

Title: A Conceptual Framework for Measuring Ecological Novelty

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Abstract:

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Background: Human pressures are driving the emergence of unprecedented, 'novel', ecological and environmental systems. The concept of novel (eco)systems is well accepted by the scientific community, but the use and measurement of novelty has outgrown initial definitions and critiques. There are still unresolved methodological and conceptual differences in
15 quantifying novelty that prevent a unified research approach.

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Framework: Here we present a conceptual framework and guidelines to unify past and future measurement of ecological novelty. Under this framework, novelty is a property of an ecological or environmental entity of interest. Novelty is quantified as the comparison between the target
entity and a reference set, measured as the summary of degrees of difference across one or more dimensions. Choices in these components of novelty, particularly the reference set, can change resulting measurements and inferences.

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Showcase: We provide a case-study to showcase our framework, measuring pre- and post-European novelty in 99 pollen assemblages in Midwest USA forests. We paired this quantitative exploration with a five-step process designed to improve the utility and outcomes of novelty

analyses.

Conclusions: Quantitative novelty has immense value in studies of abrupt ecological change,
30 linking climatic and ecological change, biotic interactions and invasions, species range shifts
and fundamental theories. Our framework offers a unified overview and is also primed for
integration into management and restoration workflows, providing consistent and robust
measurements of novelty to support decision making, priority setting and resource allocation.

35 **Keywords:** community composition, dissimilarity, multidimensional comparisons, no analog
communities, novel communities, novel ecosystems, time series

Human-driven environmental change defines the Anthropocene (Lewis & Maslin, 2015). The anthropogenic pressures altering natural systems are unprecedented in strength (Sage, 2020) and ubiquitous across local (e.g., pollution, land clearing) and global (e.g., anthropogenic warming) scales (Ricciardi, 2007; Ellis *et al.*, 2010; Ellis, 2011; Radeloff *et al.*, 2015; Waters *et al.*, 2016). Abiotic and biotic systems are consequently transitioning into ‘novel’ states distinct from past observations (Mascaro *et al.*, 2012; Hobbs *et al.*, 2013; Truitt *et al.*, 2015; Heger *et al.*, 2019), a term that has been applied to ecological communities and assemblages (Overpeck *et al.*, 1985; Williams *et al.*, 2001; Lurgi *et al.*, 2012; Young, 2014; Ordonez *et al.*, 2016; Finsinger *et al.*, 2017; Burke *et al.*, 2019; Pandolfi *et al.*, 2020; Staples *et al.*, 2022), abiotic climatic conditions (Kueffer, 2015; Radeloff *et al.*, 2015; Mahony *et al.*, 2017; Fitzpatrick *et al.*, 2018), species interactions (Saul & Jeschke, 2015; Schittko *et al.*, 2020) and entire ecosystems (Chapin & Starfield, 1997; Milton, 2003; Hobbs *et al.*, 2006, 2009; Graham *et al.*, 2014; Hobbs, 2017).

While the concept of “novel ecosystems” was initially controversial (Aronson *et al.*, 2014; Hobbs *et al.*, 2014b; Hobbs, 2017), it has become well-established (Hobbs, 2017). More recent research has advanced methods to quantify novelty in ecological systems, measuring the difference of an entity, of whatever ecological or environmental variety, from others (Radeloff *et al.*, 2015). These measurements of novelty have been used to identify when and where contemporary systems are changing to non-historic states (Morse *et al.*, 2014; Fitzpatrick *et al.*, 2018). Novelty can also be projected into the future. Forecasting potential novel climates under climate change scenarios (Radeloff *et al.*, 2015; Mahony *et al.*, 2017) offers a way to project how environmental and ecological regimes may change, particularly where existing conservation goals or ecosystem services may be threatened (Williams & Jackson, 2007; Hobbs *et al.*, 2009). Novel states that emerged in the past also provide valuable opportunities to

study how species and communities respond to changes in composition or underlying abiotic conditions (Marris, 2009; Hobbs *et al.*, 2013). These past observations can also identify potential environmental drivers and ecological consequences of novel changes (Williams & Jackson, 2007; Pandolfi *et al.*, 2020) and inform ecosystem management and forecasting (Fitzpatrick *et al.*, 2018). This diverse body of literature on how to measure novelty was absent during the initial conceptualization of novel ecosystems (Hobbs *et al.*, 2006), but current methods and terminology remain disparate (Williams & Jackson, 2007; Truitt *et al.*, 2015), with no underpinning structure or consensus. Novelty has been measured relative to a spatial suite of past assemblages or conditions (Finsinger *et al.*, 2017), to a spatial suite of future assemblages (Overpeck *et al.*, 1992) and to a temporal suite of a site's past states (Staples *et al.*, 2022), including different sub-variants of novelty (Burke *et al.*, 2019; Pandolfi *et al.*, 2020) (Figure 2). Novelty studies also differ in whether, and how, they make statistical comparisons of novelty across different sites to draw conclusions, in part because there is no overarching framework to follow. Frameworks act as both template and reporting standard. As a template, frameworks scaffold and highlight decision-making, allowing analysts to understand which choices are likely to impact their results. As a reporting standard, a framework contains the minimum set of details necessary to reproduce an analysis, improving transparency and clarity. Without a framework that explicitly describes the analytic choices that impact novelty measurements, future research cannot build consensus and progress.

Here we define a framework to standardize the measurement of ecological and environmental novelty, building upon existing definitions (Hobbs *et al.*, 2013; Morse *et al.*, 2014; Heger *et al.*, 2019) and analog-based inferential approaches in paleoecology (Overpeck *et al.*, 1985; Williams & Jackson, 2007) to provide a common set of terminology (Table 1) and structure (Fig. 1). We provide five statements that underpin our formal definition of quantitative novelty. We

then describe a methodology to apply our framework, with a five-step process that can assist research and management to understand the explicit and implicit choices in novelty measurement. This methodology is paired with a quantitative case-study as an example of framework use. Finally, we outline future research opportunities for quantitative novelty that can advance both fundamental ecology and applied ecological management.

1. Underlying statements and definition

Our novelty framework is built on top of five statements that we have derived from the overt or implicit assumptions in past novelty research. These statements ground the concept of novelty to be workable and applicable across theoretical and real-world contexts.

1. Novelty is an ecological property, not a process. Original definitions of “novel ecosystems” required pairing of processes and patterns (e.g., Hobbs *et al.*, 2013), but this contradicts both recent quantitative work (Radeloff *et al.*, 2015) and non-ecological definitions of novelty (Pimentel *et al.*, 2014). We consider the identification of drivers and processes as separate to the measurement of novelty, made either prior (e.g., quantifying novelty in response to an observed driver) or subsequently (e.g., identifying drivers behind an observed mass extinction).
2. Novelty can occur in the absence of human activities. While human-driven novel states are potentially widespread (Marris, 2009), they are a subset of broader novelty that includes past, present, and future states driven by both natural and anthropogenic forces (Hobbs *et al.*, 2009; Jackson, 2013; Heger *et al.*, 2019). Novelty simply requires a differentiation of a state, which applies to both contemporary occurrences of novelty, as well as those emerging from natural processes in pre-human time periods.

- 115 3. Novelty is a value-neutral measurement. Novelty refers to distinction, and does not
ascribe value, including assessments of system degradation or stability, the magnitude
of natural capital, or conservation or restoration potential. A “novel ecosystem” has been
defined as resulting from degradation (Hobbs *et al.*, 2006), while simultaneously
criticized as representing scientific endorsement of human landscape modification
120 (Aronson *et al.*, 2014). The value of a novel system is ultimately a matter of perspective
and preference, both socially and ecologically. A novel environment created by land
clearing for farmland may have reduced value from the perspective of conservationists,
and for native taxa. But the same system may have increased value for capital
production and provide opportunities for native and exotic weeds. In both cases the
125 novelty of the system, its uniqueness, is not linked to the system’s value or change in
value. We suggest regarding novelty as independent from these sets of values, which
can be considered either before or after novelty measurement (as in Heger *et al.*, 2019).
- 130 4. Novelty can be measured at any scale across space and through time. Novelty simply
requires the specification of observable “entities”, which include commonly made
comparisons at the community or landscape scale, but also include species or individual
organisms (Heger *et al.*, 2019). As well as scale, there is no theoretical bounds to the
direction that novelty can be measured in. Novelty for a given entity has been measured
relative to a contemporaneous reference (Hobbs *et al.*, 2013), to a selection of past
135 (Radeloff *et al.*, 2015; Burke *et al.*, 2019) or future states (Overpeck *et al.*, 1992), or for a
given time series (Pandolfi *et al.*, 2020; Schittko *et al.*, 2020). This agnosticism to time
allows us to subsume the related no-analog classification used in paleoecology under
the broader umbrella of novelty (Williams & Jackson, 2007; Truitt *et al.*, 2015). While
there are temporal and spatial limits to where novelty is a relevant property, we do not

define these limits. Appropriate scales will depend on research aims and data, and instead we promote the consideration and explicit reporting of temporal context (Kerr *et al.*, 2024).

5. Novelty is not the same as irreversibility. Novelty refers to a substantial change in some underlying system characteristics, while irreversibility requires that these changes be persistent and resilient to reversal efforts. Persistence, a core component of initial definitions of novel ecosystems (Hobbs *et al.*, 2013), was criticized for requiring the quantification of ecological thresholds (Murcia *et al.*, 2014), which remains a challenge in real-world systems (Donohue *et al.*, 2016; Van Meerbeek *et al.*, 2021). Adding to this complexity, ecological novelty may create a system that functions differently to its past, without any future observations. Ultimately it may be valuable to consider whether novelty results in a barrier to reversal, whether it be social or ecological, but this discussion is separate from the measurement of novelty itself.

2. Defining novelty

We define quantitative novelty via its calculation, which is made by comparing a target entity with a reference set, using a measurement method to define a degree of difference across one or more predefined quantitative dimensions (Fig. 1: terms defined in Table 1). This is not the only paradigm for defining novelty (Pimentel *et al.*, 2014), but comprehensively captures past use of the term in ecological and environmental science. Quantitative dimensions refer to data recorded for each entity, such as abundances of a set of species or values for a set of climatic variables (Table 1). Dimensions do not refer to the spatial or temporal context of the target entity to the reference set (Fig. 2). The reference set is used to establish an expectation by which the target entity can be evaluated. The degree of difference, an intentionally broad term, can be measured with any method that distinguishes between an expected and anomalous signal

(Pimentel *et al.*, 2014). Past research on ecological novelty has almost universally used dissimilarity indices to measure degrees of difference. Dissimilarities between the target and each reference entity are summarized, such as the minimum target-reference set dissimilarity, to represent the target's novelty (Radeloff *et al.*, 2015). Studies of novelty often repeat the measurement process for a number of target entities, either using discrete reference sets that lie outside of the pool of targets (Radeloff *et al.*, 2015), or by treating each entity in a reference set as a target in turn to sequentially estimate novelty measurements (Burke *et al.*, 2019; Pandolfi *et al.*, 2020). The specification of different reference sets has also been used to create different sub-variants of novelty for the same target entities (Burke *et al.*, 2019; Pandolfi *et al.*, 2020).

Converting continuous novelty measures into novel classifications requires defining a threshold, as does any classification into discrete classes. While this results in information loss, ecosystem management, including conservation and restoration, often prefer the simpler decision-making that can result from classifications (Samhouri *et al.*, 2010), such as inclusion in hierarchical management frameworks (Schläppy & Hobbs, 2019). Seminal work on novel ecosystems defined thresholds as ecological boundaries that cannot be easily reversed (Hallett *et al.*, 2013; Hobbs *et al.*, 2014a; Miller & Bestelmeyer, 2016), but such thresholds are not readily apparent in natural systems (Kattan *et al.*, 2016; Hillebrand *et al.*, 2020). Instead, we define thresholds as quantitative boundaries that separate novelty measurements, such as a binary threshold to divide “novel” and “not novel” classifications (Fig. 1). Past research has defined these boundaries using a particular novelty value (Jackson & Williams, 2004), quantiles of novelty measurements aggregated across several target entities (Finsinger *et al.*, 2017), or probabilistic values from more complex models (Wahl, 2004; Mahony *et al.*, 2017; Pandolfi *et al.*, 2020).

Thresholds are not required to draw inference from novelty; numeric values are interpretable

directly and can avoid boundary effects that emerge with classification (as in p-values: Wasserstein *et al.*, 2019).

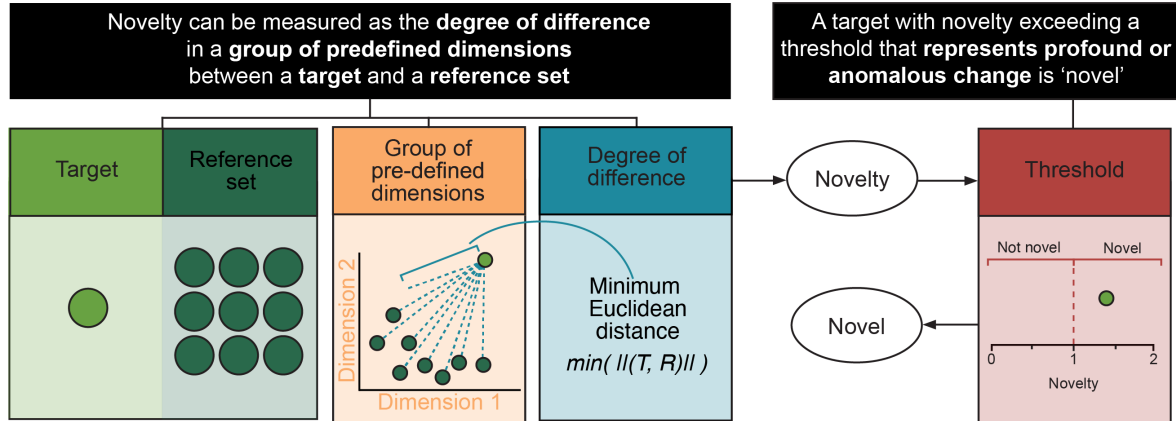


Figure 1: Conceptual framework and components of the measurement of ecological and environmental novelty. Broad definitions (black boxes) for novelty and novel are underpinned by quantitative components (colored boxes). Novelty is a comparison between a target entity and a reference set, measured as a degree of difference across one or more dimensions. In this example, novelty is the minimum Euclidean difference in the set of target-to-reference point comparisons. Each of these components are defined by the analyst, depending on the question and dataset, and alter the calculation and interpretation of novelty (e.g., Fig. 2). Finally, conversion of continuous novelty to novel classification requires defining a threshold.

