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# Emergence patterns of novelty in European vegetation assemblages over the past 15 000 years

Walter Finsinger,<sup>1\*</sup> Thomas Giesecke,<sup>2</sup> Simon Brewer<sup>3</sup> and Michelle Leydet<sup>4</sup>

## Abstract

Plant communities are not stable over time and biological novelty is predicted to emerge due to climate change, the introduction of exotic species and land-use change. However, the rate at which this novelty may arise over longer time periods has so far received little attention. We reconstruct the emergence of novelty in Europe for a set of baseline conditions over the past 15 000 years to assess past rates of emergence and investigate underlying causes. The emergence of novelty is baseline specific and, during the early-Holocene, was mitigated by the rapid spread of plant taxa. Although novelty generally increases as a function of time, climate and human-induced landscape changes contributed to a non-linear post-glacial trajectory of novelty with jumps corresponding to periods of rapid changes. Emergence of novelty accelerated during the past 1000 years. Historical cultural landscapes experienced a faster novelty development due to the contribution from anthropogenic land-cover changes.

## Keywords

Biological novelty, EPD, Europe, pollen, post-glacial.

## INTRODUCTION

The inevitable consequence of individualistic changes in species distributions (Gleason 1939) is that modern associations will be reshuffled into substantially different associations with respect to historical and present baseline conditions (Hobbs *et al.* 2009, 2014) through several mechanisms. Parts of the modern climate space may disappear and currently unavailable portions of the climate space may unfold, thereby potentially restricting suitable habitats for species lacking a pre-adaptation to abiotic novelty in climate conditions (Williams & Jackson 2007; Reu *et al.* 2014; Ordonez *et al.* 2016). Rapid rates of climate change could cause biological novelty, if suitable climate space shifts across the landscape faster than species dispersal velocity (Jackson & Overpeck 2000; Ordonez *et al.* 2016). Rates of change in radiative forcing by greenhouse gases during the 20th century already have exceeded any rates sustained during the past 22 000 years (Joos & Spahni 2008) and rates of climate change are predicted to exceed those experienced by ecosystems during the past 20 000 years (Diffenbaugh & Field 2013). In addition to the effects of climate change, human agency is considered the major driver of the rise of novelty today (Radeloff *et al.* 2015) due to widespread landscape management, the spread of alien invasive species, and land-use.

Vegetation models can be used to predict the emergence of biotic novelty (Reu *et al.* 2014). However, the predictive power of vegetation models to forecast the reshuffling of species into novel associations in future novel climate

combinations may be rather limited (Williams & Jackson 2007). Whether or not climate change propagates into the recombination of species may depend on the extent of their fundamental niches rather than on their modern realized niches, which are at the basis of most vegetation models (Reu *et al.* 2014). This difference between modern realized and fundamental niches might arise from the different climate space available at present-day, and from the effects of competition among species and actual disturbance regimes (Jackson & Overpeck 2000). Additionally, in some parts of the species' range populations were favoured or became locally extinct due to land-use pressure and anthropogenic disturbance (Bradshaw & Lindbladh 2005; Tinner *et al.* 2013). Further, vegetation models are constrained by a limited set of environmental variables, and the effects of, for example, land-use changes and disturbances by wildfires are not fully implemented (Reu *et al.* 2014; Radeloff *et al.* 2015).

The large majority of studies attempting to reconstruct the emergence of novelty are limited to relatively short time periods, typically no longer than a few centuries from past baselines to the present (Hobbs *et al.* 2009; Radeloff *et al.* 2015). Therefore, the long-term dynamics of emergence of biotic novelty and the relationships to rates of environmental change are largely unknown. However, understanding the dynamics of novelty emergence has fundamental implications for ecology, evolution and conservation (Jackson & Overpeck 2000; Jackson & Williams 2004), as it relates to the broader question of whether species associations persist over time or are ephemeral. Several open questions were recently discussed by

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Jackson (2013) including: does novelty always increase as a linear (or curvilinear) function of time from the observer, such that novelty is always high far in the future? Is novelty related to rates of environmental changes, such that it rises at times of high rates of environmental change? Can human agency accelerate the processes that lead to the rise of novelty?

