

REVIEW

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# A review of landscape ecology experiments to understand ecological processes

Yolanda F. Wiersma\*

## Abstract

**Background:** One way in which we make inferences about ecological processes is via experimentation. Many ecological processes happen at landscape extents and it is at this extent that experimentation is more challenging. This review explores the intersection between experimentation, ecological processes and landscape ecology. Specifically, this review seeks to discover how scientists design experiments to understand ecological processes at landscape scales.

**Results:** I found 87 papers where these three concepts intersected, and reviewed them in more depth to assess characteristics of scale (treatment and study area extent), replication, research question and experiment type.

**Conclusions:** The findings suggest that experimental approaches for understanding ecological processes are well established, and beginning to more readily accommodate spatial dimensions. However, there is room to integrate more spatially explicit, landscape-scale experiments into studies of ecological processes.

**Keywords:** Inference, Landscape ecology, Manipulative experiment, Observational experiment, Scale

## Introduction

A key tool for understanding mechanisms that shape patterns is via experimentation. This is true across scientific disciplines. Ecological processes, the focus of this journal, shape and influence ecological systems at all scales. Although research in this journal has traditionally examined ecological process at many different extents, ecological processes at large extents merit special consideration since these shape the systems that humans directly interact with, actively manage, and critically depend on. These include the agricultural and marine ecosystems that feed us, the forest ecosystems that provide timber and non-timber resources, and the myriad of ecosystems that provide carbon sequestration. These large extent systems of fields, forests and oceans are also the purview of the discipline of landscape ecology (Turner 2005; Turner and Gardner 2015). How to carry out experiments in landscapes to realize reliable inferences about the links

between ecological patterns and ecological processes, and vice versa, is a key challenge for researchers, and is the focus of this review.

In a perspectives essay on experimental landscape ecology, Jenerette and Shen (2012) discussed different experimental approaches to identify how landscapes affect variation in ecological processes, and how landscape structure influences these processes. They highlighted the challenge of carrying out experiments at landscape extents (generally 10–100 s of kilometres), citing difficulty with replication, and the complexity of setting up experiments in spatially heterogeneous systems (Jenerette and Shen 2012). Many landscape-scale studies rely on observational data, and rely on correlations to infer processes, which may not capture the actual mechanisms at play.

Jenerette and Shen (2012) suggested four types of experiments that landscape ecologists could apply to help identify process variation within a landscape. These include distributed in situ experiments; ex situ experiments using samples collected throughout a landscape and brought back to the lab for analysis, translocation

\*Correspondence: [ywiersma@mun.ca](mailto:ywiersma@mun.ca)

Department of Biology, Memorial University, St. John's, NL A1C 5S7, Canada

experiments and transport manipulations. Their group of experiment types to identify how processes responded to landscape structure echo many of the “classic” large-scale experiments, such as the experimental patches at the Savannah River Ecosystem, the Bowling Green fragmentation experiment, or systems such as Ecotrons (see an excellent summary of these types of experiments in Haddad 2012). Such experiments manipulate patch shape, connectivity, and fragmentation. Other experiments that can be used to infer how landscape structure affects process include manipulation of internal patch characteristics (e.g., via adding artificial structures, or adding nutrients), manipulation of landscape scale (e.g., mesocosms, microcosms, microlandscapes) or the construction of entire landscapes (Jenerette and Shen 2012). Wiersma (2022a, b) summarized these approaches (large-scale manipulations, mesocosms, microcosms) along with *in silico* experiments (i.e., computer models) in more detail to show how researchers could harness these experimental tools to do spatially explicit experimentation (See Box 1). In this review, I pay particular attention to the experimental types (according to the taxonomy in Jenerette and Shen 2012) and tools used to study ecological processes at landscape extents.