Table 1: Terminology and definitions used as a ‘nomenclature of novelty’.

Term	Definition	Example	Other names
Entity	A bounded region in space and time where observations are made.	Community, remote-sensing grid cell, population, individual organism, geographic region.	Observation, sampling unit, site
Target	The <u>entity</u> of interest for which <u>novelty</u> is calculated.	A specific current community, a set of projected climate conditions.	Focal
Reference set	One or more <u>entities</u> that are compared to the <u>target</u> and used to measure <u>novelty</u> .	Set of past community compositions, set of present global climatic conditions.	Baseline group, reference site, training set
Group of predefined dimensions	A multidimensional set of quantitative values for the <u>target</u> and each <u>reference set entity</u> that are used to measure <u>novelty</u> .	Environmental variables, species abundances, community-weighted trait means.	Feature set, data dimensions, variable set
Degree of difference	A measurement method used to compare the <u>target entity</u> ’s observations in <u>pre-defined dimensions</u> to those of <u>reference set entities</u> .	Dissimilarity index, signal processing methods.	Dissimilarity, distance, comparison, deviation
Novelty	A property of an ecological or environmental <u>entity</u> , measured as a summary of the <u>degree of difference</u> in a <u>group of predefined dimensions</u> between a <u>target</u> and a <u>reference set</u> .	Minimum target-to-reference entity difference, average of n smallest dissimilarities, signal processing methods.	Anomaly score, outlyingness, no-analog value
Threshold(s)	Value(s) beyond which the continuous <u>novelty</u> of a <u>target entity</u> is converted into classifications, such as a binary “ <u>novel</u> ” versus “not novel”.	Dissimilarity value, distribution quantile, modelled probability.	Cutoff, boundary, classification threshold
Novel	Quality of a <u>target entity</u> with <u>novelty</u> exceeding a <u>threshold</u> that represents profound or anomalous change.	A community exceeding a pre-set dissimilarity value relative to nearby communities.	Anomalous, outlier, no modern analog

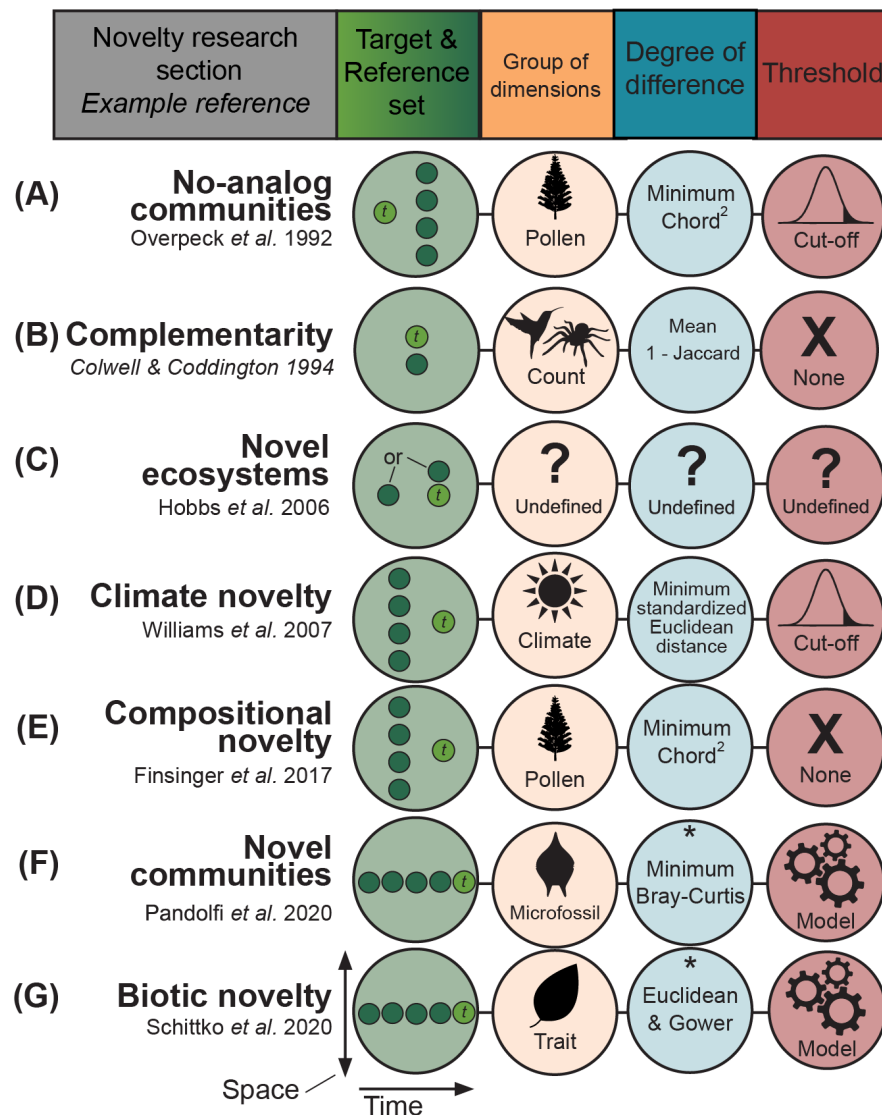


Figure 2: Past research into ecological and environmental novelty decomposed into the five components of our framework. Despite substantial differences in aims, scale and methodology, all research sections can easily be divided into framework components, highlighting similarities and differences. Under Target & Reference set, the x-axis relates to temporal position and the y-axis relates to spatial position. Target entities are indicated by “t”, with dark green circles as the reference set. Degrees of difference marked by * contain more complex methods; only the underlying dissimilarities are shown here.

3. Using the framework to describe and distinguish novelty measurements

The most effective application of ecological novelty is one that researchers and managers can use; this was the justification behind the original genesis of novel ecosystems (Hobbs *et al.*, 2009; Harris *et al.*, 2013). Ad-hoc application of measurement or classification of novelty has the potential to create confusion and sow public and scientific doubt (Aronson *et al.*, 2014), and many early attempts to define novel ecosystems were vague (Fig. 2, Truitt *et al.*, 2015).

Our framework is designed to guide and structure future quantitative research into ecological and environmental change, providing terminology and context to describe differences in research aims and methodologies. To improve the communication and transparency of novelty research, we suggest five steps during design, analysis and interpretation that clarify what novelty measurements mean and how they relate to prior work.

We describe each of the steps below alongside a quantitative case-study to act as an example: identifying novelty in pre- and post-European vegetation, using pollen sediment data in 99 palynological time series from the temperate forest region of Midwest USA (centered on Minnesota: Fig. 3B). These records have been well-studied in past analyses of ecological novelty (Overpeck *et al.*, 1992; Williams & Shuman, 2008; Burke *et al.*, 2019; Staples *et al.*, 2022). We applied four different novelty measurements, reflecting common target to reference set arrangements observed in past research, to use similarities and differences to help articulate framework recommendations (Fig. 3). The case study was analyzed in R version 4.4.0 (R Core Team, 2022), with the following packages: lme4 (Bates *et al.*, 2015), here (Müller, 2020), neotoma2 (Socorro & Goring, 2023), rworldmap (South, 2011), sf (Pebesma & Bivand, 2023), shape (Soetaert, 2024), vegan (Oksanen *et al.*, 2024) and WorldFlora (Kindt, 2020).

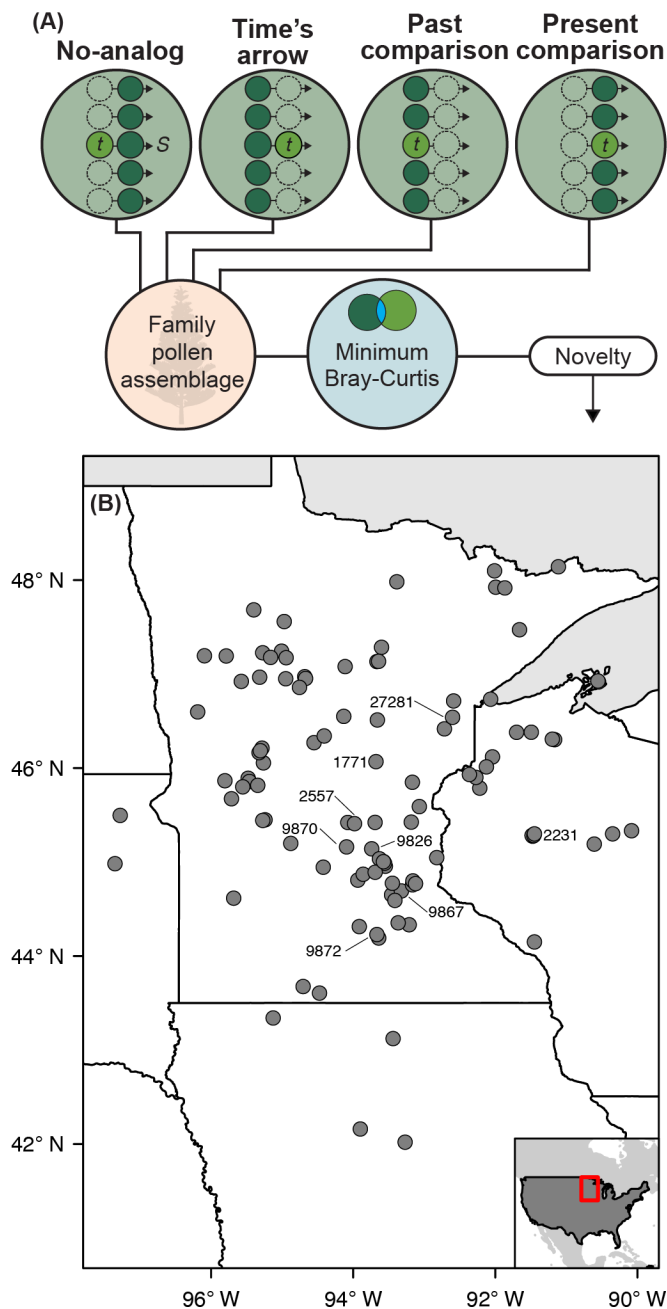


Figure 3: (A) Case study schematic of novelty measurements using outlined framework structure. Each time series ("S", rows) is represented by two temporal observations of pollen family relative abundances (columns). Each green circle describes novelty for a single target ("t") compared to a reference set (all filled circles), measured in one of four ways: "No-analog", backwards through time, using a past target ("t") compared to the entire present reference set (filled circles); "Time's arrow", forward through time with a present target compared to the past reference set; "Past comparison", a past target compared to a past reference set; and "Present comparison", a present target

compared to present reference set. Novelty was estimated as the minimum target-reference set

265 Bray-Curtis dissimilarity. (B) Distribution of case-study time series across four states of Midwest USA.

Table 2: Decomposition of novelty measurements into a minimum reporting standard that lists both data restrictions and analytic choices that may impact novelty. In the case-study data, there was no spatial arrangement of the reference set (e.g., reference sets containing only sites poleward of the target). The only differences between novelty measurements were in the temporal extent and temporal reference-target arrangement, which are clearly indicated and underlined in this table. In the context of this case study, “modern” refers to average pollen assemblages from 1500-2000AD, and “pre-modern” refers to 1000-1500AD.

Novelty measurement	Target and Reference Set							Degree of difference	Dimensions	Threshold
	Spatial scale			Temporal scale			Reference set size			
	Extent	Grain	Ref-Target arrangement	Extent	Grain	Ref-Target arrangement				
No-analog <i>"Different from any modern assemblage"</i>	368-701km	Varied (watershed)	None	1000-2000AD	500 years	<u>Subsequent to target</u>	99	Minimum Bray-Curtis dissimilarity	Relative abundance of family-level pollen grains (20)	-
Time's arrow <i>"Different to any pre-modern assemblage"</i>	368-701km	Varied (watershed)	None	1000-2000AD	500 years	<u>Prior to target</u>	99	Minimum Bray-Curtis dissimilarity	Relative abundance of family-level pollen grains (20)	-
Past comparison <i>"Distinct from assemblages in the region"</i>	368-701km	Varied (watershed)	None	<u>1000-1500AD</u>	500 years	Contemporaneous to target	98	Minimum Bray-Curtis dissimilarity	Relative abundance of family-level pollen grains (20)	-
Present comparison <i>"Distinct from assemblages in the region"</i>	368-701km	Varied (watershed)	None	<u>1500-2000AD</u>	500 years	Contemporaneous to target	98	Minimum Bray-Curtis dissimilarity	Relative abundance of family-level pollen grains (20)	-

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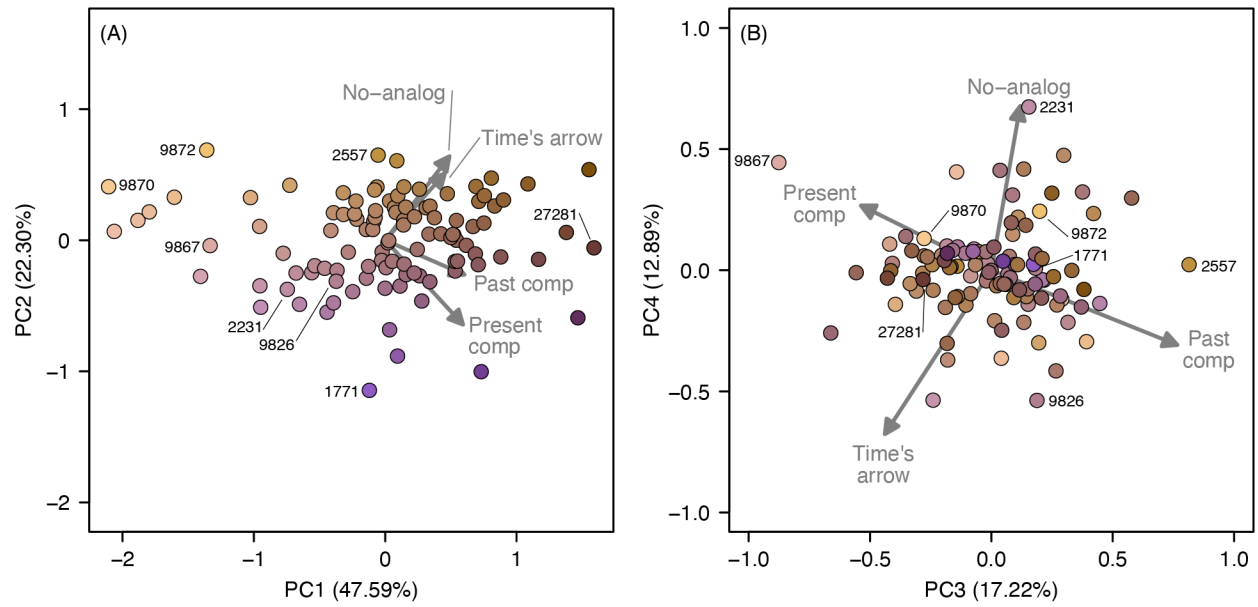


Figure 4: Novelty of pollen time series in temperate Midwest USA, measured with four different target-reference set arrangements (Table 2, Fig. 3) and collated using Principal Component Analysis (PCA). All novelties were logit-transformed prior to PCA; arrows are eigenvectors of (A) the first and second, and (B) third and fourth principal components. Color gradient reflects position on the first two principal components.