Pollen records document vegetation composition changes on centennial to millennial timescales. These archival records suggest that ecological change is a key feature in a world of continual environmental flux (Jackson & Overpeck 2000) and palaeoenvironmental databases (Brewer *et al.* 2016) shed light on the dynamics of vegetation change at subcontinental scales (Huntley & Birks 1983; Williams *et al.* 2013). The pattern of European land-cover change is increasingly well documented by fossil pollen records (Brewer *et al.* 2016) and the representation is being refined using quantitative assessments (Gaillard *et al.* 2010). These pollen records demonstrate that late-glacial to early-Holocene climatic changes triggered the spread and expansion of plant populations (Birks & Ammann 2000; Williams *et al.* 2002). The clearance of European forests for agriculture, fuel and industrial resources started during the mid-Holocene and progressed over millennia (Fyfe *et al.* 2015), reaching the lowest tree cover during the 18th century (Millennium Ecosystem Assessment 2005). Factors that are expected to cause a rise of biological novelty in the future have also acted in the past. For example, the high within-site rates of vegetation change (RoC) associated to the post-glacial spread of plants and to past anthropogenic land-cover changes (Huntley 1990; Seddon *et al.* 2015), often coupled to the spread of agriculture may be compared to the currently observed spread of alien species and land-use changes. Based on this, we use the fossil record to investigate the long-term temporal and spatial patterns of emergence of novelty and its relations with RoC.

The degree of dissimilarity between contemporary and fossil pollen assemblages has been extensively investigated for a number of regions (Overpeck *et al.* 1985; Huntley 1990; Bush *et al.* 2004). Many of these studies revealed the past occurrence of pollen assemblages without close modern counterparts ('no-modern analogues'), thereby supporting Gleason's (1939) inferences on the individualistic range dynamics (Matthews 1996) and replacing, as previously suggested (Davis 1981), the static view of coevolved plant communities.

But, rather than looking into the past with the eyes of a modern observer, here, we look forward from the past to reconstruct the long-term emergence of novelty, enabling comparisons between past and recent rates of novelty emergence. Given the presumed relationships between rates of environmental change and novelty (Jackson & Overpeck 2000; Radeloff *et al.* 2015), we expect that the rate at which novelty arises is faster at times of rapid environmental changes, such as those characterizing the late-glacial to interglacial transition and the late-Holocene anthropogenic land-cover changes, which led to high rates of vegetation change (RoC) (Huntley 1990; Seddon *et al.* 2015). Smaller amplitude Holocene climate variations (NGRIP Members 2004) and the more gradual and site-specific impact of earlier human-induced landscape changes are expected to have given rise to slower emergence of novelty.

## MATERIALS AND METHODS

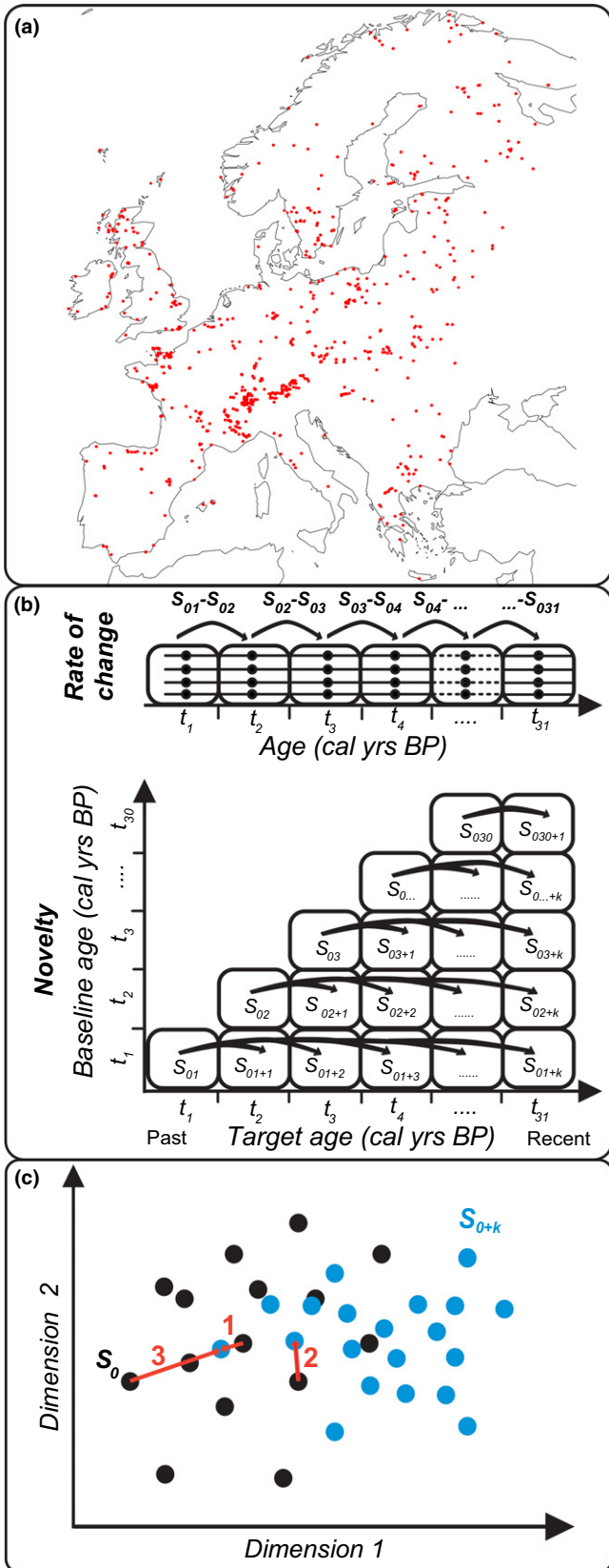
We define biological novelty as the degree of dissimilarity between entities (here pollen assemblages) in a baseline set and their closest counterpart in future target sets (Radeloff *et al.* 2015). Hence, across-site 'novelty' as defined here is distinct from within-site 'vegetation change' (RoC), because places that change the most are not necessarily the most novel (Radeloff *et al.* 2015): a similar pollen assemblage may be found at any time in a different region due to range shifts of taxa.

