the distribution of observations within the spectrum of one or more scale dimensions[1]). Empirical observations are critical for developing and testing the models that explain why

[1]This definition differs slightly from Wiens' (*3*), who defined "domain of scale" as "a portion of the scale spectrum

ecological patterns vary in time and space (*1, 7*), therefore the spatio-temporal domains of observations provide an important indicator of the field's progress towards achieving a holistic, predictive understanding of ecosystems (*1, 2*).

Our analysis focused on two dimensions of spatial scale, resolution (grain) and extent, and two of temporal scale, interval and duration (Table 1). Resolution is the area of an individual spatial replicate within which a complete measurement (as opposed to a sub-sample) of the feature of interest was made. Extent is the area enclosed by the outer-most spatial replicates, or, if the system or habitat being sampled was distinct from its surrounding matrix (e.g. forest patches in grassland habitats), the summed area of sampled patches (see SI for full definition). Interval refers to the average time elapsed between individual temporal replicates. Duration measures the time elapsed between the first and last temporal replicates, or, in the case of temporally unreplicated observations, the estimated time spent collecting the observation (SI). We also assessed observational scales within two additional dimensions, *actual* extent (the integrated area of spatial replicates) and *actual* duration (the summed observational time of temporal replicates). We evaluated these additional dimensions to gain insight into how much the actual scales of observation (i.e. how much space and time is covered by the measurement) differ from those they are intended to represent.

Table 1: The scale dimensions of ecological observations assessed in this meta-analysis.

Component		**Units**	**Description**
Spatial	Resolution	m^2	Area of an individual spatial replicate (plot)
	Extent	ha	Area encompassed by all spatial replicates
	Actual extent	ha	Summed area of all spatial replicates
Temporal	Interval	days	Time elapsed between successive temporal replicates
	Duration	days	Time elapsed between first and last temporal replicates
	Actual duration	days	Summed observational time of all temporal replicates

Our analysis was based on a review of 348 papers randomly selected from 42,918 published

within which process-pattern relationships are consistent regardless of scale."

between 2004-2014 in the top 30 (based on 2012 impact factor) ecology-themed journals. We extracted scale data from 379 observations of "natural" (i.e. non-experimentally manipulated) ecological features that were reported within 134 of the reviewed papers (plus an additional 62 that these cited as the source of observations). We excluded experiments because they tend to be of limited extent, duration, and resolution due to their higher logistical costs (*7, 9*), and would therefore likely bias our findings towards finer scales.

To account for uncertainty in the estimation of observational dimensions due to 1) unclear methodological description in the reviewed papers, and 2) observer interpretation, we conducted a resampling analysis (n=1000) in which scale values were randomly perturbed within the bounds of estimated inter-observer variation (SI). We constructed histograms for each dimension from the mean of the perturbed ensembles, and estimated 95% confidence intervals for each histogram bin (Fig. 1). We constructed kernel density estimates from the full resampled ensemble in order to assess observational distributions within different juxtapositions of the four primary (resolution, extent, interval, duration) space-time dimensions (Fig. 2).

Domains

In terms of resolution, the majority (67%) of observations were collected in plots of <1 m^2 resolution, 24% were collected within plots of 1 m^2 up to 1 ha, and the remaining 9% in plots of ≥ 1 ha (Fig. 1A). The extent of 19% of observations was <10 ha, 23% covered 10-1,000 ha, 42% 1000-1,000,000 ha, and 16% $>1{,}000{,}000$ ha (Fig. 1B).

In the temporal dimensions, 37% of observations were not repeated (Fig. 1C), 17% were repeated at short intervals (sub-second to daily), 20% at daily to monthly intervals, 18% at monthly to yearly intervals, and 8% at yearly to decadal intervals. Duration was one day or less for 31% of sampled observations, while 10% covered one day to one month, 23% lasted one month to one year, 27% covered 1-10 years, and 10% spanned a decade or more (including several paleoecological studies covering centuries to millennia; Fig. 1D).