Before discussing the literature review in more detail, a review of key terms is necessary. There has been much debate about whether we should consider observational studies to be “proper experiments” or not (Diamond 1983). In the mid-twentieth century, the increased reliance on sophisticated technology in the bench sciences, particularly molecular genetics, suggested to some ecologists that their field observational studies were too close to amateur natural history studies to be considered experimental and that manipulative experiments were the more reliable means for testing hypotheses (Kohler 2002). To clarify, by a manipulative experiment here, I mean an experiment whereby the researcher actively manipulates a factor of interest. This could be at a large extent in the field (e.g., via a controlled burn), in the field at smaller extent (e.g., via exclosures) or in a laboratory setting (e.g., experimental tanks or aquaria under controlled environments). Observational experiments (also called “natural experiments”) are those where natural processes have created the experimental treatment conditions. This treatment could be in the form of a disturbance, such as a flood or forest fire, or could be due to an underlying natural gradient (e.g., topography, soil moisture, light levels). If sampling is carried out as carefully as possible, so that experimental standards of control, replication, and randomization are applied, many suggest that observational experiments should be considered an equally credible approach as a manipulative one (Diamond

1983). Indeed, Diamond (2001) points out that heading to the field with a too narrowly focused experiment in mind can risk missing the chance to carry out an unplanned natural experiment. Laboratory/manipulative experiments have advantages of being easier to control for confounding effects, but being less realistic. Field manipulative experiments are more realistic, but can be logistically challenging to implement and have limited replication, and be influenced by stochastic events at the particular point in space and time they are implemented. Thus, it can be more challenging to meet the standards of experimental design in a manipulative field experiment (Diamond 1983; Wiersma 2022a). Observational experiments are the most realistic, but the experimenter loses control over every aspect of the study except where and when they sample. For the purposes of this review, I am considering both observational (“natural”) and manipulative approaches in my consideration of what is an experiment. Moreover, this review is limited to experiments in ecological science. While studies of ecological processes and research in landscape ecology can certainly benefit from integration of methodology from the social sciences, an assessment of methodological approaches in social science is outside the scope of this review.

The experimental aspects of a control (a set of observations identical to the experiment minus the treatment factor), and randomization (ensuring experimental treatments and/or sampling are carried out without bias to underlying conditions) should be familiar to scientists. Conceptually, they are straightforward, but when working at large landscape extents, it can be difficult to implement these (Jenerette and Shen 2012; Wiersma 2022a, b). The issue of replication can cause more confusion. Replication can happen at the experimental unit and at the sampling unit, and sometimes researcher can be confused as to what their sample size actually is. An experimental unit is defined by Krebs (1989: 269) as “the smallest division of the experimental material such that any two units may receive different treatments”. A sampling unit, on the other hand, is the thing that the scientist measures to test the effect of the treatment. These can be the same thing; such as when plants are exposed to different light treatments in a greenhouse and the dried weight of the whole plant is taken to assess how light levels affect biomass. If the dark and light halves of the greenhouse had 200 plants each, then there are a total of 400 experimental units ( $200 \times 2$  treatment levels) and 400 sampling units. However, if four leaves from each of the plants were measured instead to assess the response, then there would still be 400 experimental units (200 per treatment), but 1600 sampling units. Confounding experimental units and sampling units incorrectly in the statistical

analysis can lead to accusations of pseudoreplication (see chapter 4 in Wiersma (2022a, b) for a detailed discussion of this issue as it pertains to landscape experiments).

In this review, I examine experiments designed to understand ecological processes, where space is either an implicit or an explicit component of the study design. Most happen at the ‘typical’ landscape extents of 1–100 km, but I did not limit the review to such studies, since what a small organism perceives as a landscape may be a very small area of just a few square metres or centimetres. My focus is to examine as wide a range of experiments about ecological processes as possible to deduce trends and best practices. There is value to taking landscapes/space into consideration when studying ecological processes. Although many papers published in this journal have examined spatial dimensions of ecological processes (e.g., Webb et al. 2012; Ahmed et al. 2016; Paca et al. 2019; Sieger and Hovestadt 2021; Barik et al. 2022; Bedane et al. 2022; Datta et al. 2022; John et al. 2022), few of these have been explicitly experimental. Thus, this review examines landscape experiments on ecological processes and experiments on ecological processes carried out with a landscape ecology focus.