To explore the novelty dynamics relative to past baseline conditions, we use a compilation of  $M = 772$  pollen records (Fig. 1a) from the European Pollen Database (EPD) (Brewer *et al.* 2016) with associated age information based on calibrated-age-scale chronologies (cal BP; where 0 cal BP = AD 1950) and metadata (Appendix S1). For each record, we extracted pollen counts of the 43 most important terrestrial pollen taxa (Table S1) and collated the counts into  $N = 31$  consecutive 500-year wide age bins centred on full 500-year intervals between 15 000 and 0 cal BP (see Appendix S1). Collated counts were converted to proportions based upon the pollen sum of the 43 terrestrial pollen taxa. Thereafter, all data in each of the 30 age bins from 15 000 to 500 cal BP was considered as a data set describing the 'baseline conditions' ( $S_{0n}$ ) at a given time in the past ( $t_{0n}$ ; with  $n = 1, \dots, 30$ ), and for each baseline system, we built a series of 'target datasets' ( $S_T = \{S_{0n+1}, \dots, S_{0n+k}\}$ ; with  $k = N-n$ ) as the sets of all samples from all records for a given time that post-date the baseline. These represent the set of all 'future' systems from that baseline, and allow us to assess novelty in both time and space (Fig. 1b).

We use the chord distance (CD) as a measure for dissimilarity between pollen assemblages (Overpeck *et al.* 1985; Williams & Jackson 2007) to estimate within-site RoC and across-site novelty (for results obtained with other dissimilarity coefficients see Appendix S1). RoCs were computed as CD scores within each record between consecutive age bins [between  $S_{0n}$  and  $S_{0n+j}$ ; as CD scores  $\times (500 \text{ years}^{-1})$ ] (Huntley 1990). Across-site novelty was estimated iteratively between each  $S_{0n}$  baseline and each  $S_T$  target system in the future of  $S_{0n}$  (Fig. 1b). To estimate the degree of novelty, we used the analogue-matching technique (Overpeck *et al.* 1985), which for each record  $i$  in  $S_{0n}$  identifies among all records in the selected  $S_T$  dataset the record  $j$  giving the smallest CD score ( $CD_{ij, \min}$ ; i.e. the closest analogue) (Radeloff *et al.* 2015) (Fig. 1c).

Novelty is a continuous variable, while the categorical differentiation of 'novel' vs. 'non-novel' ecosystems has proven difficult theoretically (Aronson *et al.* 2014). We focused here on patterns of novelty rather than trying to strictly delineate novel vs. non-novel ecosystems, but used the  $n$ th percentile of all  $CD_{ij, \min}$  scores as a threshold to assess at what point novelty (the  $CD_{ij, \min}$  score) is large enough to represent a genuinely novel assemblage (see Appendix S1).

