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TITLE: Model systems for large scale ecological research: *parva sub ingenti*

SHORT TITLE: Model systems for landscapes

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Abstract

Large-scale ecological research (i.e., macroecology, biogeography, and landscape ecology) is limited by the inability to have robust experimental replication due to scale and spatial changes in ecological patterns. Model systems may offer one solution to this challenge. We propose that considering smaller patterns in the context of larger ones (here, patches of lichen thalli on the trunks of trees) as model systems for large-scale research, can provide sufficient replication. Appropriate model systems will facilitate experimentation to elucidate links between spatial ecological patterns and processes. To function as replicate landscape units, patterns of patches should not differ significantly between trees across a sampling area of interest. We compared a previously-demonstrated model system of patches of lichen on balsam fir (*Abies balsamea*) tree trunks within a single small lichen-rich forest stand on the Avalon Peninsula in Newfoundland, Canada to a set of more widely dispersed trees of two species (balsam fir and yellow birch, *Betula alleghaniensis*) to assess if this model system could be useful across broader spatial extents. We found that lichen composition generally followed consistent patterns between north and south sides of the tree, as well as along an elevational gradient up the trunk at both the more constrained, and at the more extensive, sampling extents. However, the reliability of the trees as model landscapes varied by tree species and with the suite of lichens included. Considering lichens on trees as a model landscape system can allow sufficient replication in experimentation to address questions about spatial ecological patterns and thus provide a useful model system for research in landscape ecology and biogeography.

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1. Introduction

When asked to describe what landscape ecologists study, the reply is often "what you can see from an airplane window", namely, landforms, land cover, and land use [1]. Understanding links between spatial patterns in these three elements of the landscape, and the ecological processes therein, has been the focus of landscape ecology. Scientific research in landscape ecology, in turn, has informed real-world management problems in forestry (e.g., [2]), wildlife management (e.g., [3]), and land-use planning (e.g., [4]). However, after decades of research, landscape ecologists lack comprehensive theories to explain the patterns observed, and the variation between regions. The spatial extents at which landscape ecology research is often conducted make it difficult (if not impossible) to carry out manipulative experiments [5, 6] and to sufficiently replicate experimental units to enable robust hypothesis testing [5, 7]. This, in turn, makes it difficult to elucidate mechanisms that link patterns and processes. Hargrove and Pickering [7] referred to pseudoreplication as the *sine qua non* for regional ecology, meaning that without allowing for pseudoreplication in studies, hypothesis testing (and hence, reliable information to inform management-decisions) within large-scale ecology research is not possible. However, pseudoreplication is an anathema to many researchers [8, 9], and makes it difficult to carry out hypothesis testing and draw meaningful inference from statistical analysis. Thus, the suggestion that pseudoreplication may be unavoidable can be a difficult one to accept.

Here, by experimental replicate units we refer to repeated sampling units, not full-scale replication of experiments [10], which has also been termed reproducibility [11]. We propose that considering smaller patterns in the context of larger patterns (*parva sub ingenti* – the small under the huge), that is treating microlandscapes as model systems, can provide a solution to the problem of adequate replication in large-scale ecological research. Model systems (e.g.,

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Drosophila melanogaster or *Escherischi coli*) are common in biomedical and molecular biology research as their faster processes and small size make them amendable for manipulative experiments, and their biological traits make them good analogs for other, larger and less easy-to-manipulate systems. In ecology, Vitousek [12] suggested the use of natural model systems, such as islands or lakes, to test ecological hypotheses that might apply to other, less well-delineated or more-difficult-to-manipulate systems.