**Box 1 Six approaches to landscape experiments (from Wiersma 2022a)**

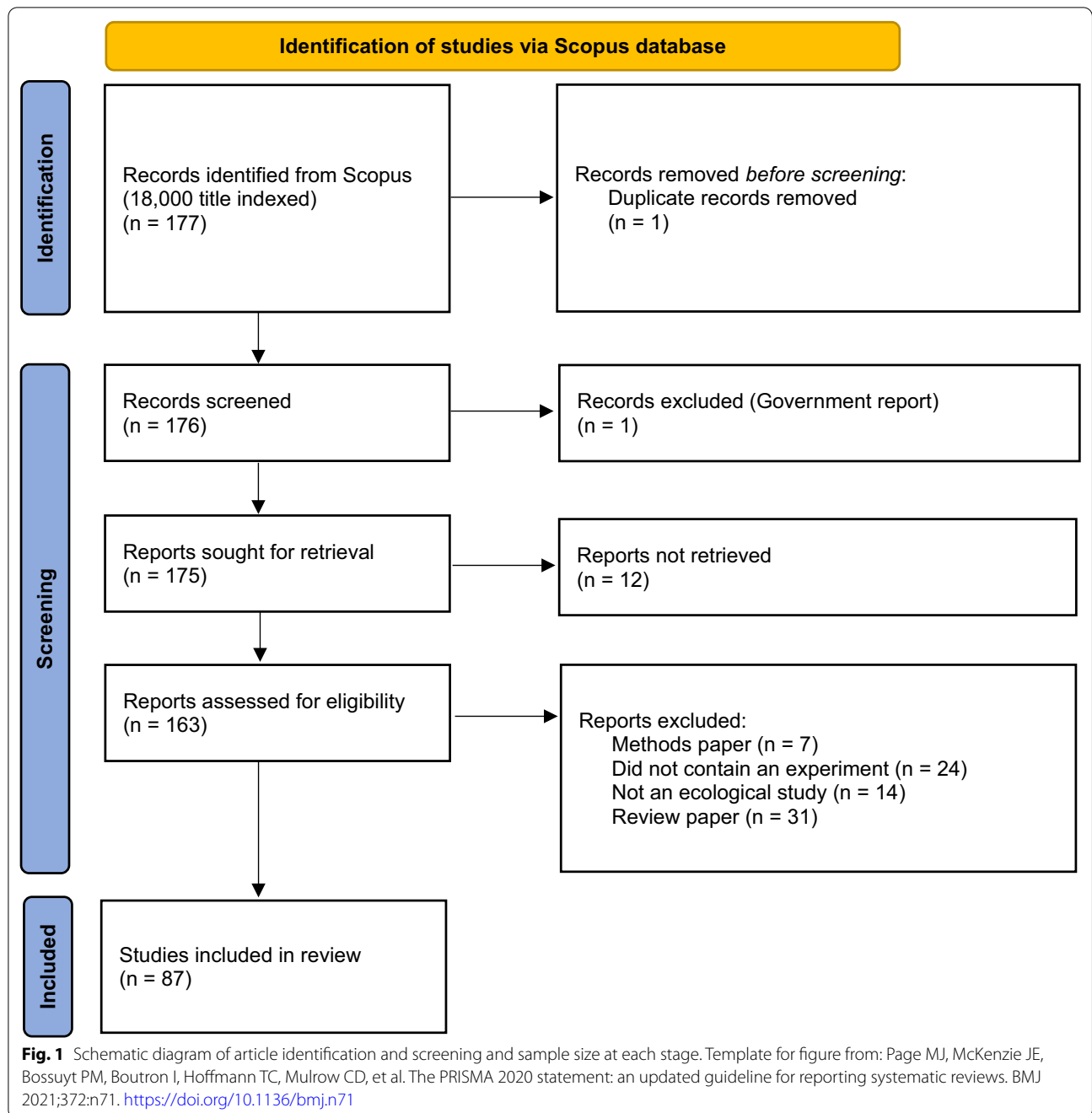
1. Large-scale manipulative experiments—these refer to landscape experiments at extents of ~ 15 ha or greater. These can be observational or manipulative. Examples of long-term manipulative experiments of this type include the Savannah River Experiment (Brinkerhoff et al. 2005), the Biological Dynamics of Forest Fragmentation Project (Bierregaard et al. 1992) and the Stability of Altered Forest Ecosystems (SAFE) Experiment (Ewers et al. 2011).
2. Experimental model landscapes—these refer to landscape experiment that manipulate a smaller area (usually on the order of 1–15 ha), usually in a more anthropogenically manipulated landscape, such as an agricultural field. Examples include the Bowling Green Fragmentation Experiment (With and Pavuk 2011) and the Kansas University Fragmentation Experiment (Holt et al. 1995).
3. Mesocosms—these refer to experiments in artificial containers (e.g., tanks, aquaria), which are either assembled by the researcher (pots with investigator controlled plants grown in them), or are subsets of natural systems (e.g., aquaria with water from an adjacent pond). The experimental design places the mesocosms in situ in the natural environment for experimentation (Srivistava et al. 2004).