1. Decompose novelty into framework terminology

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Rationale: We suggest that in an early phase of a novelty study, analysts use the structure and terminology of the framework in Figure 1 and Table 1 to decompose their novelty measurement into constituent components (e.g., Table 2). This provides both a standardized description for ease of subsequent analyses and future reference, as well as a set of minimum standards that

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allow for repeatable and transparent reporting.

Case-study: Palynological time series contain samples occurring at different times, based on stratigraphic differences in site sediments. We followed palynological convention by averaging pollen samples into standardized time windows of 500-years, a “modern” period, 1500 - 2000AD (-50 to 450 ybp), and a “pre-modern” period, 1000 – 1500AD (450 – 950 ybp). All novelty measurements were estimated using the minimum Bray-Curtis dissimilarity between each target and the reference set, using relative pollen count of the twenty most abundant plant families across all time series records (see Supplementary Material).

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We used this set of time series to estimate novelty in four ways, using consistent methods that varied only in the target-reference set arrangement (Table 2, Fig. 3). First, we treated the past sample for each site as a target, with all present samples acting as a reference set. This resembles the paleoecological “no-analog” approach (Overpeck *et al.*, 1985). Second, we treated the present samples as targets with a past reference set. These novelty values are akin to compositional novelty applied in paleoecological studies (Finsinger *et al.*, 2017), and orient comparisons along “time’s arrow”. The third and fourth novelty measures were within-time window approaches, treating each past sample as a target with a reference set containing all other past samples, and likewise for present samples. These are most akin to complementarity (Fig. 2B); we refer to these as “present comparisons” and “past comparisons”, respectively.

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310 2. Clarify the temporal and spatial scale of novelty measurement

Rationale: Many studies of novelty use data across space and time, but the actual measurement of novelty is restricted to a subset of these extents. Novelty is a measurement for a single target, and analysts need to distinguish between the extent and dimensions of the data used to generate the target and reference set, and the extent and dimensions of these novelty components. This clarification helps distinguish between novelties used in past research that appear the same on the surface. For example, differentiating novelty using reference sets with broad spatial extent but little temporal depth (e.g., Fig. 2E: “Compositional novelty”) from time series reference sets that have broad temporal extent but are restricted in space (e.g., Fig. 2F: “Novel communities”); both are compositional or assemblage comparisons, but their similar names obscure differences in reference set structure. Finally, the relative position of the reference set and target in space and time should be defined, as this contributes to the perspective that novelty measurements offer and is the major difference between past novelty research (Fig. 2). A reference set can be temporally unconstrained, or exist entirely prior to, contemporaneous with, or subsequent to the target entity. Likewise, a reference set can be spatially mixed, or constrained in any of the three spatial dimensions (e.g., westwards, polewards or lower elevation).

Case-study: Novelty measurements were made across spatially mixed pollen assemblages, with potential contributions from different vegetation types, averaged across long temporal periods. Spatial scales were consistent, while the temporal scale and arrangement of the reference set and target differed. The spatial extent of novelty measurement varied from 368-701km (median = 477km), based on the location of the target entity relative to reference set entities (Fig. 3B). Spatial grain also varied. While sediment cores were small, pollen represented

335 a space-averaged mix from vegetation in the surrounding area, potentially to the entire watershed, biased towards individuals proximate to the sample location.

Novelty was measured using pollen composition dated between 1000 and 2000 AD (representing pre- and post-European ecological context). The temporal extent was 1,000 years
340 for novelty measurements that made through-time comparisons (no-analog and time's arrow), while the within-time past and present comparisons had a temporal extent of 500 years, the width of the sampling bins. The temporal grain of time series observations, 500 years, average together seasonal and annual variation, providing coarse estimates of overall composition across multiple generations of constituent taxa. The temporal arrangement differed between
345 novelty measurements, with reference sets prior to (time's arrow), contemporaneous to (past and present comparison) and subsequent to the target (no-analog).

3. Describe novelty components, differentiate data restrictions from analytic choices

Rationale: Once it is clear where novelty is being measured, analysts should clarify the other
350 components of the framework, including measurement of the degree of difference, over which dimensions, and if, and how, a threshold was applied. Some of these components will be restricted by the dataset or research question, and some will be chosen by the analyst, and this distinction is useful. The palynological data from our case-study have been included in multiple past novelty studies (Overpeck *et al.*, 1992; Burke *et al.*, 2019; Staples *et al.*, 2022),
355 represented by Figure 2A, E and F respectively. These studies have biases and restrictions arising from the underlying data, including differences in pollen production and precision of pollen identification across taxa (Birks *et al.*, 2016). Regardless of analyst choices, these data restrictions will impact novelty measurements and what inferences can be drawn. Even with the same data, however, each of these studies used a different configuration of target and

reference entities, with different research questions, deriving unique perspectives from a singular resource. This is especially true where past research has applied more complex methods to quantify the degree of difference (Figure 2), introducing even more specificity in the meaning of novelty measurements. Realizing the utility of measuring novelty requires analysts to identify and describe these biases, distinguishing analytic choices from data restrictions, provide clear methodological descriptions, and conducting sensitivity analyses to test the robustness of their conclusions.

Case-study: We used palynological time series samples from lake sediments. Pollen composition is only a proxy for vegetation composition (Felde *et al.*, 2015; Matthias *et al.*, 2015), with structural biases which limit the accuracy and precision of novelty measurement. Alongside these structural biases, we made choices that influenced novelty measurements. These include using a 500-year pollen sampling window, using restricted reference sets over limited regions of space and time, aggregating palynomorphs into plant families and the use of relative abundance Bray-Curtis dissimilarity. We conducted an alternate analysis, aggregating palynomorphs into plant genera, as a test of how our choice of dimensions may have impacted our results (Fig. S3-6). Genera novelties were strongly correlated with equivalent family novelties ($R = 0.593 - 0.733$), but there were notable differences where intra-family variation drove, or minimized, novelty in some targets (Fig. S6). An additional sensitivity test highlighted how novelty increases as a function of dimensions included (in this case, plant families), presenting further evidence of how analytic choices can impact downstream novelty measurements (Fig. S7).

4. Derive what novelty means, and does not mean, given dataset and analytic choices

Rationale: The meaning of novelty derives from the interaction of framework components.

Analysts need to interpret novelty in the light of this interaction. For instance, novelty is only

relative to the reference set, and a novel target may not be truly unique if the reference set is biased or incomplete (such as niche truncation issues in climatic niche modelling: Peterson *et al.*, 2018). The reference set frames the context for novelty measurements, regardless of whether reference entities represent a range of states the target is expected to resemble (as in macroecological novelty research), or a restricted ideal state (such as a restoration reference site). Similarly, a target may be undetectably novel if relevant dimensions are excluded (e.g., the exclusion of grass pollen with a genus-level comparison) or may likewise be meaningless if the wrong dimensions are included (e.g., inclusion of pollen from aquatic plants). Finally, temporal and spatial scale will impact the contribution of different processes to novelty. Novelty measured with small-scale targets and reference sets will emphasize similarly scaled processes, such as stochasticity, microclimatic gradients and short-term climatic variation. Even a single year of drought may alter vegetation to the point where an assemblage appears novel at a small temporal grain. Broader scale comparisons will have the opposite effect. For instance, novelty across deep time will be strongly influenced by evolutionary processes, with variation from climate and neutral dynamics averaged within a broad temporal grain (Pandolfi *et al.*, 2020). These impacts are the case with past novelty work, even where they may have been unstated. We suggest that clarifying the meaning of novelty measurements is invaluable for interpretation as the research field moves forward.

Case-study: A summary of the meaning of case-study novelties is listed in Table 2. Overall, novelty measurements retained distinctive signals (Fig. 4A-B), despite being calculated across the same compositional data and with similar framework components (Table 2, Fig. 3). Just under half of variation in the four novelty measurements (47.59%) was correlated: sites with large novelty in one measurement tended to be large in others (Fig. 4A). Another 22.30% of variation could be explained by dividing novelty variants in those making temporal comparisons (no-analog and time's arrow) versus variants with only spatial comparisons (past and present

comparison: Fig. 4A). The remaining 30.11% of variation in novelty measurements was unique (Fig. 4B). Some sites had low (e.g., 9870) or high (e.g., 25281) novelty across all

measurements (Fig. 4); in others, novelty was elevated only with particular reference sets. Sites
415 with low novelty may be useful for studies of resilience, identifying site features or taxa traits that promote compositional stability within a landscape. Low novelty sites 9867, 9870 and 9872 contained 50-65% Fagaceae pollen, primarily *Quercus*. These oak-dominated sites were part of a compositional cluster with consistently low novelty across all four measures (Fig. S2). Despite low overall novelty, site 9867 had a Present comparison novelty that was much higher,
420 highlighting how reference set choice can have profound impacts on resulting novelty.

Novelty values should be interpreted cautiously. The assumption in novelty estimation is that the reference set reflects all relevant community types, however, high novelty may be a function of sampling gaps. Grass-dominated site 1771 had low No-analog and Time's arrow novelties
425 (0.05), with much higher Past and Present comparison novelties (0.14 and 0.15 respectively).

This site was geographically isolated (Fig. 3) and had a distinct composition similar only to one other site (Fig. S2). We might infer that site 1771's community type is regionally rare, but it is likely that high novelties are a function of an incomplete reference set. As well as sampling gaps, we used family-level taxonomic identities. While the family-level novelties we present here

430 were strongly correlated with genus-level equivalents, family data tended to underestimate novelty at a genus level (Fig. S3). There are three potential explanations for this. First, family-level data are insensitive to ecological transitions in species or genera (such as the emergence of exotic pasture grasses and grains with European expansion). Second, the taxonomic resolution of pollen is variable across taxa; sites with lower fractions of pollen identifiable to
435 genus (e.g., 1771) had much lower genus novelties as significant proportions of family-level pollen were excluded. Thirdly, there is a sampling effect to novelty. Measuring novelty across

more dimensions equates to more places to find dissimilarity, resulting in greater novelty by chance as dimensionality increases (Fig. S4).

440 High novelties act as flags for further exploration, whether they be data biases, taxa contributions, land use changes and potential risks to ecosystem services and conservation goals in the area.

5. Situate novelty measurements within existing research and understanding

445 **Rationale:** Once analysts have decomposed and interrogated the structure and meaning of their novelty measurements, the next step is to draw similarities and comparisons with existing research. Outcomes from the previous steps should facilitate this process, allowing analysts to make comparisons using our framework terminology and structure. This process includes
450 comparisons to studies using similar data but with different novelty measurements, studies using different data but with similar choices and using novelty results to generate hypotheses and processes. Some comparisons might be undertaken as additional sensitivity analyses (e.g., Fig. S19 in Staples *et al.*, 2022), but it may be sufficient to draw attention and discuss consistent and different results. In addition to formalizing and simplifying comparison of results, we
455 anticipate the use of our framework to identify research gaps: what types of reference sets have not been used to measure novelty for the target? And would such comparisons fill a knowledge gap?

Case-study: Past novelty research on these pollen assemblages has been measured
460 comparable to our no-analog (Finsinger *et al.*, 2017; Fig. 2E: Burke *et al.*, 2019) and time's arrow approaches (Fig. 2A: Williams *et al.*, 2001), as well as time-series specific reference sets (Fig. 2F: Staples *et al.*, 2022). Williams *et al.* (2001) identified that the study region underwent

substantial climatic and vegetation change since the Last Glacial Maximum, but was similar to modern vegetation over the past c. 10,000 years. Staples et al (2022) identified that overall rates of novelty relative to each time series' past was low and consistent with post-glacial averages until c. 300 years before present. Modern instances of this "temporal novelty" were higher, especially at the latitudes of our study region (Staples *et al.*, 2022).

Our framework decomposes cryptic analytic choices so that methodological differences are evident, and this utility is clear in our case study. Reference set arrangements in our case study, even with a narrow spatial and temporal focus, resulted in substantial variation between resulting novelty measurements (52.41% of total variation). This variation reflects differing results from ostensibly similar studies of novelty using the same data (Burke *et al.*, 2019; Staples *et al.*, 2022). Our case study highlights both distinct anomalous assemblages in our case study region that could be explored in more detail, as well as the potential for further research that fully unpacks and contextualizes the varied no-analog and novelty palynological work published over the last forty years.