We extracted the geographical coordinates of the records to compute the displacement distance (km) on a geodetic ellipsoid between the location of each record  $i$  and its closest counterpart  $j$ , and divided that by the age difference between  $S_{0n}$  and  $S_T$  to estimate the average velocity of displacement ( $\text{km year}^{-1}$ ) to the closest analogue in the target set.



**Figure 1** Schematic representation of the theoretical approach used in this study: (a) Spatial distribution of EPD pollen records (red circles) used in this study. (b) A data set ( $S_{0n}$ ) comprising pollen assemblages that characterize vegetation for a 500-year long snapshot is considered as representing ‘average baseline conditions’ at time  $t_{0n}$ . Rate of vegetation change within sites was calculated as chord distance (CD) between datapoints of the same site in consecutive time slices (i.e. for all  $S_{0n}-S_{0n+1}$  couplets). To reconstruct the long-term dynamics of novelty emergence, the system  $S_{0n}$  is iteratively compared to each of the 500-year wide ‘target systems’ ( $S_T = \{S_{0n+1}, \dots, S_{0n+k}\}$ ) in its contingent futures (where  $S_{0n+k}$  describes near-to modern conditions, i.e. 0 cal BP). (c) The degree of novelty is quantified as the minimum CD distance ( $CD_{ij,min}$ ) between entity  $i$  of the baseline set and the closest counterpart  $j$  in the target set in a multivariate space. In the example in (c), samples are plotted in a reduced space (axes 1 and 2), black dots indicate entities of  $S_{0n}$ , blue dots indicate entities belonging to a target set  $S_{0n+k}$ , and red arrows indicate the minimum distance ( $CD_{ij,min}$ ) between entities of the two sets. Entities 1–3 experienced increasing degrees of novelty (modified from Radeloff *et al.* 2015).

RoC and across-site novelty at time lags equal to 500 years from baseline conditions. We binned and differenced the Greenland  $\delta^{18}\text{O}$  record (NGRIP Members 2004) to represent large-scale climate changes, and used linear mixed-effect models to explore the responses of RoC and novelty to the climate changes for the time periods before and after 8ka BP (see Appendix S1). We partitioned the within-site and the site-to-site variances to estimate the level of variability in site responses. To illustrate the geographical distribution of RoC and novelty at lags +500 years, we produced gridded maps of RoC and  $CD_{ij,min}$  values grouped into quartiles for selected baseline ages. Values for grid cells of  $50 \times 50$  km were obtained by application of a tricube distance-weighting function with a horizontal search radius of 300 km.

To illustrate the temporal dynamics of novelty emergence for each baseline system  $S_{0n}$ , we computed for each set of baseline-to-target couplet ( $S_{0n} - S_T$ ) the median degree of novelty ( $CD_{ij,min}$ ), the median distance (in km) and the median displacement velocity (in  $\text{km year}^{-1}$ ) to the closest analogue. We estimated the rate of novelty change as the difference between median novelty values for consecutive  $S_T$  systems (as median novelty  $\times 500 \text{ years}^{-1}$ ). These variables are arranged in triangular matrices with dimensions of  $15 \times 15$  and were represented graphically using heat maps.