4. Microcosms—like mesocosms, microcosms are container experiments; the difference here is that microcosms are naturally occurring containers, or habitats/ecosystems with delineated boundaries, for example pitcher plants or tank bromeliads (Srivistava et al. 2004).
5. In silico landscapes—this refers to experiments involving computer models. These could include (but are not limited to) statistical models, mathematical models, cellular automata and agent-based models.
6. Novel landscapes—Wiersma (2022a) highlighted how experiments in non-terrestrial landscapes such as seascaapes (Pittman 2018) and riverscaapes (Wiens 2002) create opportunities for different kinds of experiments. Similarly, experiments that take a landscape ecology lens to other disciplines such as acoustic ecology (“soundscapes”; Farina 2014) or medical science (“tumor-scaapes”; Lloyd et al. 2015) or construct artificial landscapes in a laboratory setting (“microlandscapes”; Larsen and Hargreaves 2020) can offer new opportunities for experiments to address questions in landscape ecology.

**Methods**

I searched the journal database Scopus (which indexes 18,000 titles from over 5000 international publishers) on 30-May-2022 for papers that addressed ecological process experiments at landscape extents. The search string TITLE-ABS-KEY (“ecological process”) AND TITLE-ABS-KEY (landscape) AND TITLE-ABS-KEY (experiment\*) yielded 177 papers. After removing duplicates and government reports and those where I could not access the document (see Fig. 1 for summary), I reviewed the abstracts of all papers, and excluded review/essay/op-ed papers (31), methods papers (8), those with no explicit experiment (24), and those that did not examine an ecological process (14). This yielded 87 papers (see Additional file 1 for full list). For each paper, I noted whether the experiment was observational or manipulative and whether the experimental design was spatially implicit or explicit. I also noted the spatial extent of the study area (if this was not reported, I attempted to infer it either via estimation from included maps, or by searching the internet for details on the study area), the spatial extent of the treatment units (to calculate the scope; Frazier 2022; Wiersma and Schneider In press), the degree of replication (of both experimental units and study landscapes) and the type of ecological process under assessment.

Finally, I classified the experiment based on both type of question (following the taxonomy of Jenerette and Shen 2012) and by experimental method. For the latter, I used the six classes discussed in my book (Wiersma



2022a, b) and summarized briefly in Wiersma (2022b) and here in Box 1. For clarity, definitions of meso- and microcosm here follow that in the book (Wiersma 2022a), where mesocosms are artificial containers placed in the environment (e.g., tanks, aquaria) and microcosms are naturally occurring containers (e.g., pitcher plants, tank bromeliads). Microlandscapes refer to artificially constructed landscapes, which the experimenter manipulates under laboratory conditions (e.g., a dendritic network

of pipes and petri dishes to assess ciliate movement). Because of the focus on ecological processes, I also noted a few other experiment types (e.g., food addition, seed addition, exclosures (to exclude predators/pollinators)) in addition to the categories in Wiersma (2022a, b).

For the classification by experimental question, I tried to classify observational studies, even though Jenerette and Shen (2012) excluded such ‘natural experiments’ from their review. For example, I included observational

studies that examined a natural disturbance as Type IV.13, even if the researcher did not actively manipulate the disturbance under study. Similarly, I classified observational studies that tested for differences in species distribution under different conditions as perception experiments (Type I.1), even if they were not explicitly manipulative. I did not classify the *in silico* experiments against Jenerette and Shen's (2012) taxonomy, since their review focused on manipulative experiments.