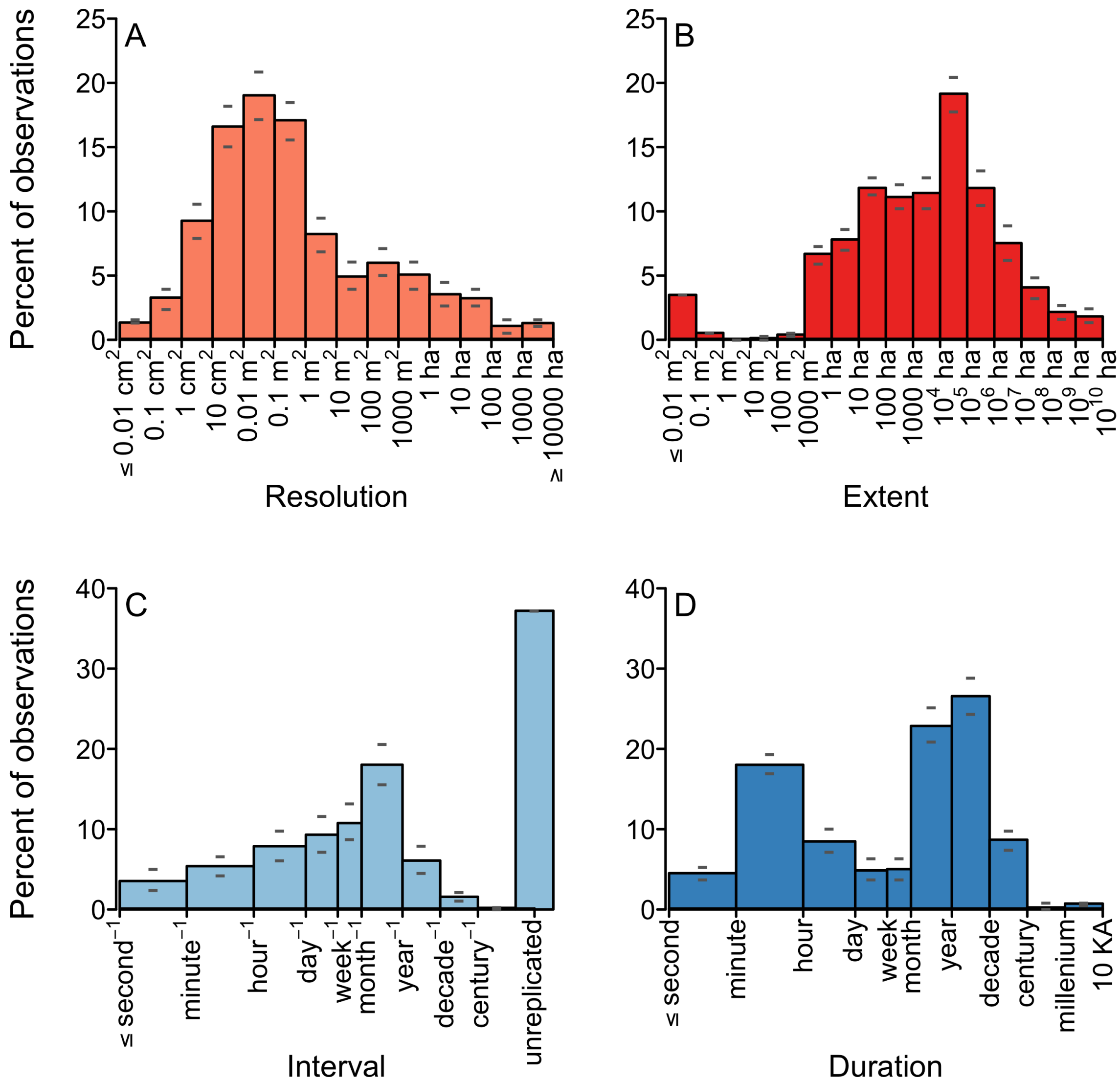

Figure 1: Histograms of the resolution (A), extent (B), interval (C), and duration (D) of observations collected from the surveyed ecological studies. Bars represent the average percentages for each bin realized after 1000 perturbed resamples, while grey bars indicate the 95% confidence interval.