Microlandscapes have been proposed (but not yet widely adopted) as model systems for landscape ecologists to examine spatial patterns and processes with replicate units [5, 13, 14). Wiens and Milne [5] proposed constructing experimental microlandscapes to assess how variation in patch configuration affected beetle movement. Bowker et al. [13] suggested using biocrusts (soil crusts comprised of fungi, algae, bryophytes, lichens and cyanobacteria) as a model system for research in community, ecosystem, and landscape ecology. Wiersma and McMullin [14] demonstrated that arboreal lichens growing on the trunk of trees could be considered as analogues to patches of landcover on a landscape. Both of the systems proposed previously [13, 14] differ from the system described by Wiens and Milne [5] in that they are naturally occurring as opposed to artificially constructed. The advantage of Wiersma and McMullin's [14] model system over Bowker et al.'s [13] is that the boundaries of the proposed microlandscapes (tree trunks) can be very clearly defined and delineated *in situ*. In fact, others [15] have posited that trees could be considered as "islands". A disadvantage is that it is infeasible to transport tree trunks to the lab for controlled experiments as can be done with soil crusts [13]. Nonetheless, having microlandscapes that can be continually monitored within a natural setting has the potential to advance the science of landscape ecology. Below, we discuss the standards for replicate experimental units and replicate landscapes in more detail, before

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introducing the sampling and testing carried out to evaluate whether the model system described for a smaller area [14] has traction across a broader region.

1.1 Standards for replicate experimental units and replicate landscapes

To have true replication in any study, replicates should be independent but as closely similar as possible except for the factor of interest (the treatment). In laboratory experiments, this is achieved through replicate model organisms which are bred explicitly to be virtual clones of each other. Outside the controlled lab environment, observational experiments are designed to collect data from individual organisms or sites which share certain traits (e.g., age, sex, soil pH, sun exposure) but differ in a single trait of interest (e.g., diet, disturbance history). Much of the lack of perfect replication can be dealt with in various ways at the analysis stage. Statistical tests can treat individuals as random effects to separate variation due to individual replicates from variation due to the experimental treatment (but see critiques of this approach in [16]). Although proper replication is emphasized in classical statistical tests, others [17] have suggested alternatives for experiments in large-scale systems, including replicated controls, or to conduct unreplicated experiments and acknowledge and accommodate the lack of replication through Bayesian statistics or through analysis of spatial and temporal variation. However, both Hurlbert [8] and Oksanen [17] acknowledge that replication is still necessary for inductive approaches to experimentation.

To determine how landscapes might be replicated, and to properly evaluate the proposed model system of lichen-covered tree trunks, it is important to understand how the term "landscape" is defined and understood. In their foundational paper, Forman and Godron [18] describe landscapes as being comprised of interacting stands or patches, which are repeated

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across kilometers-wide extents in similar form. The "patch" has been described as the fundamental unit of landscapes and is defined as a relatively homogenous area that differs from its surroundings [1, 18]. The spatial pattern of patches can be quantified using a wide range of landscape metrics [19] and is assumed to be driven by abiotic and biotic factors and processes operating at multiple spatial and temporal scales [18]. For example, climate dictates the range of plant species that can occur, while topography might influence the plant cover within a specific patch as a function of microclimate.

To meet the standards of replicate units described above, replicate landscapes have to have similar spatial configuration of patches (i.e., landscape pattern) and thus similar landscape structure, but yet be spatially independent to avoid problems of spatial autocorrelation and pseudoreplication. In natural systems, we can expect that no two landscapes will be identical as might be the case in artificial ecosystems (e.g., [20]), but we do know that there are predictable patterns. For example, von Humboldt's early biogeographical thinking (which influenced the development of the field of landscape ecology in Europe) on the geography of plants described predictable patterns of vegetation as a function of climate that were similar across continents [21]. Similarly, Merriam's "life zones" concept describes patterns of similar plant communities as a function of elevation in mountainous regions [22]. While the exact patterns of vegetation patches along an elevational gradient will differ between mountain ranges in different continents, patterns will be similar along two slopes within a single mountain chain. Similarly, there are predictable differences in vegetation patterns on north-facing vs. south-facing slopes, which are generally consistent across different hillsides. A landscape study along different slopes within a single mountain chain might appear to constitute robust replicates for experimentation, but the spatial extent of these landscapes provides logistical challenges while also introducing

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confounding factors that might be correlated with altitude or location [17]. Thus, we propose replicating within model systems of tree trunks to more efficiently increase sample size, while making studies more amenable to manipulation.