## Results

### Experiment types

The 87 papers reviewed represented a wide range of journals and disciplines (Table 1). Of these 87 papers, 15 were experiments *in silico* (discussed in further detail below). Of the remaining 72 papers, 17 were observational experiments, 45 were manipulative and 10 included a combination of an observational and manipulative experiment. Only one (Hess and Tschinkel 2017) used a full BACI (Before-After-Control-Impact) design. Three papers (Gornall et al. 2007; Lu et al. 2018; Menzies Puer et al. 2020) had a lab component in addition to a field study, and one (Heggenes et al. 2017) transferred microcosms (lichen mats) from the field to the lab for the experimental treatment. The experimental methods are summarized in Table 2. After *in silico* experiments, large-scale manipulative and large-scale observational experiments were most common (15 and 10 papers, respectively). As well, there were 11 experiments with some kind of addition, including food (6), artificial nests (1), seeds (2) and nutrients (2).

### Research questions

The types of ecological processes addressed did not cover all the categories of Jenerette and Shen (2012); most common were manipulations of internal patch characteristics (Type III.7) and manipulation of disturbances (Type IV.13; although this count included natural disturbances; hence the number of observational studies in Table 3 does not match what is reported above.

### Scale characteristics and replication

The spatial extent of the studies ranged from 78.5 m<sup>2</sup> to 20,300 km<sup>2</sup> and the size of the treatments from 4 cm<sup>2</sup> to ~500 km<sup>2</sup> for terrestrial studies, and 20 mL to 1000 L for aquatic/marine studies. The scope (ratio of extent to resolution/grain; Frazier 2022) ranged from 1.60 to  $3.125 \times 10^{10}$ , with a mean of  $4.17 \times 10^8$ . Variation in scope was narrowest for observational experiments and highest when studies combined both observational and manipulative experiments (Fig. 2). Replication of treatment units had a mean of 14.1 and median of 5 (range 1–320). Landscape replication was generally low, with

**Table 1** Journals in which the papers reviewed here appeared

Journal	Count
Agriculture, Ecosystems and Environment	1
Arthropod-Plant Interactions	1
Austral Ecology	2
Biological Conservation	1
Biological Control	1
Biological Reviews	1
Biotropica	1
Canadian Journal of Zoology	1
Conservation Biology	1
Copeia	1
Ecography	2
Ecohydrology	1
Ecological Applications	1
Ecological Engineering	1
Ecological Entomology	1
Ecological Management and Restoration	1
Ecological Modelling	1
Ecological Processes	1
Ecological Restoration	1
Ecology	6
Ecology and Evolution	1
Ecosphere	4
Ecosystem Ecology	1
Ecosystems	1
Estuarine, Coastal and Shelf Science	1
Forest Ecology and Management	2
Functional Ecology	2
Hydrobiologia	1
International Journal of Applied Earth Observation and Geoinformation	1
Journal of Applied Ecology	6
Journal of Arid Environments	2
Journal of Ecology	3
Journal of Environmental Management	2
Journal of Insect Conservation	1
Journal of Mammalogy	1
Journal of Plant Nutrition and Soil Science	1
Journal of Tropical Ecology	1
Journal of Urban Ecology	1
Land Degradation and Development	1
Landscape and Urban Planning	1
Landscape Ecology	4
Methods in Ecology and Evolution	3
Molecular Ecology	1
Nature Communications	2
Oecologia	3
Oikos	1
Oryx	1
Plant Ecology	1
PLoS ONE	1

**Table 1** (continued)

Journal	Count
Population Ecology	1
Proceedings of the National Academy of Sciences	1
Regional Environmental Change	1
Restoration Ecology	2
Revista de Biología Tropical	1
Science of the Total Environment	1
Water, Air, & Soil Pollution	1
Wildlife Monographs	1

**Table 2** Summary of experimental methods found in the 85 papers reviewed that examined spatial dimensions of ecological processes

Experimental method	Count
Large-scale manipulative experiment	16
Experimental model landscape	3
Mesocosm	5
Microcosm	1
In silico experiment	15
Microlandscape	5
Novel landscape	8
Large-scale observational experiment	10
Exclosures	7
Artificial nests	1
Food addition	6
Nutrient addition	2
Seed addition	2
Transplants	3
Mark-recapture	1

The first 7 methods in the list are discussed in detail in Wiersma (2022a, b)