Juxtaposing these observational dimensions provides further insight into the spatio-temporal domains of ecological observations (Fig. 2). Contrasting resolution with interval reveals that the majority of temporally replicated observations (the 37% that were unreplicated were excluded because they lack interval values) had resolutions of 10 cm^2-1 m^2 and were revisited at daily to yearly intervals (Fig. 2A). A less dense, oblong concentration of observations bounded on the lower right by monthly to yearly observations at 100 m^2 and on the upper left by near-daily to monthly observations with 1-10 ha resolution is also evident. This lower right to upper left orientation reflects the tradeoff between resolution and interval that is typical of satellite imaging (*8*), and stands in contrast to the upper right to lower left line that stretches between this concentration and the high frequency (minute-hour intervals), high spatial resolution (0.1-100 cm^2) observations. This line demonstrates the opposite tradeoff that occurs with field-based observations, where larger plot sizes demand greater effort that in turn reduces sampling frequency (*9*).

Contrasting duration and extent (for all observations) reveals two primary domains of observational concentration. The first consists of observations spanning one month to one decade in time and 10-1000 ha in space, while the second is defined by observations of one year to several decades that cover 10,000 to 1,000,000 ha (Fig. 2B). Three other notable, but lesser areas of concentration are also evident, including small area observations (0.1-1 ha) covering one month to decade, and short duration, temporally unreplicated observations ($<$1 day) of either 1-10 ha or 10,000-1,000,000 ha.

Comparing the two spatial dimensions against one another (for all observations) shows a primary concentration of observations with 10 cm^2 to 100 m^2 resolution that have extents ranging between slightly over 1,000 to nearly 1,000,000 ha (Fig. 2C). The second-most prominent concentration consists of higher resolution (1 cm^2-1 m^2), smaller extent (10-1,000 ha) observations, beneath which lies a third and fainter concentration of 1-1,000 cm^2 resolution, 1000 m^2 to $<$10 ha. These three concentrations suggest a tendency for observational extent to increase with resolution,