The more targeted nature of our analysis provides opportunities to explore unusual results in more detail. Novelities in our data were consistently low, with few Bray-Curtis dissimilarities exceeding 0.2, reflecting the general compositional stability in forest compositional data with a small temporal extent and large grain. For instance, many higher-than-expected novelities result from shifts in Betulaceae, Fagaceae and Pineaceae pollen, reflecting, respectively, dominant tree genera: *Betula* (birch) and *Alnus* (aspen); *Fagus* (beech) and *Quercus* (oak); and *Picea* (spruce) and *Pinus* (pine) respectively. Past shifts in these taxa have been driven by climatic change (Davis, 1981) and these genera have distinct successional responses to fire regimes (Anoszko *et al.*, 2022). The unusual grass-dominated sites also warrant further investigation, including

additional sampling to fill reference set gaps, and overlaying historical and current land use context onto these broad novelty patterns.

4. The future of quantifying novelty

Measuring novelty has shifted over the last decade from qualitative to quantitative, advancing our understanding of ecological and environmental change across time and space. Research has linked novel climates to novel communities (Williams *et al.*, 2001), assessed the ability of species distribution models to accurately forecast under novel climates (Fitzpatrick *et al.*, 2018) and estimated the role of extinction in the transition to novel states (Pandolfi *et al.*, 2020). Our conceptual framework provides a structure to describe the overlap, and research gaps, in this past work. We believe our framework will allow the next generation of quantitative research into novelty to build on this existing knowledge base and advance both fundamental and applied research priorities (Radeloff *et al.*, 2015).

Research on quantitative novelty offers a direct agenda: studying and understanding how environmental and ecological systems change into unprecedented states, and the drivers and implications of these changes (Turner *et al.*, 2020). Our summary of novelty research suggests there is still work to be done to understand novelty across different taxa, regions and scales. This includes expanding correlative links between abiotic and biotic novelty and estimating the strength of environmental, ecological and anthropogenic mechanisms to drive novelty (Blois *et al.*, 2013). At a fundamental level, there is a need to capture background distributions of novelty for given time periods, ecosystems and spatial regions, which can be used to benchmark present and future changes (Staples *et al.*, 2022).

Furthermore, the concept of novelty has value for testing and expanding ecological theory, as the identification and study of anomalies has led to fundamental shifts in related biological fields (Panero & Funk, 2008). While original treatments of ecological novelty were linked to

515 Hutchinsonian niche theory (Jackson & Overpeck, 2000), there are opportunities to study how novel systems alter biotic interactions (Blois *et al.*, 2013), such as through ecological networks (Ings *et al.*, 2009). Understanding changes in community-scale interactions under novelty may in turn benefit from an organism-centric view (Heger *et al.*, 2019), identifying whether, and how, novel conditions drive species invasions (Schittko *et al.*, 2020) and rapid evolution (Yeh, 2004; 520 Mackin *et al.*, 2021). Both ecological and environmental novelty are expected to alter ecosystem functions and services (Hobbs *et al.*, 2009). This theoretical link could be studied by integrating novelty methodologies with remote sensing data, trait databases (e.g., TRY plant trait database: Kattge *et al.*, 2011) or long-term global experiment networks (e.g., Nutrient Network: Borer *et al.*, 2014)). Environmental novelty has conceptual overlap with measurements of climate 525 velocity (Ordonez *et al.*, 2016), with potential to be integrated into ecological forecasting (Fitzpatrick *et al.*, 2018), such as in models of species range shifts. Finally, some quantifications of novelty have both theoretical and empirical links to core ecological concepts such as beta diversity (Anderson *et al.*, 2011; Godsoe *et al.*, 2021). Novelty in species composition, for instance, increases when beta diversity between the target and reference set exceeds beta 530 diversity within the reference set. Understanding conceptual overlap and correlation between similar terms could simplify and synchronize parallel research.

Another key need is to better integrate the tools and lessons from quantitative novelty research to ecosystem monitoring, management, and recovery (Williams & Jackson, 2007; Hobbs *et al.*, 535 2018; Heger *et al.*, 2019). Ecosystem management needs to consider multiple ecological and

environmental aspects holistically, not just in isolation (e.g., species abundance, value of one ecosystem service) or as aggregate statistics (e.g., diversity, productivity). Current indicators lack relevance to specific ecosystems or biomes and tend to be poorly tested (Nicholson *et al.*, 2021). Our framework can be used to explicitly measure and detect novelty across multiple dimensions, and across space or through time. This could allow restoration projects to be monitored using novelty to a target environmental or ecological reference state containing multiple features, with lower novelty over time representing a successful outcome. Our framework can also be used in time series (e.g., Fig. 2F-G) to monitor system change, providing early-warning signs (via increased novelty) of potentially deleterious change. This has benefits both for monitoring the progress of restoration projects, with early identification of sites that may need follow-up planting or management, but also in natural systems that may be at risk of degrading into lower-value states (e.g., bleaching on coral reefs: Anderson & Thompson, 2004). Measurement of novelty could also offer opportunities to identify anomalous recovery or resilient “bright spots” (Cinner *et al.*, 2016), stable systems that may have value as refuges. All these potential applications offer comparable measurement of distinctiveness that can easily be incorporated into existing frameworks (e.g., Resist-Accept-Direct framework: Schuurman *et al.*, 2022), improving cost-effectiveness of restoration and conservation efforts and value-adding to long-term monitoring programs.

While novelty has been defined in restoration ecology, conservation biology has considered complementarity, alongside measures of species endemism, for prioritization in protected area design (Margules & Pressey, 2000; Astudillo-Scalia & Albuquerque, 2020). Complementarity makes comparisons among areas, in either environment or ecological composition, to identify high priorities for conservation action (Justus & Sarkar, 2002). Hence, complementarity is a measurement of novelty as defined here; exploration of quantitative complementarity under our

framework may offer improvements to the design and maintenance of conservation plans. In addition to planning and managing protected areas, conservation has shifted from trying to protect static areas of nature to understanding and predicting species movements and shifts (Pech *et al.*, 2017; Hobbs *et al.*, 2018). Novelty measured under our framework offers a valuable tool to quantify these shifts in consistent and comparable terms, as well as making explicit how measurements can differ based on constituent components. Rather than a limitation, the component-dependency of novelty offers benefits, such as understanding the uniqueness of future climates at multiple spatial scales, which could feed into and improve decision-making and management.

5. Conclusion

Research on ecological novelty has shifted from early conceptual outlines to formal and quantifiable definitions. However, a profusion of quantitative analyses, each employing different and often incompletely described analytical approaches, has limited interpretability and synthesis of novelty analyses. The framework highlighted here provides a common structure to the variety of quantitative approaches, with clear definitions and language to assess differences among them and thereby better interpret findings. Our framework facilitates explicit and transparent choices about the measurement of novelty that up until now have been left implicit or outright ignored. These choices can change both the measurement and interpretation of novelty, limiting the potential for novelty to advance research and management goals. Our framework provides a structure and lexicon to describe novelty that can help guide decision-making via defining research goals and selection of appropriate data sources and analytic approaches. The combination of framework components distills novelty to aid analysts in defining what resulting measurements may, and may not, mean. Our unification of a fast-growing area of facilitates exploration of fundamental and theoretical questions, opens potential

integrate novelty measurements into biological applications, amid a background of rapid and unprecedented global change.

590 **Data accessibility statement:** Data were obtained from the North American Pollen Database (accessed via the Neotoma Paleoecological Database). R code to conduct analyses and reproduce all figures and tables is housed in Zenodo at <https://doi.org/10.5281/zenodo.12524200> . This is a blinded record for review and will be replaced with a full version linked to GitHub on manuscript acceptance.

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Author contributions: This manuscript is the result of the PaleoNovelty workshop, led by Timothy L. Staples and John M. Pandolfi. Timothy L. Staples conducted all analyses. All authors contributed substantially to study design, manuscript writing and revisions.

600 **Acknowledgements:** This paper developed from discussions at the PaleoNovelty workshop, held remotely and supported by the Paleosynthesis program, funded by Volkswagen Foundation and awarded to WK and others. This work was funded by ARC Discovery Early Career Research Award DE240100398 awarded to Timothy L. Staples and Discovery Project grant DP210100804 awarded to John M. Pandolfi and Wolfgang Kiessling. Anne E. Magurran, 605 Maria Dornelas and Amelia M. Penny acknowledge support from the Leverhulme Trust (RPG-2019-402). The *Sistema Nacional de Investigación* of SENACYT (Panamá) supported Aaron O'Dea. Jessica Blois was supported by the National Science Foundation (EAR-1750597). Tina Heger was supported by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation, project number HE 5893/8-1). Data were obtained from the Neotoma Paleoecology Database (<http://www.neotomadb.org>) and its constituent database, the North American Pollen Database. The work of data contributors, data stewards, and the Neotoma community is gratefully acknowledged. Open access publishing facilitated by The University of Queensland,

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as part of the Wiley - The University of Queensland agreement via the Council of Australian University Librarians.

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References:

- Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H. v, Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C. & Swenson, N.G. (2011) Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology Letters*, **14**, 19–28.
- 620 Anderson, M.J. & Thompson, A.A. (2004) Multivariate control charts for ecological and environmental monitoring. *Ecological Applications*, **14**, 1921–1935.
- Anoszko, E., Frelich, L.E., Rich, R.L. & Reich, P.B. (2022) Wind and fire: Rapid shifts in tree community composition following multiple disturbances in the southern boreal forest. *Ecosphere*, **13**, e3952.
- 625 Aronson, J., Murcia, C., Kattan, G.H., Moreno-Mateos, D., Dixon, K. & Simberloff, D. (2014) The road to confusion is paved with novel ecosystem labels: A reply to Hobbs et al. *Trends in Ecology and Evolution*, **29**, 646–647.
- Astudillo-Scalia, Y. & Albuquerque, F. (2020) Why should we reconsider using species richness in spatial conservation prioritization? *Biodiversity and Conservation*, **29**, 2055–2067.
- 630 Bates, D., Mächler, M., Bolker, B.M. & Walker, S.C. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **67**, 1–48.
- Birks, H.J.B., Felde, V.A., Bjune, A.E., Grytnes, J.-A., Seppä, H. & Giesecke, T. (2016) Does pollen-assemblage richness reflect floristic richness? A review of recent developments and future challenges. *Review of Palaeobotany and Palynology*, **228**, 1–25.
- 635 Blois, J.L., Zarnetske, P.L., Fitzpatrick, M.C. & Finnegan, S. (2013) Climate change and the past, present, and future of biotic interactions. *Science*, **341**, 499–504.
- Borer, E.T., Harpole, W.S., Adler, P.B., Lind, E.M., Orrock, J.L., Seabloom, E.W. & Smith, M.D. (2014) Finding generality in ecology: a model for globally distributed experiments. *Methods in Ecology and Evolution*, **5**, 65–73.
- 640 Burke, K.D., Williams, J.W., Brewer, S., Finsinger, W., Giesecke, T., Lorenz, D.J. & Ordóñez, A. (2019) Differing climatic mechanisms control transient and accumulated vegetation novelty in Europe and eastern North America. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **374**, 20190218.
- 645 Chapin, F.S. & Starfield, A.M. (1997) Time lags and novel ecosystems in response to transient climatic change in arctic Alaska. *Climatic Change*, **35**, 449–461.
- Cinner, J.E., Huchery, C., MacNeil, M.A., Graham, N.A.J., McClanahan, T.R., Maina, J., Maire, E., Kittinger, J.N., Hicks, C.C., Mora, C., Allison, E.H., D’Agata, S., Hoey, A., Feary, D.A., Crowder, L., Williams, I.D., Kulbicki, M., Vigliola, L., Wantiez, L., Edgar, G., Stuart-Smith, R.D., Sandin, S.A., Green, A.L., Hardt, M.J., Beggs, M., Friedlander, A., Campbell, S.J., Holmes, K.E., Wilson, S.K., Brokovich, E., Brooks, A.J., Cruz-Motta, J.J., Booth, D.J., Chabanet, P., Gough, C., Tupper, M., Ferse, S.C.A., Sumaila, U.R. & Mouillot, D. (2016) Bright spots among the world’s coral reefs. *Nature*, **535**, 416–419.
- 650

- Davis, M.B. (1981) *Quaternary History and the Stability of Forest Communities*. (ed. by D.C. West), H.H. Shugart), and D.B. Botkin), pp. 132–153. Springer New York, New York, NY.
- 655 Donohue, I., Hillebrand, H., Montoya, J.M., Petchey, O.L., Pimm, S.L., Fowler, M.S., Healy, K., Jackson, A.L., Lurgi, M., McClean, D., O'Connor, N.E., O'Gorman, E.J. & Yang, Q. (2016) Navigating the complexity of ecological stability. *Ecology Letters*, **19**, 1172–1185.
- Ellis, E.C. (2011) Anthropogenic transformation of the terrestrial biosphere. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, **369**, 1010–1035.
- 660 Ellis, E.C., Klein Goldewijk, K., Siebert, S., Lightman, D. & Ramankutty, N. (2010) Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography*, **19**, 589–606.
- 665 Felde, V.A., Peglar, S.M., Bjune, A.E., Grytnes, J.-A. & Birks, H.J.B. (2015) Modern pollen–plant richness and diversity relationships exist along a vegetational gradient in southern Norway. *The Holocene*, **26**, 163–175.
- Finsinger, W., Giesecke, T., Brewer, S. & Leydet, M. (2017) Emergence patterns of novelty in European vegetation assemblages over the past 15 000 years. *Ecology Letters*, **20**, 336–
- 670 346.
- Fitzpatrick, M.C., Blois, J.L., Williams, J.W., Nieto-Lugilde, D., Maguire, K.C. & Lorenz, D.J. (2018) How will climate novelty influence ecological forecasts? Using the Quaternary to assess future reliability. *Global Change Biology*, **24**, 3575–3586.
- Godsoe, W., Bellingham, P.J. & Moltchanova, E. (2021) Disentangling Niche Theory and Beta
- 675 Diversity Change. *The American Naturalist*, 0.
- Graham, N.A.J., Cinner, J.E., Norström, A. v. & Nyström, M. (2014) Coral reefs as novel ecosystems: EMBRACING new futures. *Current Opinion in Environmental Sustainability*, **7**, 9–14.
- Hallett, L.M., Standish, R.J., Hulvey, K.B., Gardener, M.R., Suding, K.N., Starzomski, B.M.,
- 680 Murphy, S.D. & Harris, J.A. (2013) Towards a Conceptual Framework for Novel Ecosystems. *Novel Ecosystems*, 16–28.
- Harris, J.A., Murphy, S.D., Nelson, C.R., Perring, M.P. & Tognetti, P.M. (2013) *Characterizing Novel Ecosystems: Challenges for Measurement. Novel Ecosystems: Intervening in the New Ecological World Order*, pp. 192–204. John Wiley & Sons, Ltd.
- 685 Heger, T., Bernard-Verdier, M., Gessler, A., Greenwood, A.D., Grossart, H.-P., Hilker, M., Keinath, S., Kowarik, I., Kueffer, C., Marquard, E., Müller, J., Niemeier, S., Onandia, G., Petermann, J.S., Rillig, M.C., Rödel, M.-O., Saul, W.-C., Schittko, C., Tockner, K., Joshi, J. & Jeschke, J.M. (2019) Towards an Integrative, Eco-Evolutionary Understanding of Ecological Novelty: Studying and Communicating Interlinked Effects of Global Change.
- 690 *BioScience*, **69**, 888–899.
- Hillebrand, H., Donohue, I., Harpole, W.S., Hodapp, D., Kucera, M., Lewandowska, A.M., Merder, J., Montoya, J.M. & Freund, J.A. (2020) Thresholds for ecological responses to global change do not emerge from empirical data. *Nature Ecology & Evolution*, **4**, 1502–1509.
- 695 Hobbs, R.J. (2017) *Novel ecosystems: Can't we just pretend they're not there? Effective Conservation Science: Data Not Dogma*, pp. 45–50. Oxford University Press, Oxford.

- Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., Epstein, P.R., Ewel, J.J., Klink, C.A., Lugo, A.E., Norton, D., Ojima, D., Richardson, D.M., Sanderson, E.W., Valladares, F., Vilà, M., Zamora, R. & Zobel, M. (2006) Novel ecosystems: Theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography*, **15**, 1–7.
- Hobbs, R.J., Higgs, E., Hall, C.M., Bridgewater, P., Chapin, F.S., Ellis, E.C., Ewel, J.J., Hallett, L.M., Harris, J., Hulvey, K.B., Jackson, S.T., Kennedy, P.L., Kueffer, C., Lach, L., Lantz, T.C., Lugo, A.E., Mascaro, J., Murphy, S.D., Nelson, C.R., Perring, M.P., Richardson, D.M., Seastedt, T.R., Standish, R.J., Starzomski, B.M., Suding, K.N., Tognetti, P.M., Yakob, L. & Yung, L. (2014a) Managing the whole landscape: Historical, hybrid, and novel ecosystems. *Frontiers in Ecology and the Environment*, **12**, 557–564.
- Hobbs, R.J., Higgs, E. & Harris, J.A. (2009) Novel ecosystems: implications for conservation and restoration. *Trends in Ecology and Evolution*, **24**, 599–605.
- Hobbs, R.J., Higgs, E.S. & Hall, C.M. (2013) *Defining Novel Ecosystems. Novel Ecosystems: Intervening in the New Ecological World Order* Wiley Online Books., pp. 58–60.
- Hobbs, R.J., Higgs, E.S. & Harris, J.A. (2014b) Novel ecosystems: Concept or inconvenient reality? A response to Murcia et al. *Trends in Ecology and Evolution*, **29**, 645–646.
- Hobbs, R.J., Valentine, L.E., Standish, R.J. & Jackson, S.T. (2018) Movers and Stayers: Novel Assemblages in Changing Environments. *Trends in Ecology and Evolution*, **33**, 116–128.
- Ings, T.C., Montoya, J.M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C.F., Edwards, F., Figueroa, D., Jacob, U., Jones, J.I., Lauridsen, R.B., Ledger, M.E., Lewis, H.M., Olesen, J.M., van Veen, F.J.F., Warren, P.H. & Woodward, G. (2009) Review: Ecological networks – beyond food webs. *Journal of Animal Ecology*, **78**, 253–269.
- Jackson, S.T. (2013) *Perspective: Ecological Novelty is not New. Novel Ecosystems: Intervening in the New Ecological World Order* Wiley Online Books., pp. 63–65.
- Jackson, S.T. & Overpeck, J.T. (2000) Responses of Plant Populations and Communities to Environmental Changes of the Late Quaternary. *Paleobiology*, **26**, 194–220.
- Jackson, S.T. & Williams, J.W. (2004) Modern Analogs In Quaternary Paleoecology: Here Today, Gone Yesterday, Gone Tomorrow? *Annual Review of Earth and Planetary Sciences*, **32**, 495–537.
- Justus, J. & Sarkar, S. (2002) The principle of complementarity in the design of reserve networks to conserve biodiversity: A preliminary history. *Journal of Biosciences*, **27**, 421–435.
- Kattan, G.H., Aronson, J. & Murcia, C. (2016) Does the novel ecosystem concept provide a framework for practical applications and a path forward? A reply to Miller and Bestelmeyer. *Restoration Ecology*, **24**, 714–716.
- Kattge, J., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M., Reich, P.B., Wright, I.J., Cornelissen, J.H.C., Violle, C., Harrison, S.P., Van Bodegom, P.M., Reichstein, M., Enquist, B.J., Soudzilovskaia, N.A., Ackerly, D.D., Anand, M., Atkin, O., Bahn, M., Baker, T.R., Baldocchi, D., Bekker, R., Blanco, C.C., Blonder, B., Bond, W.J., Bradstock, R., Bunker, D.E., Casanoves, F., Cavender-Bares, J., Chambers, J.Q., Chapin, F.S., Chave, J., Coomes, D., Cornwell, W.K., Craine, J.M., Dobrin, B.H., Duarte, L., Durka, W., Elser, J., Esser, G., Estiarte, M., Fagan, W.F., Fang, J., Fernández-Méndez, F., Fidelis, A., Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G.T., Fyllas, N.M., Gallagher, R.

- V., Green, W.A., Gutierrez, A.G., Hickler, T., Higgins, S.I., Hodgson, J.G., Jalili, A., Jansen, S., Joly, C.A., Kerkhoff, A.J., Kirkup, D., Kitajima, K., Kleyer, M., Klotz, S., Knops, J.M.H., Kramer, K., Kühn, I., Kurokawa, H., Laughlin, D., Lee, T.D., Leishman, M., Lens, F., Lenz, T., Lewis, S.L., Lloyd, J., Llusià, J., Louault, F., Ma, S., Mahecha, M.D., Manning, P.,
745 Massad, T., Medlyn, B.E., Messier, J., Moles, A.T., Müller, S.C., Nadrowski, K., Naeem, S., Niinemets, Ü., Nöllert, S., Nüske, A., Ogaya, R., Oleksyn, J., Onipchenko, V.G., Onoda, Y., Ordoñez, J., Overbeck, G., Ozinga, W.A., Patiño, S., Paula, S., Pausas, J.G., Peñuelas, J., Phillips, O.L., Pillar, V., Poorter, H., Poorter, L., Poschlod, P., Prinzing, A., Proulx, R., Rammig, A., Reinsch, S., Reu, B., Sack, L., Salgado-Negret, B., Sardans, J., Shiodera, S.,
750 Shipley, B., Siefert, A., Sosinski, E., Soussana, J.F., Swaine, E., Swenson, N., Thompson, K., Thornton, P., Waldram, M., Weiher, E., White, M., White, S., Wright, S.J., Yguel, B., Zaehle, S., Zanne, A.E. & Wirth, C. (2011) TRY - a global database of plant traits. *Global Change Biology*, **17**, 2905–2935.
- Kerr, M.R., Ordonez, A., Riede, F. & Svenning, J.-C. (2024) A biogeographic–macroecological perspective on the rising novelty of the biosphere in the Anthropocene. *Journal of Biogeography*, **51**, 575–587.
- Kindt, R. (2020) WorldFlora: An R package for exact and fuzzy matching of plant names against the World Flora Online taxonomic backbone data. *Applications in Plant Sciences*, **8**, e11388.
- 760 Kueffer, C. (2015) *Ecological Novelty: Towards an Interdisciplinary Understanding of Ecological Change in the Anthropocene. Grounding Global Climate Change: Contributions from the Social and Cultural Sciences* (ed. by H. Greschke) and J. Tischler), pp. 19–37. Springer Netherlands, Dordrecht.
- Lewis, S.L. & Maslin, M.A. (2015) Defining the Anthropocene. *Nature*, **519**, 171–180.
- 765 Lurgi, M., López, B.C. & Montoya, J.M. (2012) Novel communities from climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**, 2913–2922.
- Mackin, C.R., Peña, J.F., Blanco, M.A., Balfour, N.J. & Castellanos, M.C. (2021) Rapid evolution of a floral trait following acquisition of novel pollinators. *Journal of Ecology*, **109**, 2234–2246.
- 770 Mahony, C.R., Cannon, A.J., Wang, T. & Aitken, S.N. (2017) A closer look at novel climates: new methods and insights at continental to landscape scales. *Global Change Biology*, **23**, 3934–3955.
- Margules, C.R. & Pressey, R.L. (2000) Systematic conservation planning. *Nature*, **405**, 243–253.
- 775 Marris, E. (2009) Ecology: Ragamuffin earth. *Nature*, **460**, 450–453.
- Mascaro, J., Hughes, R.F. & Schnitzer, S.A. (2012) Novel forests maintain ecosystem processes after the decline of native tree species. *Ecological Monographs*, **82**, 221–228.
- Matthias, I., Semmler, M.S.S. & Giesecke, T. (2015) Pollen diversity captures landscape structure and diversity. *Journal of Ecology*, **103**, 880–890.
- 780 Van Meerbeek, K., Jucker, T. & Svenning, J.-C. (2021) Unifying the concepts of stability and resilience in ecology. *Journal of Ecology*, **109**, 3114–3132.
- Miller, J.R. & Bestelmeyer, B.T. (2016) What's wrong with novel ecosystems, really? *Restoration Ecology*, **24**, 577–582.

Milton, S.J. (2003) "Emerging ecosystems" - a washing-stone for ecologists, economists and sociologists? *South African Journal of Science*.

785 Morse, N.B., Pellissier, P.A., Cianciola, E.N., Brereton, R.L., Sullivan, M.M., Shonka, N.K., Wheeler, T.B. & McDowell, W.H. (2014) Novel ecosystems in the Anthropocene: A revision of the novel ecosystem concept for pragmatic applications. *Ecology and Society*, **19**.

Müller, K. (2020) here: A Simpler Way to Find Your Files.

790 Murcia, C., Aronson, J., Kattan, G.H., Moreno-Mateos, D., Dixon, K. & Simberloff, D. (2014) A critique of the "novel ecosystem" concept. *Trends in Ecology and Evolution*, **29**, 548–553.

Nicholson, E., Watermeyer, K.E., Rowland, J.A., Sato, C.F., Stevenson, S.L., Andrade, A., Brooks, T.M., Burgess, N.D., Cheng, S.-T., Grantham, H.S., Hill, S.L., Keith, D.A., Maron, M., Metzke, D., Murray, N.J., Nelson, C.R., Obura, D., Plumptre, A., Skowno, A.L. & Watson, J.E.M. (2021) Scientific foundations for an ecosystem goal, milestones and indicators for the post-2020 global biodiversity framework. *Nature Ecology & Evolution*, **5**, 1338–1349.

795 Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H.B.A., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M.O., Lahti, L., McGlenn, D., Ouellette, M.-H., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C.J.F. & Weedon, J. (2024) vegan: Community Ecology Package.

800 Ordonez, A., Williams, J.W. & Svenning, J.C. (2016) Mapping climatic mechanisms likely to favour the emergence of novel communities. *Nature Climate Change*, **6**, 1104–1109.

805 Overpeck, J.T., Webb, R.S. & Webb, T. (1992) Mapping eastern North American vegetation change of the past 18 ka: no-analogs and the future. *Geology*, **20**, 1071–1074.

Overpeck, J.T., Webb, T. & Prentice, I.C. (1985) Quantitative interpretation of fossil pollen spectra: Dissimilarity coefficients and the method of modern analogs. *Quaternary Research*, **23**, 87–108.

810 Pandolfi, J.M., Staples, T.L. & Kiessling, W. (2020) Increased extinction in the emergence of novel ecological communities. *Science*, **370**, 220–222.

Panero, J.L. & Funk, V.A. (2008) The value of sampling anomalous taxa in phylogenetic studies: Major clades of the Asteraceae revealed. *Molecular Phylogenetics and Evolution*, **47**, 757–782.

815 Pebesma, E. & Bivand, R. (2023) *Spatial Data Science: With applications in R*, Chapman and Hall/CRC.

Pecl, G.T., Araújo, M.B., Bell, J.D., Blanchard, J., Bonebrake, T.C., Chen, I.-C., Clark, T.D., Colwell, R.K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R.A., Griffis, R.B., Hobday, A.J., Janion-Scheepers, C., Jarzyna, M.A., Jennings, S., Lenoir, J., Linnetved, H.I., Martin, V.Y., McCormack, P.C., McDonald, J., Mitchell, N.J., Mustonen, T., Pandolfi, J.M., Pettorelli, N., Popova, E., Robinson, S.A., Scheffers, B.R., Shaw, J.D., Sorte, C.J.B., Strugnell, J.M., Sunday, J.M., Tuanmu, M.-N., Vergés, A., Villanueva, C., Wernberg, T., Wapstra, E. & Williams, S.E. (2017) Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, **355**, eaai9214.