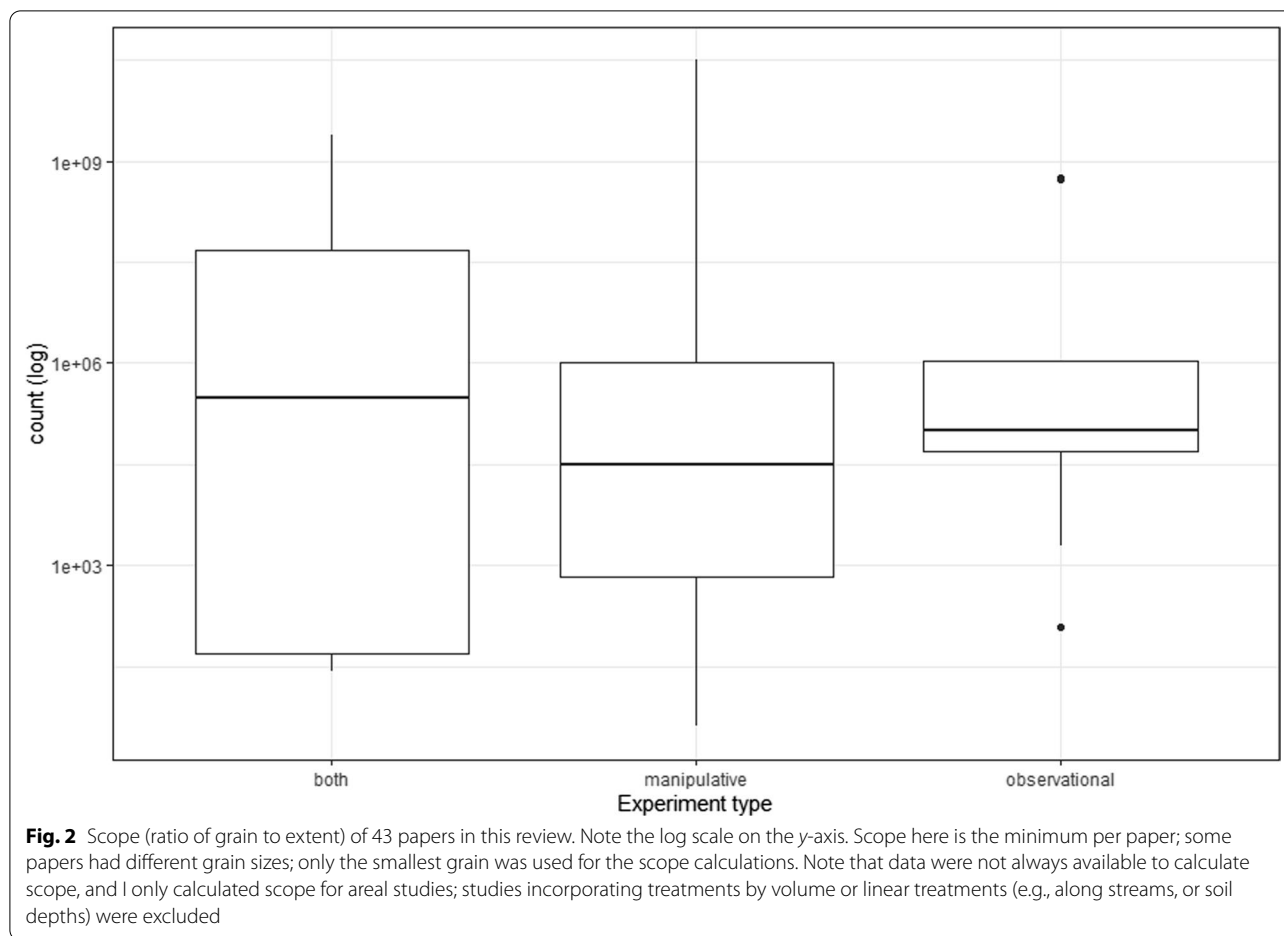
**Table 3** Summary of the type of experimental question (sensu Jenerette and Shen 2012) for the 73 non in silico experiments reviewed here