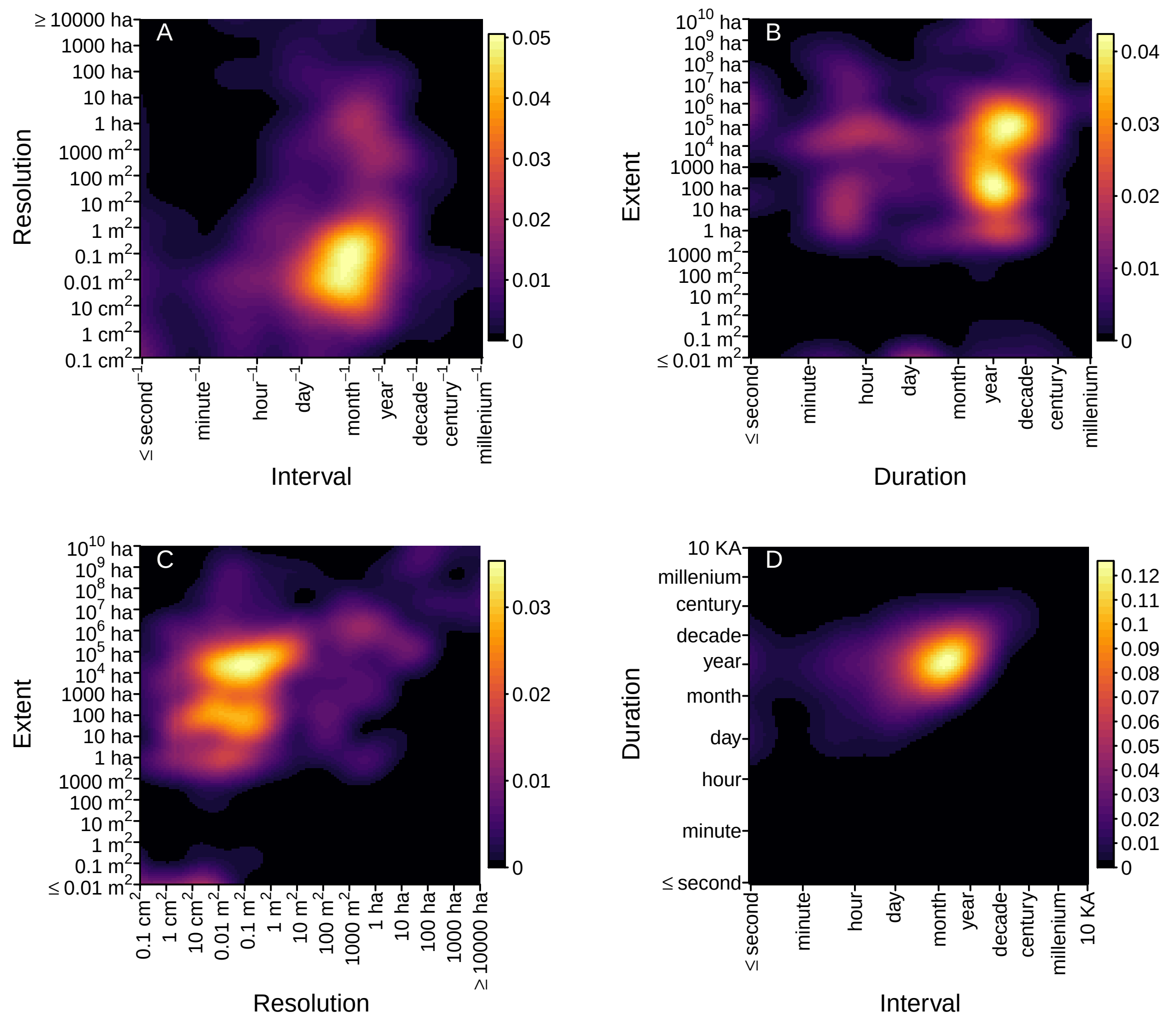

Figure 2: Kernel density estimates of observational densities within the domains defined by A) interval and resolution (of temporally replicated observations only), B) duration and extent, C) resolution and extent, and D) interval and duration (of temporally replicated observations). Density estimates were applied to the log-transformed values of each observational dimension, and density estimates are rescaled to represent percentages.

which is a relationship that becomes more pronounced in the (less densely observed) portion of the domain where resolutions $\geq$100 m^2.

A similar tendency for duration to increase with interval was also evident amongst temporally replicated observations (Fig. 2D), with the majority of repeated at daily to decadal intervals and spanning $\geq$ 1 month to 1 decade. The orientation of this concentration shows that interval increases with duration; observations lasting one month to one year tend to have daily to monthly intervals, while those lasting one year to one decade tend to have yearly to decadal intervals. The low densities of observations having sub-daily intervals shows that relatively few high frequency, long duration ecological measurements are undertaken.

To provide further insight into observational domains, we also evaluated the degree to which the scales *represented* by observations differed from those that were actually observed. To make this assessment, we first $\log_1 0$ transformed and then subtracted the values of i) actual extent from extent and ii) actual duration from duration, in order to calculate the magnitude of difference (or decade) between each pair of dimensions for each observation. We then compared how these magnitudes varied in relation to the scale of the actual dimension (Fig. 3). This comparison showed that a majority (81%) of the assessed observations had actual extents of $\leq$1 ha, which on average were 4 to nearly 8 orders of magnitude smaller than the quantified extent (Fig 3.A). Actual extent converged with extent above 100,000 ha, but this applies to just 5% of observations. The actual duration of 64% of observations was $<$ 1 day, which on average was 3 to nearly 9 orders of magnitude shorter than the time span covered by temporal replicates (Fig. 3B). The two duration measures were approximately equal for the 16% of observations exceeding one month of actual duration.