825

- Peterson, A.T., Cobos, M.E. & Jiménez-García, D. (2018) Major challenges for correlational ecological niche model projections to future climate conditions. *Annals of the New York Academy of Sciences*, **1429**, 66–77.
- 830 Pimentel, M.A.F., Clifton, D.A., Clifton, L. & Tarassenko, L. (2014) A review of novelty detection. *Signal Processing*, **99**, 215–249.
- R Core Team (2022) R: A Language and Environment for Statistical Computing.
- Radeloff, V.C., Williams, J.W., Bateman, B.L., Burke, K.D., Carter, S.K., Childress, E.S., Cromwell, K.J., Gratton, C., Hasley, A.O., Kraemer, B.M., Latzka, A.W., Marin-Spiotta, E.,
- 835 Meine, C.D., Munoz, S.E., Neeson, T.M., Pidgeon, A.M., Rissman, A.R., Rivera, R.J., Szymanski, L.M. & Usinowicz, J. (2015) The rise of novelty in ecosystems. *Ecological Applications*, **25**, 2051–2068.
- Ricciardi, A. (2007) Are Modern Biological Invasions an Unprecedented Form of Global Change? *Conservation Biology*, **21**, 329–336.
- 840 Sage, R.F. (2020) Global change biology: A primer. *Global Change Biology*, **26**, 3–30.
- Samhuri, J.F., Levin, P.S. & Ainsworth, C.H. (2010) Identifying Thresholds for Ecosystem-Based Management. *PLOS ONE*, **5**, e8907.
- Saul, W.-C. & Jeschke, J.M. (2015) Eco-evolutionary experience in novel species interactions. *Ecology Letters*, **18**, 236–245.
- 845 Schittko, C., Bernard-Verdier, M., Heger, T., Buchholz, S., Kowarik, I., von der Lippe, M., Seitz, B., Joshi, J. & Jeschke, J.M. (2020) A multidimensional framework for measuring biotic novelty: How novel is a community? *Global Change Biology*, **26**, 4401–4417.
- Schläppy, M.L. & Hobbs, R.J. (2019) A triage framework for managing novel, hybrid, and designed marine ecosystems. *Global Change Biology*, **25**, 3215–3223.
- 850 Schuurman, G.W., Cole, D.N., Cravens, A.E., Covington, S., Crausbay, S.D., Hoffman, C.H., Lawrence, D.J., Magness, D.R., Morton, J.M., Nelson, E.A. & O'Malley, R. (2022) Navigating Ecological Transformation: Resist–Accept–Direct as a Path to a New Resource Management Paradigm. *BioScience*, **72**, 16–29.
- Socorro, D.V. & Goring, S. (2023) Working with the Neotoma Paleoecology Database. *GitHub*.
- 855 Soetaert, K. (2024) shape: Functions for Plotting Graphical Shapes, Colors.
- South, A. (2011) rworldmap: A New R package for Mapping Global Data. *The R Journal*, **3**, 35–43.
- Staples, T.L., Kiessling, W. & Pandolfi, J.M. (2022) Emergence patterns of locally novel plant communities driven by past climate change and modern anthropogenic impacts. *Ecology Letters*, **25**, 1497–1509.
- 860 Truitt, A.M., Granek, E.F., Duveneck, M.J., Goldsmith, K.A., Jordan, M.P. & Yazzie, K.C. (2015) What is Novel About Novel Ecosystems: Managing Change in an Ever-Changing World. *Environmental Management*, **55**, 1217–1226.
- Turner, M.G., Calder, W.J., Cumming, G.S., Hughes, T.P., Jentsch, A., LaDeau, S.L., Lenton, T.M., Shuman, B.N., Turetsky, M.R., Ratajczak, Z., Williams, J.W., Williams, A.P. &
- 865 Carpenter, S.R. (2020) Climate change, ecosystems and abrupt change: science priorities. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **375**, 20190105.
- Wahl, E.R. (2004) A general framework for determining cutoff values to select pollen analogs with dissimilarity metrics in the modern analog technique. *Review of Palaeobotany and*
- 870 *Palynology*, **128**, 263–280.

Wasserstein, R.L., Schirm, A.L. & Lazar, N.A. (2019) Moving to a World Beyond “ $p < 0.05$.” *The American Statistician*, **73**, 1–19.

Waters, C.N., Zalasiewicz, J., Summerhayes, C., Barnosky, A.D., Poirier, C., Gałuszka, A., Cearreta, A., Edgeworth, M., Ellis, E.C., Ellis, M., Jeandel, C., Leinfelder, R., McNeill, J.R.,
875 Richter, D.D.B., Steffen, W., Syvitski, J., Vidas, D., Waple, M., Williams, M., Zhisheng, A., Grinevald, J., Odada, E., Oreskes, N. & Wolfe, A.P. (2016) The Anthropocene is functionally and stratigraphically distinct from the Holocene. *Science*, **351**.

Williams, J.W. & Jackson, S.T. (2007) Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, **5**, 475–482.

880 Williams, J.W. & Shuman, B. (2008) Obtaining accurate and precise environmental reconstructions from the modern analog technique and North American surface pollen dataset. *Quaternary Science Reviews*, **27**, 669–687.

Williams, J.W., Shuman, B.N. & Webb, T. (2001) Dissimilarity analyses of late-Quaternary vegetation and climate in eastern North America. *Ecology*, **82**, 3346–3362.

885 Yeh, P.J. (2004) Rapid evolution of a sexually selected trait following population establishment in a novel habitat. *Evolution*, **58**, 166–174.

Young, K.R. (2014) Biogeography of the Anthropocene: Novel species assemblages. *Progress in Physical Geography: Earth and Environment*, **38**, 664–673.

890

Supplementary Information for:
A conceptual framework for measuring ecological novelty

Supplementary Methods

We acquired palynological data from the North American Pollen Database (Illinois State Museum & National Geophysical Data Center) from the Neotoma Paleoecology Database (Goring *et al.*, 2015; Williams *et al.*, 2018). We restricted the dataset to pollen samples from a small geographic area with high time series density: Midwest USA centered on Minnesota (Fig. 3B). The region covered western Wisconsin, eastern North and South Dakota and northern Iowa, containing a total of 99 time series. Taxa were synonymized using the World Flora Index (Kindt, 2020). Within each time series, we averaged pollen counts for each plant family into two 500-year sampling bins: a pre-modern bin, 1000-1500AD, and a modern bin, 1500-2000AD. This period was chosen as it covered the European occupation of the study region, representing the most recent pre-European sample of pollen composition.

Novelty was calculated by calculating Bray-Curtis dissimilarity on the square-root transformed relative abundances (divided by total sampling bin count) of the twenty most abundant plant families (measured across the entire study region). Square-root transformation amplified change in rarer taxa relative to dominant taxa, a common practice in ecological studies, and were strongly correlated with novelty measures made without transformation ($R = 0.624 - 0.745$).

Novelty was calculated with four different target-reference set arrangements (see Table 2, Fig. 3), resulting in four measurements for each study site. These novelties were compared by Principal Component Analysis (princomp function) after logit-transformation. To visualize assemblage composition, we used non-metric multidimensional scaling of pollen composition to generate the ordination in Figure 4 (metaMDS function: vegan package).

We repeated the above process using genus identities as distinct taxa in the Bray-Curtis measurement, including the 50 most abundant genera.

Finally, we tested for how the number of taxa ("dimensions") in novelty calculation may impact measurements. For each site, we measured "no-analog" novelty with restricted taxa, using two to 20 plant families (with 20 families reflecting the main analysis). This was repeated 999 times with families randomly ordered each time. We then calculated the novelty deviation when we reduced taxa dimensionality by subtracting novelty values from the "true" novelty when family count = 20. We present this as a boxplot, and predictions from a linear mixed-effects model, with deviation from true novelty fit as a response variable against $\log(\text{taxa number})$, with each iteration and site fitted as crossed random intercepts. This model found a positive log-relationship: novelty measurements increased as additional dimensions were added. The mixed-effects model had a marginal R^2 (fixed effects only) of 0.289, and a conditional R^2 (fixed and random effects) of 0.545.

Table S1: Twenty most abundant families in pollen data included in novelty analysis. Abundance was estimated using the mean relative abundance across all sites (as a percentage), which corrected for different sampling effort (number of pollen grains counted) in

different sites. MDS1 and MDS2 are taxa centroids in the non-metric multidimensional scaling in Fig. S2 (represented via red points and labels).

Family	Mean relative abundance across sites (%)	MDS 1	MDS 2
Fagaceae	14.97	0.33	-0.35
Pinaceae	7.79	-0.74	0.03
Poaceae	6.36	0.71	0.34
Betulaceae	4.80	-0.58	-0.11
Cyperaceae	4.16	0.06	0.63
Asteraceae	3.28	0.14	0.00
Ulmaceae	2.09	0.10	-0.23
Amaranthaceae	1.30	-0.03	1.01
Salicaceae	1.00	-0.29	0.03
Oleaceae	0.75	-0.28	0.00
Cupressaceae	0.70	-0.78	0.04
Sapindaceae	0.60	-0.30	-0.14
Malvaceae	0.60	0.19	-0.30
Juglandaceae	0.33	-0.21	0.07
Platanaceae	0.27	-0.12	0.07
Ranunculaceae	0.24	-0.12	0.09
Fabaceae	0.21	0.07	0.29
Polygonaceae	0.20	-0.28	0.01
Rosaceae	0.19	-0.31	0.26
Ericaceae	0.17	-0.94	0.23

Table S2: Fifty most abundant genera in pollen data included in supplementary novelty analysis. Abundance was estimated using the mean relative abundance across all sites (as a percentage), which corrected for different sampling effort (number of pollen grains counted) in different sites. MDS1 and MDS2 are taxa centroids in the non-metric multidimensional scaling in Fig. S5 (represented via red labels and points).

Family	Genus	Mean relative abundance across sites (%)	MDS1	MDS2
Pinaceae	<i>Pinus</i>	14.92	-0.62	0.14
Fagaceae	<i>Quercus</i>	12.09	0.69	0.22
Asteraceae	<i>Ambrosia</i>	5.78	0.59	-0.48
Betulaceae	<i>Betula</i>	5.5	-0.46	-0.12
Asteraceae	<i>Artemisia</i>	2.18	0.41	-0.30
Betulaceae	<i>Alnus</i>	1.63	-0.44	0.00
Ulmaceae	<i>Ulmus</i>	1.56	0.54	-0.02
Pinaceae	<i>Picea</i>	0.84	-0.69	-0.04
Oleaceae	<i>Fraxinus</i>	0.67	0.08	-0.29
Salicaceae	<i>Populus</i>	0.55	-0.22	-0.12
Salicaceae	<i>Salix</i>	0.51	0.19	-0.36
Betulaceae	<i>Corylus</i>	0.49	0.04	-0.03
Sapindaceae	<i>Acer</i>	0.48	0.11	-0.19
Malvaceae	<i>Tilia</i>	0.37	0.75	0.13
Betulaceae	<i>Ostrya</i>	0.33	1.21	0.67
Pinaceae	<i>Larix</i>	0.29	-0.58	-0.02
Pinaceae	<i>Tsuga</i>	0.26	-0.88	-1.07
Pinaceae	<i>Abies</i>	0.21	-0.85	-0.07
Juglandaceae	<i>Carya</i>	0.19	0.50	-0.28
Asteraceae	<i>Cyclachaena</i>	0.13	0.35	-0.94
Juglandaceae	<i>Juglans</i>	0.12	0.36	-0.31
Platanaceae	<i>Platanus</i>	0.12	0.44	-0.31
Ranunculaceae	<i>Thalictrum</i>	0.08	0.18	-0.23
Poaceae	<i>Phragmites</i>	0.07	-0.98	0.69
Ruppiaceae	<i>Ruppia</i>	0.06	0.43	-1.99
Cupressaceae	<i>Juniperus</i>	0.06	0.39	-0.14
Sarcobataceae	<i>Sarcobatus</i>	0.05	0.19	-0.59
Fabaceae	<i>Amorpha</i>	0.05	0.32	-0.86
Amaranthaceae	<i>Salsola</i>	0.04	0.55	-0.94
Polygonaceae	<i>Rumex</i>	0.04	0.02	-0.31
Poaceae	<i>Zizania</i>	0.04	0.17	-0.77
Araceae	<i>Lemna</i>	0.04	0.03	-0.92
Asteraceae	<i>Iva</i>	0.03	0.19	-0.89

Vitaceae	<i>Vitis</i>	0.03	0.52	-0.47
Asteraceae	<i>Xanthium</i>	0.02	0.26	-0.55
Cannabaceae	<i>Celtis</i>	0.02	0.29	-0.24
Plantaginaceae	<i>Plantago</i>	0.02	0.35	-0.69
Moraceae	<i>Morus</i>	0.02	0.14	-0.32
Fabaceae	<i>Dalea</i>	0.02	0.35	-1.05
Cannabaceae	<i>Humulus</i>	0.01	0.16	-0.61
Cupressaceae	<i>Thuja</i>	0.01	-0.89	0.20
Ephedraceae	<i>Ephedra</i>	0.01	0.36	-0.53
Urticaceae	<i>Urtica</i>	0.01	0.56	-0.43
Polygonaceae	<i>Persicaria</i>	0.01	0.35	-0.07
Fagaceae	<i>Fagus</i>	0.01	-0.35	-0.42
Myricaceae	<i>Myrica</i>	0.01	-0.83	0.17
Euphorbiaceae	<i>Euphorbia</i>	<0.01	0.19	-0.29
Ranunculaceae	<i>Ranunculus</i>	<0.01	0.63	-1.10
Asteraceae	<i>Bidens</i>	<0.01	0.66	-1.23
Asteraceae	<i>Eupatorium</i>	<0.01	0.81	-1.54

950 **Table S3:** Site ID numbers from Neotoma, site coordinates and raw novelty measurements used in Figure 4 Principal Component Analysis.