Group	Type	Count
I. Identification of landscape structure	1. Perception experiments	4
	2. Tracer experiments	1
II. Identification of process variation within landscapes	5. Translocation experiments	4
	6. Transport manipulation	8
III. Identification of process sensitivity to landscape structure	7. Manipulation of internal patch characteristics	17
	8. Manipulation of patch shape	3
	9. Manipulation of patch connectivity	1
	10. Fragmentation experiments	8
	11. Manipulation of landscape scale	1
	12. Construction of entire landscapes	6
IV. Identification of landscape pattern formation factors	13. Manipulate disturbances	15
Strictly observational studies		5

60 papers documenting an experiment in a single landscape, and only 7 papers documenting experiments in more than 2 landscapes (Marini 1997; Beckmann and Berger 2003; Cardoso et al. 2007; Hovel and Wahle 2010; Caballero-López et al. 2012; Bergerot et al. 2013; Augustine and Derner 2014; Giometto et al. 2014; Smith et al. 2014; Fronhofer and Altermatt 2015; Gillespie et al. 2017; Aristizábal and Metzger 2019; DiFiore et al. 2019; Menzies Puer et al. 2020; Boone et al. 2022; Nunes and Byrne 2022).

### Modelling tools

The in silico experiments used a range of modelling/computer tools, including cellular automata models (3), demographic models (1), agent-based models (1), process models (2), GIS/remote sensing (3), habitat models (2), scenario models (1) and mathematical models (2). Interestingly, the only paper in the collection obtained with the keyword search above to appear in this journal, was an in silico scenario model of the influence of ecological, economic and social drivers on future ecosystem goods and services (Huber et al. 2014). The majority of the in silico experiments modelled some kind of response to disturbance: either fire (Davies et al. 2021), grazing (King and Franz 2016; Verma et al. 2020), or climate change (Keane et al. 2017; Cui et al. 2021). Others modelled species movement (Samarasin et al. 2017; Baggio et al. 2019) or habitat use (Rowland et al. 2018; Muñoz et al. 2021) and still others modelled abiotic processes such as carbon (Güneralp et al. 2014; Xu et al. 2017), vegetation dynamics (Rango et al. 2002) or hydrology (Govind et al. 2011).



## Discussion

This review is an exploration of whether and how the themes of ecological processes, experiments and landscape ecology intersect. My findings suggests that experiments on ecological processes that have spatial dimensions occur in many kinds of ecological systems, including oceans (e.g., Cardoso et al. 2007), forests (e.g., Hylander 2005), urban areas (e.g., Visscher et al. 2018) and agricultural systems (e.g., Ouyang et al. 2020). Several of the experiments took place in long-term landscape-scale experimental sites, such as the Biological Dynamics of Forest Fragments Project (Laurance et al. 2002), the Savannah River Experiment (Levey et al. 2016), the Inner Mongolia Grassland Experiment (Yuan et al. 2015) and the Kansas Fragmentation Experiment (Alexander et al. 2012). Leveraging such long-term projects is a strategic approach to integrating landscape ecology perspectives into studies of ecological processes, since these sites have long-term data, as well as logistical resources and supports for researchers (Wiersma 2022a).

The papers I reviewed examined a wide range of ecological processes, ranging from dispersal of organisms

(e.g., Fronhofer and Altermatt 2015) or seeds (e.g., Miguel et al. 2018) to nutrient stocks and flows (e.g., Yuan et al. 2015). I also found papers carrying out experiments on species interactions such as pollination (e.g., Schmucki and De Blois 2009), predation (e.g., Gering and Blair 1999) and herbivory (e.g., DiFiore et al. 2019). A number of papers had an “applied” focus to restoration or management of ecological systems as evidenced by papers in the *Journal of Applied Ecology* (6), *Restoration Ecology* (2), *Journal of Environmental Management* (2), *Forest Ecology and Management* (2), *Ecological Applications* (1) and *Ecological Management and Restoration* (1) (Table 1).