Observational methods

We classified the method used to collect each observation into several broad categories, which were field methods (manual *in situ* data collection), automated (*in situ*) sensing, remote sensing, other geographic data, and paleo-reconstruction approaches. Field methods were used for 80% of observations, automated sensing for 12.4%, remote sensing for 6.3%, and paleo-reconstruction and other geographic data each for less than 1%. Using linear regression (weighted by the number of

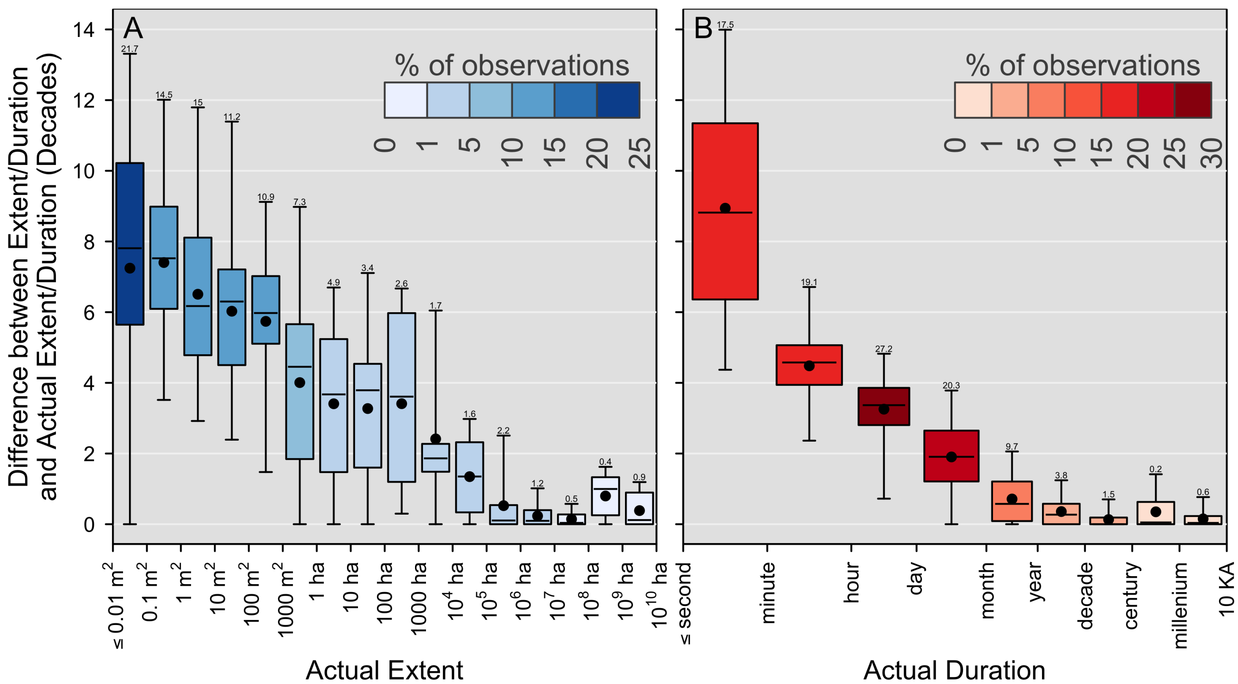

Figure 3: The difference between *actual* extent (the summed area of spatial replicates) and extent (A) and *actual* duration (the summed sampling duration across temporal replicates) and duration (B). Differences are expressed as decades, or how many orders of magnitude greater the extent or duration is then the actual extent or duration, and are summarized (as box plots, with circle in box representing the mean and line the median) in bins representing different levels of actual extent/duration. The percentages of observations falling within each bin are indicated by the color of the inter-quartile and the numeric value above the upper whisker.

observations per publication year) to assess whether the relative frequency of observing methods changed during the 10 year study period, the use of remote sensing appeared to increase by 1.3% per year from 2004-2014 (R^2 = 0.25, p<0.12), and field methods declined by the same percentage (R^2 = 0.1, p<0.18), although both slopes failed to meet the customary threshold for statistical significance. Automated sensing methods showed no trend over time (SI).