Neotoma site ID	Longitude	Latitude	Novelty measurements				PC scores			
			No analog	Time's arrow	Past comp	Present comp	PC1	PC2	PC3	PC4
9871	-93.212992	44.333012	0.040	0.042	0.047	0.026	-2.063	0.067	0.290	-0.120
9870	-94.094046	45.16118	0.052	0.051	0.026	0.029	-2.106	0.408	-0.277	0.131
9824	-93.641746	44.192116	0.060	0.040	0.032	0.038	-1.883	0.151	-0.143	0.406
9876	-94.07615	45.42133	0.041	0.063	0.047	0.029	-1.797	0.216	0.041	-0.363
9873	-93.46048	44.65102	0.051	0.060	0.063	0.026	-1.606	0.328	0.392	-0.295
9825	-93.367772	44.353702	0.045	0.045	0.066	0.048	-1.406	-0.276	0.217	-0.041
9867	-93.321848	44.692808	0.064	0.060	0.026	0.082	-1.334	-0.041	-0.876	0.444
9872	-93.666674	44.229034	0.094	0.060	0.050	0.030	-1.359	0.687	0.199	0.243
10412	-92.0406	46.11894	0.051	0.051	0.070	0.082	-0.948	-0.511	-0.072	0.088
9875	-93.914954	44.313454	0.066	0.093	0.047	0.054	-1.026	0.325	-0.395	-0.141
9688	-94.879268	45.198736	0.070	0.075	0.047	0.068	-0.956	0.105	-0.419	0.108
531	-91.475	45.275	0.037	0.085	0.071	0.070	-0.954	-0.348	-0.240	-0.536
1593	-91.48333	45.28333	0.064	0.070	0.071	0.070	-0.777	-0.100	-0.085	-0.023
2231	-91.45833	45.28333	0.087	0.037	0.075	0.087	-0.745	-0.375	0.154	0.674
27245	-91.701074	46.38043	0.066	0.066	0.070	0.086	-0.679	-0.250	-0.183	0.100
9953	-95.478928	45.891414	0.054	0.054	0.121	0.070	-0.652	-0.489	0.447	-0.137
799	-93.165416	44.757618	0.077	0.095	0.085	0.044	-0.726	0.419	0.195	-0.300
8567	-91.1662	46.30222	0.068	0.068	0.085	0.083	-0.560	-0.248	-0.015	0.027
7531	-95.2408	45.44962	0.063	0.071	0.113	0.066	-0.536	-0.194	0.316	-0.215
2786	-93.16778	45.84889	0.066	0.074	0.103	0.076	-0.461	-0.214	0.152	-0.140
10132	-95.273974	47.226802	0.059	0.059	0.113	0.092	-0.443	-0.549	0.210	-0.040
1598	-91.113124	48.14179	0.066	0.066	0.087	0.110	-0.393	-0.478	-0.139	0.096
9869	-94.474636	43.606022	0.075	0.069	0.107	0.082	-0.367	-0.230	0.182	0.008
7540	-95.46186	45.85698	0.101	0.078	0.086	0.068	-0.394	0.210	0.088	0.148
307	-93.547946	44.95588	0.066	0.111	0.085	0.074	-0.414	0.074	-0.180	-0.370
9826	-93.740124	45.14107	0.051	0.092	0.125	0.075	-0.373	-0.313	0.188	-0.537
10240	-92.126	46.0128	0.087	0.108	0.073	0.082	-0.318	0.196	-0.309	-0.086
485	-93.27	42.02	0.072	0.072	0.095	0.111	-0.247	-0.393	-0.107	0.070
9874	-93.935746	44.807836	0.080	0.094	0.072	0.105	-0.281	-0.091	-0.408	0.028
7539	-95.26402	46.0551	0.118	0.082	0.086	0.066	-0.320	0.362	0.110	0.219
1586	-92.824634	45.047734	0.085	0.105	0.100	0.074	-0.216	0.160	0.013	-0.208
824	-94.421536	44.945278	0.077	0.077	0.113	0.100	-0.144	-0.290	0.068	-0.015
7542	-95.34356	45.81656	0.132	0.063	0.099	0.073	-0.233	0.200	0.298	0.474
9768	-92.219194	45.786366	0.097	0.115	0.073	0.083	-0.223	0.298	-0.335	-0.055
13349	-92.2734	45.9006	0.100	0.066	0.103	0.102	-0.127	-0.200	0.087	0.311
8573	-90.6084	45.19114	0.096	0.096	0.085	0.094	-0.144	0.081	-0.205	0.061
13348	-92.3654	45.9316	0.101	0.098	0.095	0.087	-0.087	0.143	-0.065	0.022
1901	-94.1142	47.0798	0.087	0.102	0.117	0.077	-0.095	0.081	0.134	-0.215
9762	-95.272972	45.443186	0.101	0.101	0.100	0.083	-0.077	0.173	-0.017	-0.028
10211	-95.39968	47.683194	0.089	0.093	0.109	0.098	-0.023	-0.089	-0.021	-0.044
2235	-93.859794	44.870322	0.100	0.099	0.123	0.069	-0.074	0.225	0.270	-0.143
1548	-93.16014	44.79964	0.082	0.082	0.103	0.126	-0.001	-0.366	-0.160	0.082
1078	-94.13333	46.55	0.110	0.062	0.129	0.092	-0.027	-0.154	0.376	0.323
7538	-95.5546	45.8003	0.121	0.107	0.091	0.076	-0.063	0.406	-0.053	0.077
8551	-93.41352	44.5921	0.110	0.066	0.104	0.115	0.006	-0.209	0.036	0.412
11606	-94.682444	46.972092	0.100	0.089	0.113	0.095	0.021	-0.020	0.074	0.057
1771	-93.68	46.06833	0.050	0.050	0.144	0.153	-0.120	-1.145	0.173	0.025
1544	-93.692446	45.42213	0.136	0.080	0.119	0.064	-0.081	0.383	0.421	0.234
8572	-91.4942	46.3812	0.094	0.087	0.111	0.109	0.054	-0.161	-0.023	0.076
8561	-96.189	46.59746	0.070	0.070	0.119	0.146	0.033	-0.683	-0.076	0.077
9987	-95.8058	45.8653	0.105	0.122	0.100	0.083	0.033	0.299	-0.105	-0.144
1701	-95.00834	47.243982	0.078	0.110	0.145	0.077	0.027	-0.003	0.266	-0.416
318	-91.99472	47.92417	0.106	0.123	0.092	0.094	0.070	0.249	-0.240	-0.083
1815	-92.011594	48.098118	0.081	0.081	0.152	0.104	0.113	-0.350	0.284	-0.106

10134	-93.069822	45.590222	0.144	0.079	0.105	0.091	0.081	0.212	0.133	0.418
1766	-95.12645	43.34114	0.089	0.089	0.131	0.113	0.159	-0.262	0.078	-0.031
1729	-93.386654	47.981836	0.097	0.097	0.092	0.136	0.144	-0.182	-0.353	0.139
1991	-95.575	46.92222	0.063	0.063	0.144	0.153	0.094	-0.884	0.098	0.024
2293	-91.86667	47.91667	0.116	0.126	0.087	0.094	0.096	0.338	-0.283	-0.012
10352	-91.198582	46.307116	0.104	0.116	0.109	0.095	0.141	0.152	-0.086	-0.097
269	-94.55197	46.270324	0.098	0.122	0.104	0.100	0.139	0.116	-0.190	-0.154
2933	-93.573634	45.004374	0.112	0.112	0.125	0.081	0.157	0.252	0.144	-0.109
2557	-93.98205	45.408746	0.146	0.088	0.154	0.044	-0.054	0.649	0.815	0.023
1772	-94.408428	46.341438	0.137	0.131	0.090	0.076	0.089	0.606	-0.142	0.016
10135	-95.324986	46.164476	0.126	0.127	0.090	0.092	0.142	0.407	-0.244	0.023
10146	-94.670324	46.953096	0.100	0.099	0.139	0.102	0.244	-0.070	0.150	-0.077
2548	-95.787316	47.192748	0.093	0.093	0.130	0.125	0.262	-0.272	-0.001	-0.001
1833	-93.9	42.16	0.117	0.119	0.095	0.111	0.223	0.179	-0.277	0.059
2550	-96.093656	47.194632	0.083	0.083	0.155	0.127	0.278	-0.464	0.181	-0.057
1645	-91.45	45.3	0.074	0.137	0.088	0.153	0.221	-0.250	-0.662	-0.259
1814	-93.631152	45.034798	0.125	0.126	0.124	0.081	0.260	0.389	0.093	-0.113
245	-93.18333	45.425	0.110	0.110	0.133	0.105	0.333	0.046	0.059	-0.059
2937	-90.08333	45.33333	0.116	0.132	0.112	0.101	0.311	0.248	-0.140	-0.109
26673	-92.066748	46.732492	0.089	0.089	0.178	0.109	0.340	-0.317	0.371	-0.152
274	-93.66667	47.13333	0.123	0.123	0.125	0.095	0.341	0.260	0.021	-0.064
1827	-95.31667	46.96667	0.124	0.125	0.104	0.119	0.375	0.172	-0.264	0.055
10156	-93.559052	44.98797	0.117	0.119	0.118	0.123	0.423	0.049	-0.167	0.015
2849	-91.66	47.47167	0.105	0.105	0.146	0.140	0.533	-0.235	-0.010	-0.008
1979	-95.28417	46.21194	0.144	0.124	0.135	0.095	0.473	0.354	0.108	0.023
478	-93.439296	43.121856	0.119	0.119	0.143	0.117	0.522	0.041	0.037	-0.055
2534	-91.45	44.15	0.117	0.097	0.160	0.126	0.532	-0.162	0.182	0.067
11620	-94.705204	43.67599	0.117	0.117	0.148	0.120	0.543	-0.001	0.052	-0.058
1128	-92.71694	46.41694	0.113	0.142	0.096	0.153	0.501	0.021	-0.557	-0.010
1483	-93.12302	44.77054	0.097	0.123	0.160	0.126	0.550	-0.160	0.043	-0.248
1813	-97.279598	45.496484	0.108	0.156	0.131	0.116	0.542	0.150	-0.182	-0.302
292	-95.16281	47.1774	0.152	0.078	0.183	0.098	0.515	0.044	0.578	0.298
7534	-93.448984	44.774484	0.137	0.101	0.147	0.132	0.618	-0.039	0.082	0.196
1721	-94.756512	46.858288	0.150	0.108	0.152	0.122	0.669	0.105	0.142	0.186
2851	-94.95	46.95	0.115	0.115	0.180	0.125	0.686	-0.105	0.207	-0.115
1676	-97.352702	44.98282	0.123	0.107	0.155	0.150	0.709	-0.187	0.010	0.095
7541	-95.7134	45.6736	0.156	0.153	0.124	0.116	0.691	0.410	-0.172	0.011
6515	-93.66042	46.51172	0.157	0.125	0.161	0.106	0.713	0.296	0.209	0.048
2519	-93.69167	44.89167	0.142	0.142	0.120	0.151	0.752	0.131	-0.328	0.080
1652	-94.944158	47.173866	0.161	0.127	0.178	0.099	0.755	0.339	0.331	-0.001
30329	-90.54762	46.9164	0.078	0.078	0.192	0.221	0.731	-1.003	0.048	0.037
1590	-93.601798	47.284892	0.143	0.161	0.143	0.130	0.833	0.261	-0.149	-0.113
30327	-90.55597	46.92654	0.125	0.125	0.185	0.145	0.880	-0.127	0.116	-0.081
1119	-93.64361	47.13556	0.172	0.143	0.171	0.097	0.808	0.474	0.256	-0.027
10169	-93.574622	45.003678	0.156	0.173	0.120	0.151	0.900	0.307	-0.415	-0.002
7532	-95.6825	44.6159	0.144	0.144	0.170	0.196	1.168	-0.146	-0.194	0.040
2792	-95.30694	46.18444	0.223	0.128	0.179	0.124	1.087	0.429	0.249	0.318
1410	-90.35	45.3	0.162	0.189	0.159	0.212	1.379	0.060	-0.429	-0.033
1510	-92.587352	46.714106	0.131	0.131	0.212	0.274	1.467	-0.592	-0.182	0.070
27281	-92.601862	46.540106	0.168	0.185	0.196	0.231	1.590	-0.058	-0.281	-0.038
266	-94.971068	47.558974	0.229	0.187	0.254	0.126	1.552	0.538	0.381	-0.079

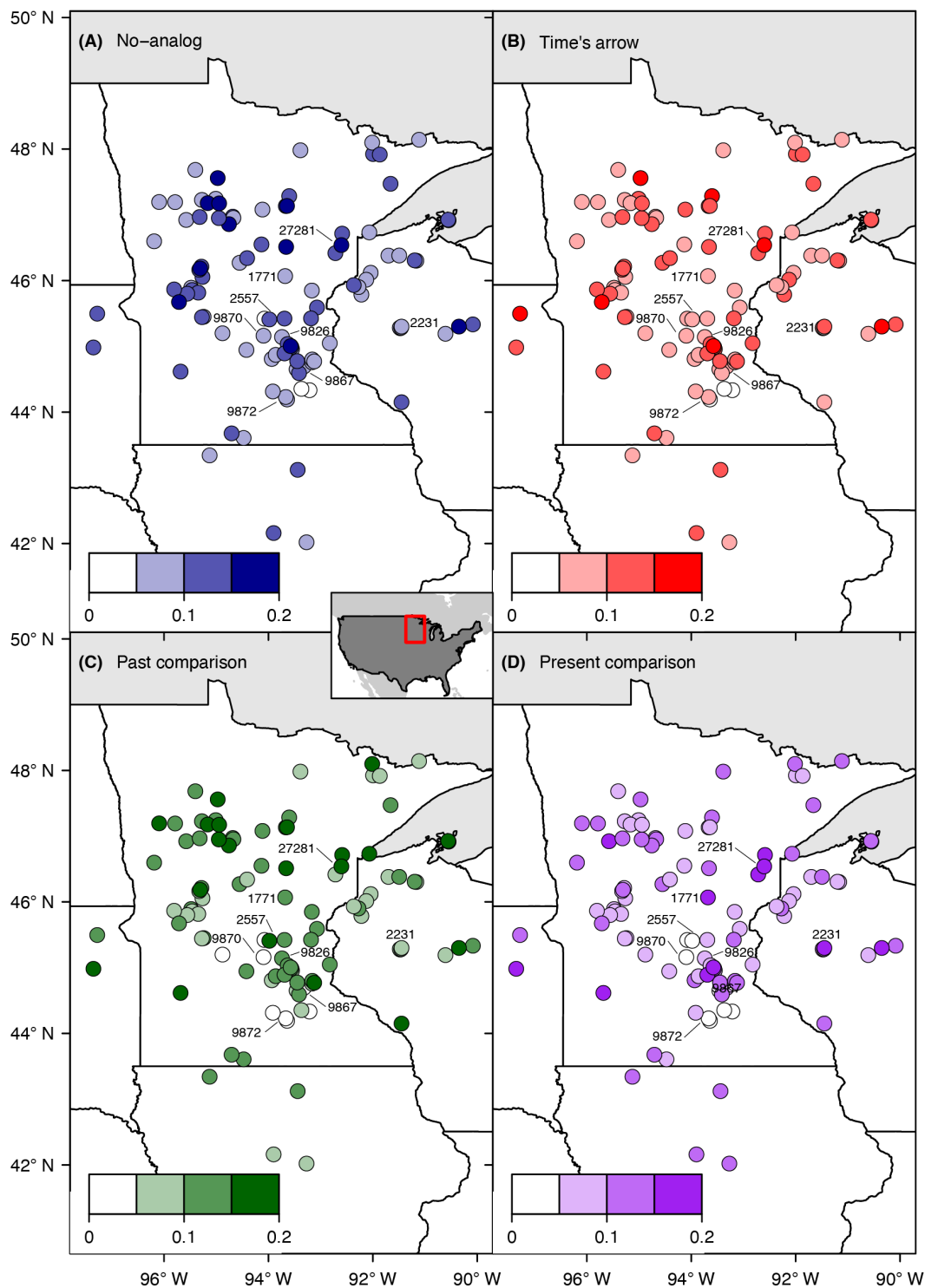


Figure S1: Raw novelty measurements overlaid on study region. Point color represents novelty value. Definitions of each novelty measurement are in Fig. 3 and Table 2. Labelled points are discussed in the main.