Wiersma and McMullin [14] showed that tree trunks growing in a single, small homogeneous stand (< 1 ha is area) had similar "patch" patterns of lichen distribution along both the gradient of the trunk and between the north and south sides of the trunk. Given the hierarchical structure of ecological systems, we posit that microlandscapes sampled across a wider spatial extent than a single stand will still adequately function as replicate experimental units. Here, we test whether the micolandscape patterns documented earlier [14] within a single stand hold within the wider ecoregion in which their original study was located.

2. Methods

Study area - The stand studied by Wiersma and McMullin [14] is in the Avalon Forest Ecoregion on the island of Newfoundland, Canada. The Avalon Forest is the smallest (500 km^2) ecoregion in the province of Newfoundland and Labrador, characterized by high humidity and precipitation, cool summers, and mild winters [23]. The forested areas are on rolling hills called ribbed moraines, landscape features created by glaciers [24]. Interspersed between the moraines are open, sphagnum-dominated wetlands [23]. Forests are dominated by balsam fir (*Abies balsamea*) with black spruce (*Picea mariana*) in wet areas and occasional yellow birch (*Betula alleghaniensis*) stands on north facing slopes [23]. In this study, we test whether the consistent microlandscape patterns previously observed on 24 balsam fir trees in a single stand [14] are consistent across a broader region on the same species, and whether such patterns are also found on a less-common deciduous tree, yellow birch.

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2.1. Experimental Design

We expanded our study area from the previous study [14]. In this new study, our spatial extent encompassed the entirety of the Avalon Forest Ecoregion (Fig. 1). Sites were all similar to those in Wiersma and McMullin [14] in that they were balsam-fir dominated stands, mostly occurring on moraines. We visited 21 sites across the region (Fig. 1) and at each site selected two trees, one balsam fir and one yellow birch that were similar in diameter and within 25 m of each other. On each tree we sampled the north and south sides of the trunk using a 10 cm x 50 cm "lichen ladder", divided into five 10 x 10 cm "blocks", placed from 1.1 m to 1.6 m up the trunk (Fig. 2). This is similar to the 10 cm by 1 m "transect" that Wiersma and McMullin [14] placed on each side of the trunk (theirs was positioned from 0.9-1.9 m along the bole). For the purposes of comparing the pattern within the single stand and across the wider ecoregion, we only used data from the 10 cm blocks in Wiersma and McMullin's [14] data that matched those of the expanded survey (i.e., we used the data from Wiersma and McMullin [14] only from the 10 cm blocks between 1.1 m and 1.6 m up the tree trunk). In the present study, we identified and counted all lichen species within each 10 cm block. Species that could not be identified in the field were collected for identification using standard processes, including microscopy, chemical spot tests [25], and thin-layer chromatography [26]. In addition, we inventoried both macro- (those with a more three-dimensional growth from, and growing on the substrate, which includes foliose and fruticose growth forms) and micro-lichens (those growing within the substrate, i.e., crustose growth forms); this is in contrast to Wiersma and McMullin [14], who limited their study to field-identifiable macro-lichens. Thus, we analyzed the new data with macro-lichens only to compare to the previous study; we also repeated the analysis for more dispersed trees using data

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on both macro- and micro-lichens to assess whether the landscape patterns observed by Wiersma and McMullin [14] held when examining a broader suite of lichen species and when looking across a larger sampling area.

2.2. Statistical analysis

We used a perMANOVA analysis [27] to assess whether the pattern of lichen patches along the trunk was consistent across all trees when stratifying for aspect, and whether the patterns between the north and south sides were consistent when stratifying by height up the trunk. Wiersma and McMullin [14] found significant patterns in both cases along a 1 m transect along the trunk across 24 trees. We re-tested their data using a 50 cm transect that covered the same distance up the trunk as in this expanded study. We separately analysed the data from the 21 balsam fir and the 21 yellow birch in the expanded study area and did not combine the data from the 21 balsam fir in the wider ecoregion with the data from the 24 balsam fir in the single stand because of differences in geographic sampling intensity. We carried out all statistical analysis using R (version 1.0.136 [28]) with the package vegan [29].

