The Spatial and Temporal Domains of Modern Ecology OR Ecology's Spatio-temporal Domains OR Space, Time, and Ecology

Lyndon Estes*1,2, Labeeb Ahmed³, Kelly Caylor², Jason Chang³, Jonathan Choi⁴, Erle Ellis³, Paul Elsen⁴, and Tim Treur⁴

¹Woodrow Wilson School, Princeton University, Princeton, NJ 08544, USA
²Civil and Environmental Engineering, Princeton University, Princeton, NJ 08544, USA
³Geography and Environmental Systems, University of Maryland Baltimore County,
Baltimore, MD 21250, USA

⁴Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA

*To whom correspondence should be addressed; E-mail: lestes@princeton.edu.

An abstract

- The scales at which ecosystems are observed plays a critical role in shaping our understand-
- $_{2}$ ing of how they are structured and function (1, 2). Ecological patterns emerge within temporal
- and spatial domains that may be coarser or finer than the processes that shape them, which means
- 4 that investigation across multiple scales is the *sine qua non* for understanding ecological phenom-
- ena (1). Awareness of the importance of scale has grown rapidly since the 1980s, accelerated by
- 6 the need to understand how changes in the global climate, ocean, and land systems are affecting
- everything from individual populations (e.g. cite) to entire biomes (e.g. cite), while technolog-
- 8 ical advances in areas such as remote sensing and genetics are making it ever-easier to quantify
- ecological features across a broad range of scales (2, 3).

Given the importance of multi-scale studies for providing ecological understanding, and the 10 growing ability to undertake them, it is important to rigorously assess whether ecology is becoming a multi-scale discipline. One approach to answering this question is to quantify the spatial and temporal domains within which observations in ecological studies are collected. Observations provide the necessary means for developing and testing the models that explain why ecological patterns vary in time and space (1,4), thus it stands to reason that the temporal and spatial range of ecological observations, and their density within different portions of those ranges, will shed light on modern ecology's progress towards a holistic, predictive understanding of ecosystems (1, 2). In this study, we quantified the spatio-temporal domain of current ecological studies, using a representative sample of papers published between 2004-2014 in the top 30 ecological journals (by 2014 impact factor) to measure two key dimensions of spatial observation, resolution (grain) and total spatial extent, and their temporal corollaries, sampling interval and total temporal duration. We 21 collected this information from 367 ecological observations (defined here as data collected from non-experimentally manipulated, or "natural" (4), systems) reported within a 148 paper subset of 299 randomly selected articles (1.4% of all papers).

In terms of spatial resolution, here defined as the two-dimensional space in which all measurable features of a natural object were recorded (as opposed to sub-sampled), the majority 63% were collected in plots having resolutions $<1 \text{ m}^2$, while 25% were collected within plots of 1 m² up to 1 ha, and the remaining 12% in plots of ≥ 1 ha (Fig. 1A). The total spatial extent covered (the number of sampled sites multiplied by the spatial resolution) by 85% of observations was <10 ha, while 31% covered less than 1 m² (Fig. 1B). Only 7% covered an extent ≥ 10 ha, with just 1.1% spanning areas ≥ 10 million ha.

In the temporal dimensions, 30% of the assessed observations were "once-offs" that were not repeated (Fig. 1C). High frequency observations (ranging between as or more frequent than once per second up to daily) comprised 25% of observations, 20% were made at daily to monthly time

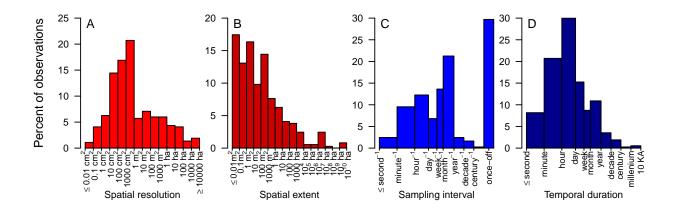


Figure 1: Histograms of the spatial resolution (A) and extent (B), sampling interval (C) and temporal duration (D) of ecological observations collected from the surveyed ecological studies. Bars represent percentage of the 367 collected records falling within each bin.

steps, while 35% and 4% were respectively made at monthly up to yearly and yearly to decadal intervals. The temporal duration of studies—the total amount of time the ecological feature was observed (the number of repeat observations multiplied by the effective sampling duration, SI)—was less than 1 day for 59% of sampled observations, 35% between 1 day and 1 year, and just 6% covering greater than 1 year (including several paleoecological studies covering centuries to millenia; Fig. 1D).