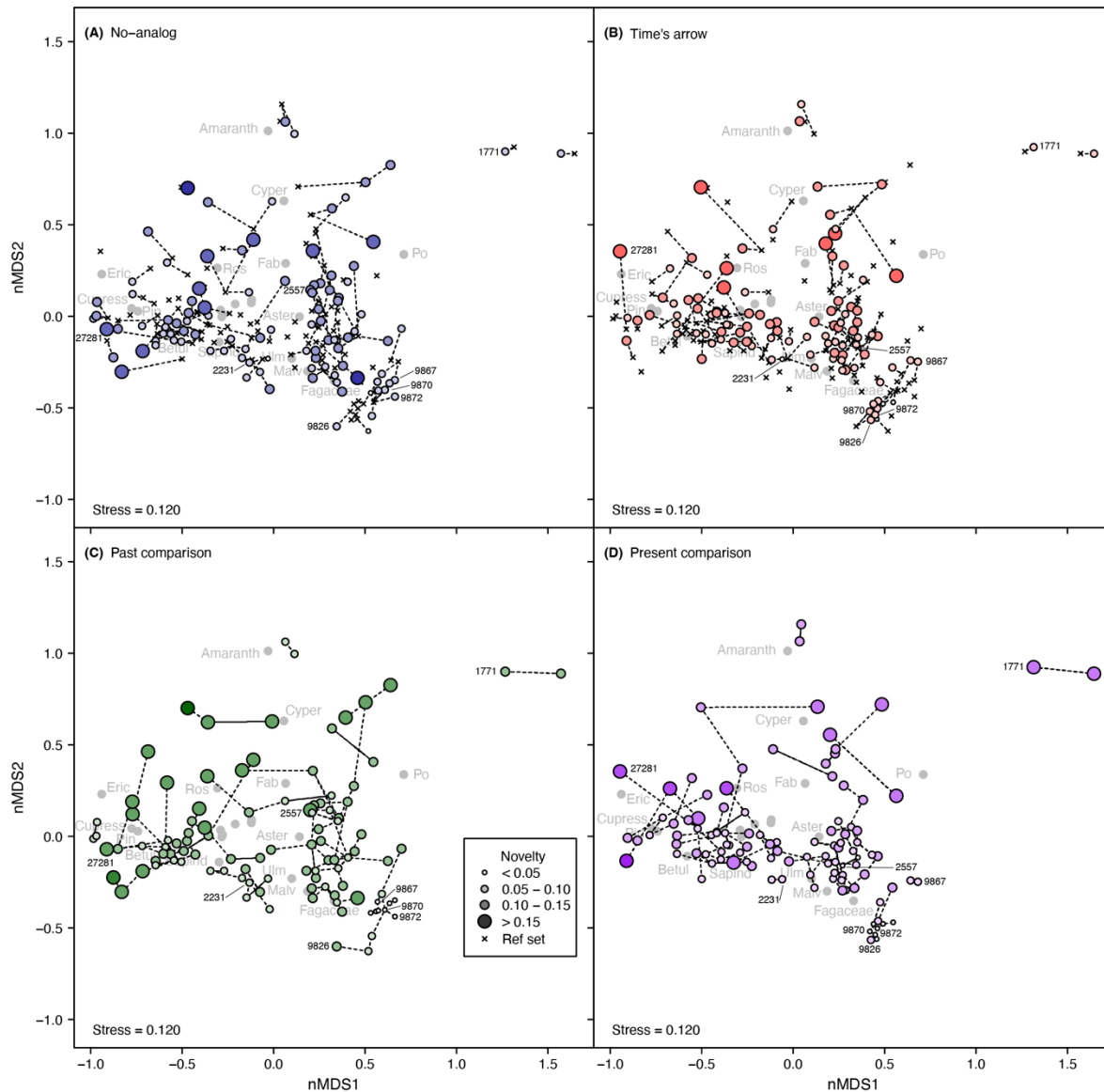


Figure S2: Non-metric multidimensional scaling of pollen assemblages based on family pollen relative abundance. Grey labels and circles are family taxa centroids (Family names have been shortened). Colored points are target entities for each novelty measurement, sized and colored based on novelty value. Crosses are reference set entities for temporal comparisons (A-B): Reference sets in C-D are within-time and reference sets comprised all entities minus each target (in sequence). Dashed lines link each target to the closest reference set entity, used to estimate novelty value in our case study. Labelled points are discussed in the main text.

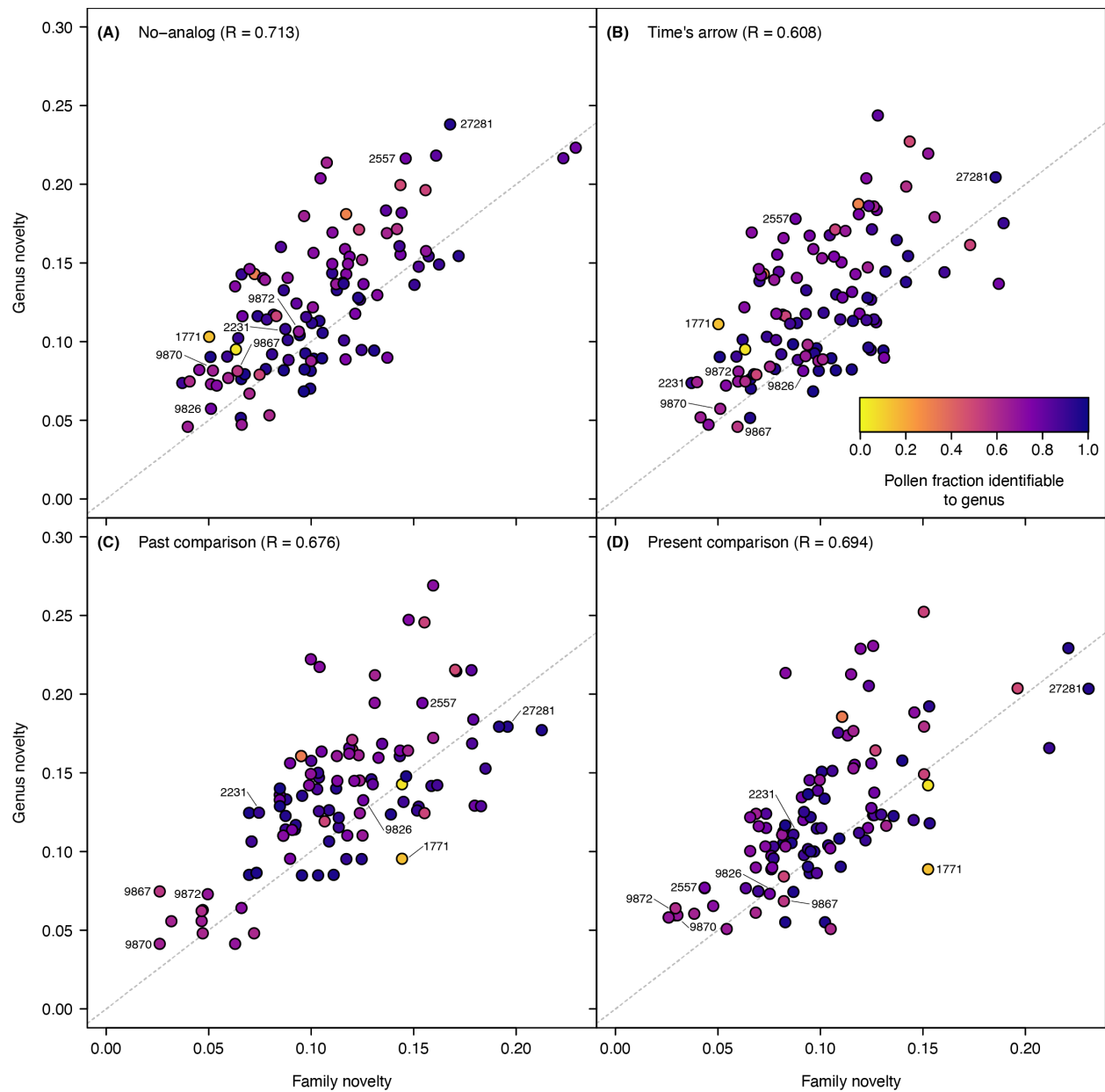


Figure S3: Comparison of four novelty measurements from the case study measured using family and genus pollen IDs. Each point represents a site, with x and y position reflecting family and genus novelty respectively. Point color reflects the fraction of pollen that was identifiable to genus; almost all pollen was identifiable to family. Grey dashed line is a 1:1 novelty line. R values in subplot labels are Pearson's Product Moment Correlation between genus and family novelties.

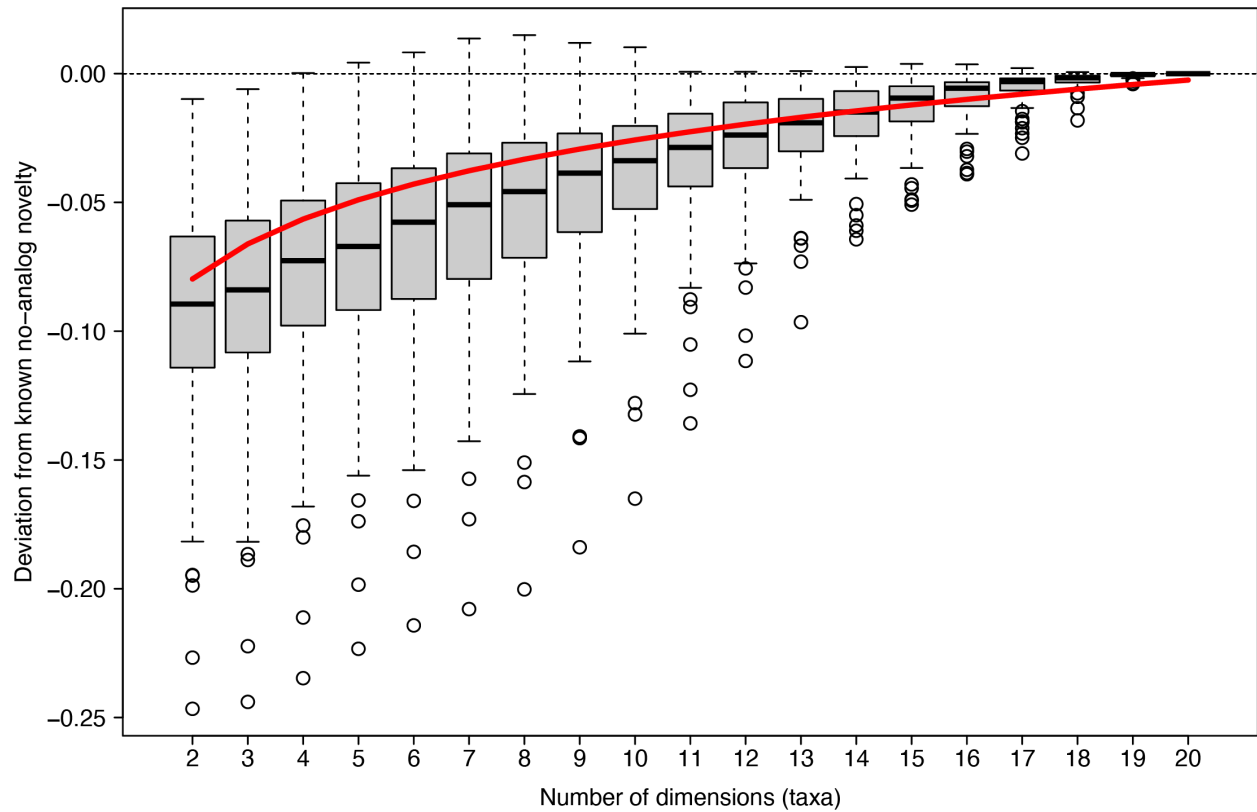


Figure S7: Deviation of novelty measurements from novelty with 20 plant families, when the number of families was restricted. Novelty was “No-analog” measurements, with a past target entity compared to a set of present reference samples, using family-level pollen assemblages from the study area identified in the main text. Novelty was calculated for each site, restricting the number of taxa from two to 20, with taxa order shuffled randomly 999 times. Boxplots are summaries of raw novelty deviations. Red line represents population predictions from a linear mixed effects model of novelty deviation against $\ln(\text{taxa count})$, with each random iteration and each site fitted as crossed random effects (marginal $R^2 = 0.289$, conditional $R^2 = 0.545$).