3. Results

The 24 balsam fir trees in the single stand (that were previously analyzed for lichen diversity along a 1 m "microtransect" along the north and south sides) showed a significantly consistent lichen patch pattern between the north and south sides when we re-analyzed only a 50 cm portion of the trunk, when stratifying by tree (perMANOVA $R^2 = 0.00552$, $p = 0.05$) but not when we controlled for position along the trunk (perMANOVA $R^2 = 0.00552$, $p = 0.223$). There was also a significant pattern for position along the trunk when controlling for the tree (perMANOVA R^2

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= 0.001727, p = 0.024) but not for position along the trunk when we stratified for aspect (perMANOVA R^2 = 0.01727, p = 0.412).

The perMANOVA results for the 21 more spatially dispersed balsam fir also showed a significant pattern for macrolichens between the north and south sides of the tree, when stratifying by tree (perMANOVA R^2 = 0.00988, p = 0.009) but not when controlling for position along the trunk (perMANOVA R^2 = 0.0098, p = 0.081). Unlike for the trees in the single stand, there was no significant pattern for position along the trunk when controlling for the tree (perMANOVA R^2 = 0.00476, p = 0.157) nor for position along the trunk when stratified for aspect (perMANOVA R^2 = 0.00476, p = 0.444). When examining a different tree species, yellow birch, there was no significantly consistent pattern of lichen between the north and south sides of the trunk, either when stratifying by tree (perMANOVA R^2 = 0.00147, p = 0.772) or by position along the trunk (perMANOVA R^2 = 0.00147, p = 0.85). Nor was there any significant pattern along the trunk of the yellow birch when stratifying by tree (perMANOVA R^2 = 0.00143, p = 0.721) or when controlling for aspect (perMANOVA R^2 = 0.00143, p = 0.811). Overall patterns for macro-lichens are summarized in Table 1.

When we looked at both macro- and micro-lichens, the patterns were different. Balsam fir did not show any significant pattern (aspect stratified by tree perMANOVA R^2 = 0.00497 p = 0.051; aspect stratified by position along trunk perMANOVA R^2 = 0.00497, p = 0.439; position along trunk stratified by tree perMANOVA R^2 = 0.00245, p = 0.471; position along trunk stratified by aspect perMANOVA R^2 = 0.00245, p = 0.843). In contrast, there was a significant pattern for aspect for yellow birch, both when stratifying by tree (perMANOVA R^2 = 0.01528, p = 0.001) and by position along the trunk (perMANOVA R^2 = 0.01528, p = 0.002). However, there was not a significant pattern for location up the trunk for yellow birch, neither when

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stratifying by tree (perMANOVA $R^2 = 0.00373$, $p = 0.297$) nor by aspect (perMANOVA $R^2 = 0.00373$, $p = 0.647$). Table 2 summarizes the overall patterns for macro- and micro-lichens combined.

4. Discussion

The consistent lichen patterns of macrolichens along the trunks of balsam fir which had previously been observed within a single stand [14] showed some similarities when we looked at 21 balsam fir trees scattered across a wider region. The lichen pattern along the north vs. south sides of trees held between the single stand and the wider region. The pattern along the gradient of the tree trunk that was observed in the initial study did not hold in the new study. However, in this more spatially dispersed sampling, we only looked at lichen patterns along a 50 cm microtransect along the tree bole. Thus, it is possible that balsam fir across a wider region exhibit consistent patterns, but only when examining at least a 1 m "microtransect". Yellow birch, on the other hand did not show any of the landscape patterns posited by Wiersma and McMullin [14] for macro-lichens. However, when micro-lichens were included, yellow birch did show significant patterns by aspect and thus might be considered potential replicate landscapes when the full suite of lichen species is included.