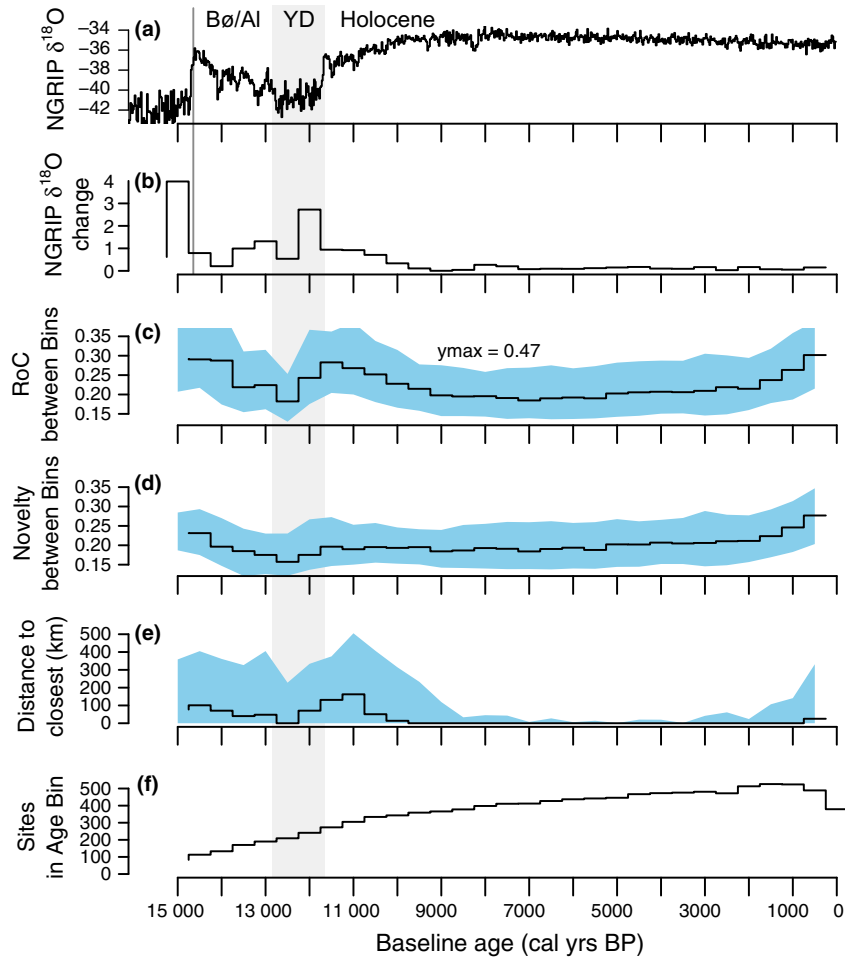
All data analyses were carried out using the R statistical language and associated packages (see Appendix S1).

## RESULTS

### Rates of vegetation change and novelty between consecutive time slices

Median RoC scores are highest ( $> 0.2$ ) during the Bølling, the early-Holocene (from 11 500 to 10 000 cal BP) and the past 1500 years (Fig. 2c), indicating that these are the periods with highest within-site rate of vegetation change. Lowest values are detected when evaluating within-site vegetation change from 12 500 to 12 000 cal BP and during the mid-Holocene (9000–5500 cal BP).

Based on the values obtained above, we calculated median RoC and novelty scores for each  $S_{0n}$  to  $S_{0n+1}$  couplet to detect periods characterized by overall higher within-site



**Figure 2** Comparison between (a) Greenland oxygen-isotope ( $\delta^{18}\text{O}$ ) record (NGRIP Members 2004) as a template of climate change over Europe [plotted on the GICC05 age scale (Rasmussen *et al.* 2014)], (b) difference between average of binned  $\delta^{18}\text{O}$  values among consecutive age bins as a template of rate of climate change, (c) median rate of vegetation change (RoC) within sites between consecutive age bins (note that  $y$ -axis was cropped between 0.375 and 0.47 CD), (d) median degree of novelty across sites between consecutive age bins, (e) geographical distance to the closest analogue in time slice +500 years relative to the baseline conditions, (f) number of records included in each time slice. The blue-shaded areas: range of values between the first and third quartiles within each age bin, and the vertical grey-shaded area marks the Younger Dryas (YD). Bø/Al: Bølling/Allerød.

The closest analogues were allowed to occur in any of the sites of the target dataset, including the same site. This allows a check as to whether the closest analogues occur within the baseline sites. In this case, the RoC and novelty scores would be equivalent, which they are not (Fig. 2). Compared to RoC, the median and the quartile novelty scores are equally elevated for the last 9000 years, while they are lower for the late-glacial, and the early- and late-Holocene indicating that in those periods the baseline assemblages and the closest analogues are not from the same sites. This is confirmed by the geographical distances to the closest analogue (Fig. 2d), which are high during the late-glacial, the early-Holocene, and the late-Holocene. The highest distances to the closest analogue are found for the early-Holocene, while novelty is relatively low for the same period. By contrast, baseline assemblages between 8000 and 2000 cal BP have lowest geographical distances to the closest analogue. Varying site density (Fig. 2f) has no significant effects on the displacement–distance trends (see Appendix S1).