Potential biases and uncertainties in quantifying scales

There were several potential methodological aspects that could have influenced our assessment of ecology's spatial and temporal domains. The first stems from our finding that many studies did not precisely report observational scales, which meant that we had to estimate–rather than simply record–these values for most observations (specifically, in 63, 60, and 67% of cases for resolution, extent, and actual extent, and 36%, 64%, and 83% of cases for interval, duration, and effective duration, respectively). The inevitable estimation errors may have biased our overall findings. However, we attempted to quantify this error by assessing inter-rater disagreement and incorporating this uncertainty into our resampling methodology. The resulting confidence intervals (Fig. 1) suggest that it was unlikely that estimation errors unduly influenced our findings.

Another potential source of bias lies within our scale-estimation protocols, chiefly with respect to our rule for estimating resolution (the smallest areal unit of *complete* measurement). We selected this definition for the sake of consistency, but some papers reported resolution as a larger area in which sub-samples were taken. For these, our estimates are finer than what the studies' authors apparently considered to be plot resolution. Additionally, our domain estimates would presumably be somewhat different if we had included experimentally manipulated observations. For example, average resolution and duration would likely be finer (*7, 9*).

Finally, because our review did not include papers beyond 2014, the omission of studies from the most recent years could have introduced bias into our domain estimates. Indeed, if the trend towards increasing use of remote sensing between 2004-2014 was not spurious, we can project that a repeated study applied to papers published between 2004-2017 would find remote sensing used for 7.7% of observations (a 22% increase), which would increase mean extent by 17.4% (95% CI = -1.3-67%; or 0.07 orders of magnitude) above the 2004-2014 average (see SI for details of calculation). Further evidence for this trend lies within the extent values themselves, which increased 0.25 orders of magnitude per year between 2004-2014 ($R^2 = 0.25$, $p<0.07$). This somewhat clearer trend also suggests that including more recent studies would show extent to be somewhat larger, although in this case by a more modest 5.5% (0.02 orders of magnitude).

Broader implications

Our results show that modern ecological observations most observations are collected at small spatial scales, are either unrepeated or relatively infrequent ($\geq$1 month interval), and in aggregate cover relatively narrow periods of time ($\leq$1 month).

1. General patterns of scales

   - Duration hasn't improved much since Tilman (check this).

   Implications for missing scales–what isn't being covered/observed?

   The continued dominance of field-based research, and the limited use of methods that allow larger areas to be comprehensively observed, such as remote sensing.

   Though the Tilman (1989) reference that one of the reviewers definitely wanted to see updated was mostly focused on field experiments, there's a couple allusions to it that we could make. One of them could go here: 387/749 of the papers he looked at from the journal Ecology (1977-1984) were mainly experimental or had an experimental component. 99 papers were mainly theoretical or conceptual. Remainder observational. We could compare our results to that here.

   Another Tilman (1989) comparison that's a little apples to oranges: of his 623 field based studies (including 180 experiments), $\sim$41% lasted less than one year, $\sim$85% less than three years, most studies >10 years and all >50 years were paleoecology/chronosequences.

   Maybe mention here (or probably better later in the discussion), that our decision has the unfortunate consequence of not being directly comparable to previous assessments that included experiments. More of just a caveat or note for the reader who is familiar with the earlier work and their summary statistics

   But there do seem to be trends increasing extent (and duration, but need to put this above), perhaps due to increasing use of remote sensing

2. Scales are not well-documented

Furthermore, the unclear documenting of observational scales implies that scale is not a primary concern in much ecological research (*2, 18*). (Scale is not a concern that cuts across the entire discipline of ecology).

3. Represented scale is very different from actual scale of observations.

In heeding Levin's call to think at multiple and appropriate ecological scales, we also need to give pause to think about whether our data are overextrapolated/overleveraged.