The comparison of the microlandscape pattern in the 24 balsam fir in the single stand (from [14]) to the 21 more widely dispersed trees sampled here, suggests that the idea of 'trees as replicate landscapes' has support across the Avalon Forest Ecoregion. The lichen pattern on the more widely dispersed trees was consistent when examining lichen patterns on north- vs. south-facing sides of the trunks. Although we did not observe the same strong pattern of a gradient along the trunk, we believe that this might be due to the shorter microtransect in this new study (50 cm vs. 1 m). The consistency of pattern with aspect in the more widely dispersed balsam fir

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is especially notable given that the canopy cover and size of the more dispersed trees was quite different (more open canopy and larger trees) in the 21 dispersed trees compared to the 24 trees in the single stand (Table 3).

Although this study shows support for the concept of treating lichens on tree trunks as analogous to patches on a larger landscape [14] for balsam fir, it also illustrates that the proposed model system may not hold true for all tree species, nor for all lichens. There was no consistent pattern for yellow birch when we included only macro-lichens, and when assessed macro- and micro-lichens together, there was a consistent pattern for yellow birch but the patterns on balsam fir disappeared. This might be due to the fact that the lichen community on the two trees differed [30]; yellow birch had higher overall lichen diversity (mean of 11.9 ± 2.86 species on yellow birch vs. 9.86 ± 3.26 on balsam fir [30]). There were nine lichen species found on yellow birch that were not on the balsam fir in either study site; of these, six species were micro-lichens. Thus, the possibility to treat trees as landscapes is only supported partially by this study. Assessments of whether trees are replicate units need to consider variation between host species tree and the extent of lichen sampling taxonomically. Micro-lichens require a much higher degree of specialization to recognize in the field and identify than macro-lichens. We only saw consistent landscape patterns on yellow birch when we included micro-lichens. Thus, in this ecosystem at least, researchers wishing to use yellow birch as replicates need to be mindful of the need for specialized lichen expertise. In other systems, some pre-sampling to assess whether certain trees are substrates for a wider array of specialized species may be useful before assessing the potential of any one tree to function as an experimental microlandscape.

There are several implications for research based on the consistent landscape patterns across more widely dispersed trees, as we have shown here for macro-lichens on balsam fir and

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for macro- and micro-lichens on yellow birch. For one thing, this means that there are replicate experimental units across a broader spatial extent against which different hypotheses can be tested than would be possible with replicate trees in a single stand (e.g., [31]). The wider extent of replicate "landscapes" allows for natural-experiments to see how landscapes respond to meso-scale conditions such as distance to different types of habitat (e.g., open bogs), or broader gradients in elevation and climate. It also allows for manipulative experiments at larger extents that might mimic real-world processes, for example, looking at responses to different disturbance levels. We suggest that future research focuses on testing whether the concept of replicate microlandscapes holds for lichens along tree trunks in different forest types, beyond the boreal. Such patterns would allow for more extensive and expansive experimentation.

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Figure Captions

Figure 1. Location of sampling sites in the Avalon Forest Ecoregion on the island of Newfoundland, Canada. Inset map shows the location of the Avalon Forest Ecoregion (black polygon). Black stars on the main map are sampling locations for the 21 sites where we sampled both balsam fir and yellow birch. The location labelled "Halls Gullies" designates the stand within which 24 balsam fir were sampled.

Figure 2. A lichen ladder, which was used to sample lichen diversity on tree trunks. Each square is 10 x 10 cm; the ladder is 50 cm in length and was placed with the top rung at 1.6 m from the ground.

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Table 1. Summary of perMANOVA analysis for trees from two studies within the Avalon Forest Ecoregion; one for 24 balsam fir in a single stand; and for 21 more widely dispersed sites with one balsam fir and one yellow birch at each site. Analysis here is for consistency in lichen patterns on the tree trunks for macro-lichens only along a 50 cm section of the tree trunk on the north- and south-facing sides.