The juxtaposition of these observational scales provides further insight into the spatio-temporal distribution of ecological observations and the domains in which they are concentrated (illustrated using two-dimensional kernel density estimates of the log-transformed scale values; Fig. 2). A comparison between the sampling interval and spatial resolution of ecological observations reveals three primary regions of observational concentration (Fig. 1A), the greatest being once-off samples with resolutions of 100 cm² to 1 m², followed next by observations of daily to monthly frequency of slightly finer resolution domain (10 cm² to slightly less than 1 m²), and then a smaller center of monthly to yearly measurements collected at scales of 0.1-10 ha. Almost no observations were

collected with intervals greater than a decade, at all spatial resolutions, while high frequency (daily to sub-daily) observations were rare and collected at very fine resolutions ($<1000 \text{ cm}^2$). Almost no observations with $\ge 1 \text{ m}^2$ resolution were collected with sub-second (effectively continuous) to hourly frequency, and the density of 10-1000 m² resolution, sub-daily to sub-monthly frequency observations was also low.

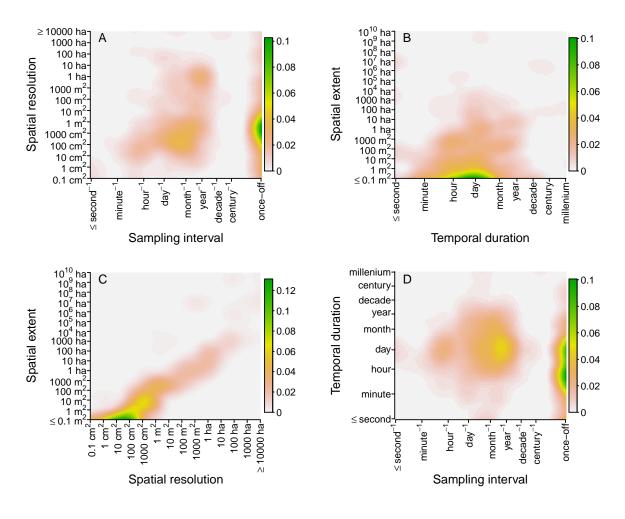


Figure 2:

In terms of temporal duration and spatial extent (Fig. 1B), the highest frequency ecological observations span time periods of 1 hour to <1 month, and cover ≤ 1 m² of space. The duration-

extent domain extent appears to reach its apex at one day of duration and 1000-10,000 ha of extent.

The very few observations collected that cover >1,000,000 ha were of sub-second duration, as these were collected by satellites that make instantaneous measurements.

Comparing the two spatial scales of measurements against one another shows that observational extent scales log-linearly with resolution (Fig. 1C), revealing a nearly 1:1 correspondence up to 100 ha of both resolution and extent. This relationship indicates that the larger the plot size, the fewer the number of replicates, which is a characteristic of field-based studies because effort and cost typically increases with plot size (5). In our sample, 85% of the observations were collected using manual, field-based methods. These stand in contrast to remotely sensed observations, which made up just 4% of the sample, but which are characterized by plot resolutions that are very high relative to their spatial extent—these are the low density patches above the 1:1 line defined by the denser concentration of field studies, namely the patches at the following resolution/extent domains; 1-10 m²/100-10,000 ha; 0.1-10 ha/10 million ha; 10-10,000 ha/100,000-10 billion ha.

Comparing sampling interval to temporal duration shows that the bulk of once-off observations last between a minute to a week in duration (Fig. 1D). For repeated observations, the greatest density of observations were those made at monthly to yearly intervals and an aggregate duration of hours to weeks. Very few repeat observations exceeded a total duration measured in years, and those that did were of daily to yearly frequency.

Reflect nature of observation approaches.

Use of remote sensing still relatively rare in ecological studies—thus the synoptic view of ecosystems not being seen.

High frequency, high resolution sampling also rare—gap into which UAS is only just allowing to be filled.

Don't forget to mention automated approaches. Limitation for ocean studies, we did not study third dimension, volume (might be more relevant). Notes: Wheatley and Johnson (2009) citing

- arbitrariness of scales in wildlife studies (cited by Chave).
- Although limited sample size, insight into the scales at which science of ecology is making
- bulk of observations Despite recognized importance of making observation across scales (1), this
- does not appear to be happening. Technical capabilities for making observations are not achieving
- adoption, despite potential of remote sensing to provide multi-scale ecological data

References and Notes

- 87 1. S. A. Levin, *Ecology* **73**, 1943 (1992).
- 88 2. J. Chave, *Ecology Letters* **16**, 4 (2013).
- 89 3. D. C. Schneider, *BioScience* **51**, 545 (2001).
- 4. D. Tilman, *Long-term studies in ecology* (Springer, 1989), pp. 136–157.
- 5. P. Kareiva, M. Andersen, *Community ecology* (Springer, 1988), pp. 35–50.
- 92 6. L. D. Estes, A. G. Mwangi, P. R. Reillo, H. H. Shugart, Animal Conservation 14, 521 (2011).
- 7. L. D. Estes, G. Okin, A. Mwangi, H. H. Shugart, *Remote Sensing of Environment* **112**, 2033 (2008).