How over-leveraged/under-leveraged might depend on the auto-correlation properties of feature being observed. Maybe use example of fire process

Maybe we should go further here to explain why this is an important (and overlooked) assessment to make (actual versus effective comparison)

4. Where to from here? What do we need to improve?

Satellite observations typically have lower information content than field measurements for a given location, and in many cases only provide proxy measures for the ecological features of interest, such as forest understorey structure (*26*), thereby making ecologists less inclined to use the technology (*21*).

Narrowness and poor documentation (a tendency that is also evident in the geographical sciences (*19*)) Ecological understanding drawn from many of these observations may have limited generalizability (*3, 18, 19*), a concern that has been previously noted due to ecology's geographical bias towards anthropogenically undisturbed and temperate ecosystems (*20*).

Our results provide valuable insight into the spatial and temporal domains being addressed by modern ecological research. Our results show that most observations are collected at small spatial scales, are either unrepeated or relatively infrequent ($\geq$1 month interval), and in aggregate cover relatively narrow periods of time (≤1 month). Very little research is conducted at high spatial and temporal resolutions over large areas or for long time periods, indicating that, despite the well-established understanding of the importance of multi-scale assessments for understanding ecological patterns and processes (*1, 3*), efforts focused on larger scales are still relatively sparse within the discipline (*1, 3*). Furthermore, the unclear documenting of observational scales implies that scale is not a primary concern in much ecological research (*2, 18*). Taken together, this narrowness and poor documentation (a tendency that is also evident in the geographical sciences (*19*)) suggests that the ecological understanding drawn from many of these observations may have limited generalizability (*3, 18, 19*), a concern that has been previously noted due to ecology's geographical bias towards anthropogenically undisturbed and temperate ecosystems (*20*).

The generally small spatial scales of observation is a consequence of the continued dominance of field-based research, and the limited use of methods that allow larger areas to be comprehensively observed, such as remote sensing. Despite early and repeated calls for ecologists to use remote sensing because it provides a synoptic view that field measurements cannot (*21–23*), and subsequent demonstration of its importance for multi-scale studies (*24, 25*), our results indicate this method has not yet been widely adopted in ecological research. Two reasons lie behind this slow uptake. First, remote sensing can be a challenging method for ecologists to learn, many of whom may not have access to appropriate training (*23*). Second, satellite observations typically have lower information content than field measurements for a given location, and in many cases only provide proxy measures for the ecological features of interest, such as forest understorey structure (*26*), thereby making ecologists less inclined to use the technology (*21*).

In contrast to remote sensing, ecologists have made broader use of technologies that increase the temporal resolution of observations. Automated sensors were used to record 12% of all observations, and accounted for most very high frequency measurements (intervals ≤1 hour). As with spatial data, finely resolved temporal data can be aggregated to facilitate multi-scale analyses (and many of the reviewed studies that used automated sensing aggregated the resulting observations before analyzing them), whereas longer-interval data (e.g. annual biomass accumulation) cannot be disaggregated into shorter interval measurements (e.g. weekly biomass accumulation) without interpolation, which turns data into modeled, rather than direct, observations.

In the coming years, rapid technological advances should increase the concentration of ecological observations in currently under-represented domains. The growing numbers of high-resolution satellite sensors, together with new analytical platforms that provide free access to large volumes of pre-processed data and computational power (*27*), will lower technical barriers that have so far prevented ecologists from adopting this observational technology (*23*). Similarly, the advent of unmanned systems offers the ability to measure ecological features at high spatial and temporal frequencies over large areas (*28*), which were scales that were previously impractical to access. The ever-falling cost of sensor technology and the ubiquity of cell phones also means that ecologists, together with a growing army of citizen-scientists, have the unprecedented ability to make spatially dense, high frequency observations over large areas (*29–32*). A greater attentiveness to scale in general, including more meticulous documentation of observed dimensions, may help to facilitate the spread of ecological research to sparsely studied scales, while improving transferability of knowledge within the discipline.

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