Variable	**Balsam fir in a single stand (*n* = 24)**	**Balsam fir dispersed (*n* = 21)**	**Yellow birch dispersed (*n* = 21)**
Aspect controlling for tree	significant	significant	non-significant
Aspect controlling for location up tree	non-significant	non-significant	non-significant
Location up tree controlling for tree	significant	non-significant	non-significant
Location up tree controlling for aspect	non-significant	non-significant	non-significant

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Table 2. Summary of perMANOVA analysis for 21 widely dispersed sites across the Avalon Forest Ecoregion with one balsam fir and one yellow birch at each site. Analysis here is for consistency in lichen patterns along 50 cm of the tree trunks along the north and south-facing sides, for macro-lichens and mirco-lichens combined.

Variable	**Balsam fir dispersed (*n* = 21)**	**Yellow birch dispersed (*n* = 21)**
Aspect controlling for tree	non-significant	significant
Aspect controlling for location up tree	non-significant	significant
Location up tree controlling for tree	non-significant	non-significant
Location up tree controlling for aspect	non-significant	non-significant

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Table 3. Comparison of balsam fir tree measurements. dbh = diameter at breast height (1.3 m). Values are given as mean (+/- standard deviation)

Sample trees	dbh (cm)	Canopy (%)	Height (m)
Dispersed trees (n = 21)	24.5 (5.9)	25 (9.4)	7.9 (1.6)
Trees in a single stand (n = 24)	10.6 (2.7)	82 (12.8)	7.1 (2.2)

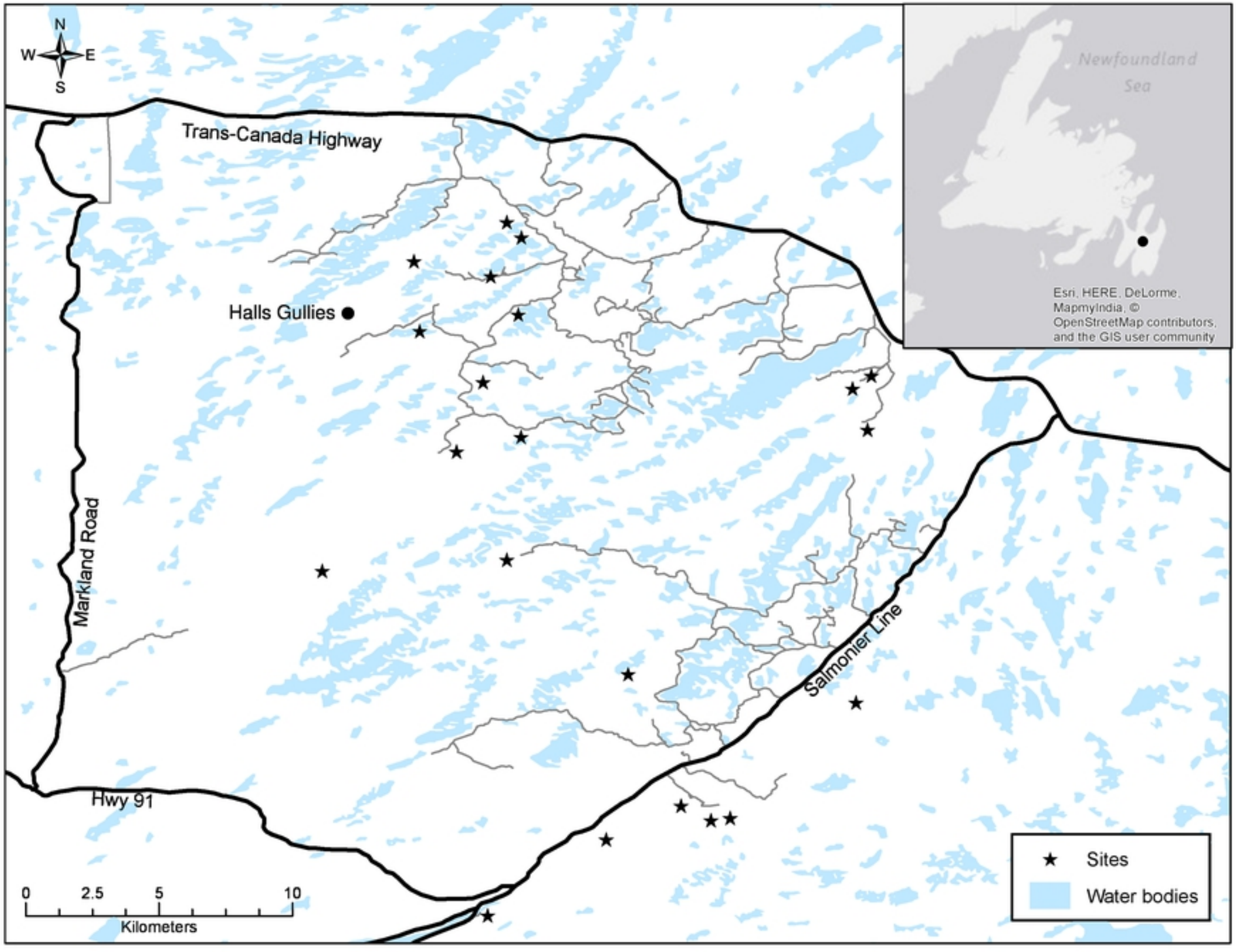
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Figure 1