Overall, it appears that many experiments concerned with ecological processes have taken a spatial/landscape approach, and at a range of extents and landscape types. This is not surprising, but what may be more surprising is the relatively low number (87 papers) of papers that are explicitly experimental. If we limit our characterization of an “experiment” to just manipulative experiments and exclude observational experiments, then this number drops to 55. Moreover, for a review focused on ecological

processes, there was only a single paper from this journal (Huber et al. 2014); this documenting an *in silico* experiment. Although other papers in *Ecological Processes* are spatially explicit and borrow concepts and tools from landscape ecology, these did not appear in the keyword search, and were not presented by their authors as experiments. This is likely due to the challenges of doing robust experiments in landscape ecology (Jenerette and Shen 2012; Wiersma 2022a, b).

Even where there are robust spatial experiments, as evidenced here, there can be challenges for researchers to meet the criteria of good experimental design. The majority of experiments occurred in a single landscape, thus making it difficult to assess if the inferences gained from one study would apply in a different landscape. This finding speaks, perhaps to the “case study” approach that characterized early work in landscape ecology (Opdam et al. 2002). Although case studies, whether qualitative or quantitative may not be fully replicable experiments, they certainly have a place in research; indeed in the medical and psychological fields, case studies are a major element of knowledge advancement (Stake 2008). Thus, researchers and reviewers should not dismiss case studies just because they may not be fully reproducible. Indeed, well-documented case studies can form the basis for valuable meta-analyses (Harrison 2011; Koricheva et al. 2013; Gerstner et al. 2017).

Where there was high replication (more than 2) of the experiment in different landscapes, this was often in anthropogenic systems, such as agricultural fields (Caballero-López et al. 2012; Augustine and Derner 2014), or when investigating dispersal of organisms that operate at smaller extents, such as butterflies (Bergerot et al. 2013) and ciliates (Giometto et al. 2014). A few were able to replicate landscapes across a broader extent, such as DiFiore et al. (2019), who examined two distinct coral reef systems in the Caribbean. Experiments in this review generally had limited treatment replication; with 39 of the studies having 10 or fewer treatment replicates, and 25 having fewer than 5. All of the manipulative experiments had some kind of control; observational studies generally were comparisons in space and/or time and did not always have a strict control.

Overall, it appears that ecologists of all types and throughout the world are applying a great deal of creativity to experiments on ecological processes in landscapes. Most are meeting criteria of control and treatment replication; replication at landscape extents in more challenging, which is understandable. While many of the papers reviewed did not explicitly focus on landscape ecology, thinking about ecological process experiments in landscape context could yield useful insights. Experiments at smaller extents may

be a strategic way to meet criteria of good experimental design, and with some effort, the inferences might be able to be scaled up to the extents at which human management happens. The experiment on soil organisms’ feeding activities by Joschko et al. (2008) is a good example of cross-scale work on ecological processes in a landscape. Since ecological processes are scaled in space and time, and landscape ecologists are familiar with scaling issues, considering how to extrapolate from small-scale process experiments to larger-extent landscapes is likely the next frontier to explore. A recent review by Wiersma and Schneider (In press) examined whether microlandscapes and sampling at small scales can usefully be extrapolated to make inferences at larger scales. Larsen and Hargreaves (2020) reviewed the broad array of microlandscape experiments, but did not examine scaling up in detail. Cross-scaling is facilitated when experiments are at different scales, but have the same scope; where scope is defined as the ratio of the extent to the grain (Frazier 2022). The scope of studies in this review varied several orders of magnitude (Fig. 2), making it difficult to compare across experiments. Ecologists considering experimental approaches as a means of understanding ecological processes in space would be wise to consider scale effects when designing the experiment. Whether experiments are manipulative or observational, researchers should make careful consideration of sampling design (including grain/extent, and hence scope), and degree of replication, randomization, experimental control and reproducibility in their studies. Although case studies have their place, experiments facilitate better understanding of the mechanisms influencing ecological processes, and thus should not be cast aside simply because they are difficult to do at landscape scales.

### Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-022-00401-0>.

**Additional file 1.** The list of all papers reviewed is provided as an Excel spreadsheet.

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### Author contributions

YFW collected and reviewed the articles, wrote and revised the paper. The author read and approved the final manuscript.

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### Availability of data and materials

The list of all papers reviewed is provided as an Excel spreadsheet in the additional material.



## Declarations

### Ethics approval and consent to participate

Not applicable.

### Consent for publication

Not applicable.

### Competing interests

The author declares that they have no financial and non-financial competing interests.

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