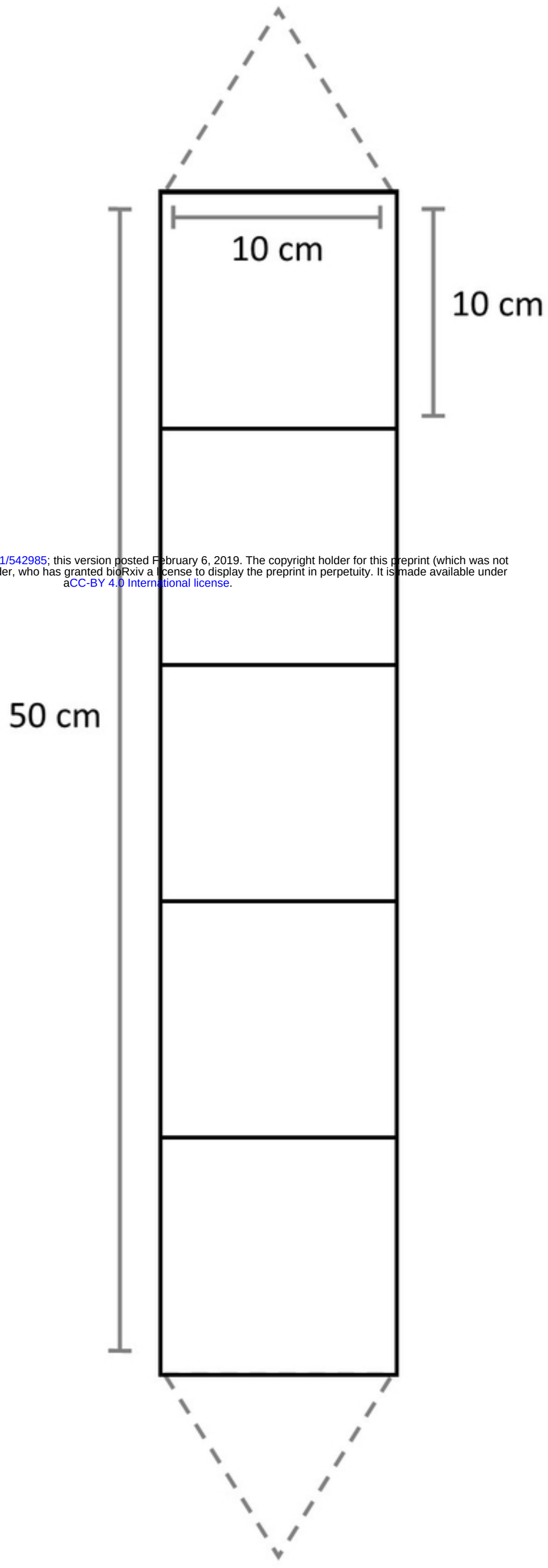

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Figure 2