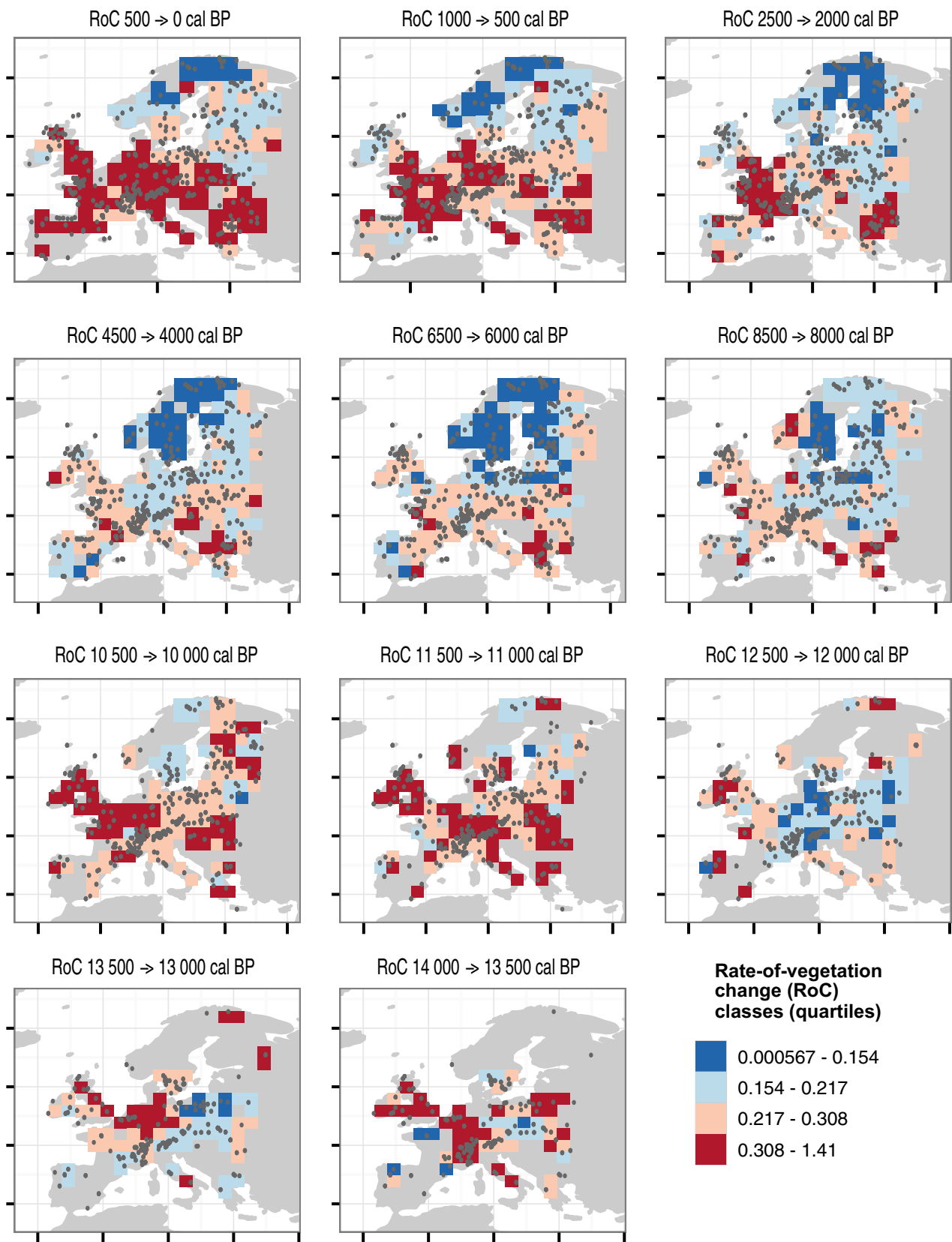
Linear mixed-effect models show significant relationships between climatic changes (differenced NGRIP  $\delta^{18}\text{O}$  values)

and RoC and novelty for both pre-8ka and post-8ka periods. However, the relationships are strongest for RoC in the pre-8ka BP period (see Appendix S1). This can be further seen in the variance components of the models, with a larger amount of variance explained within sites (*c.* 88%) for RoC pre-8ka BP, than in the other models (*c.* 54–67%), indicating higher spatial variability in RoC response post-8ka BP, and novelty in both periods.

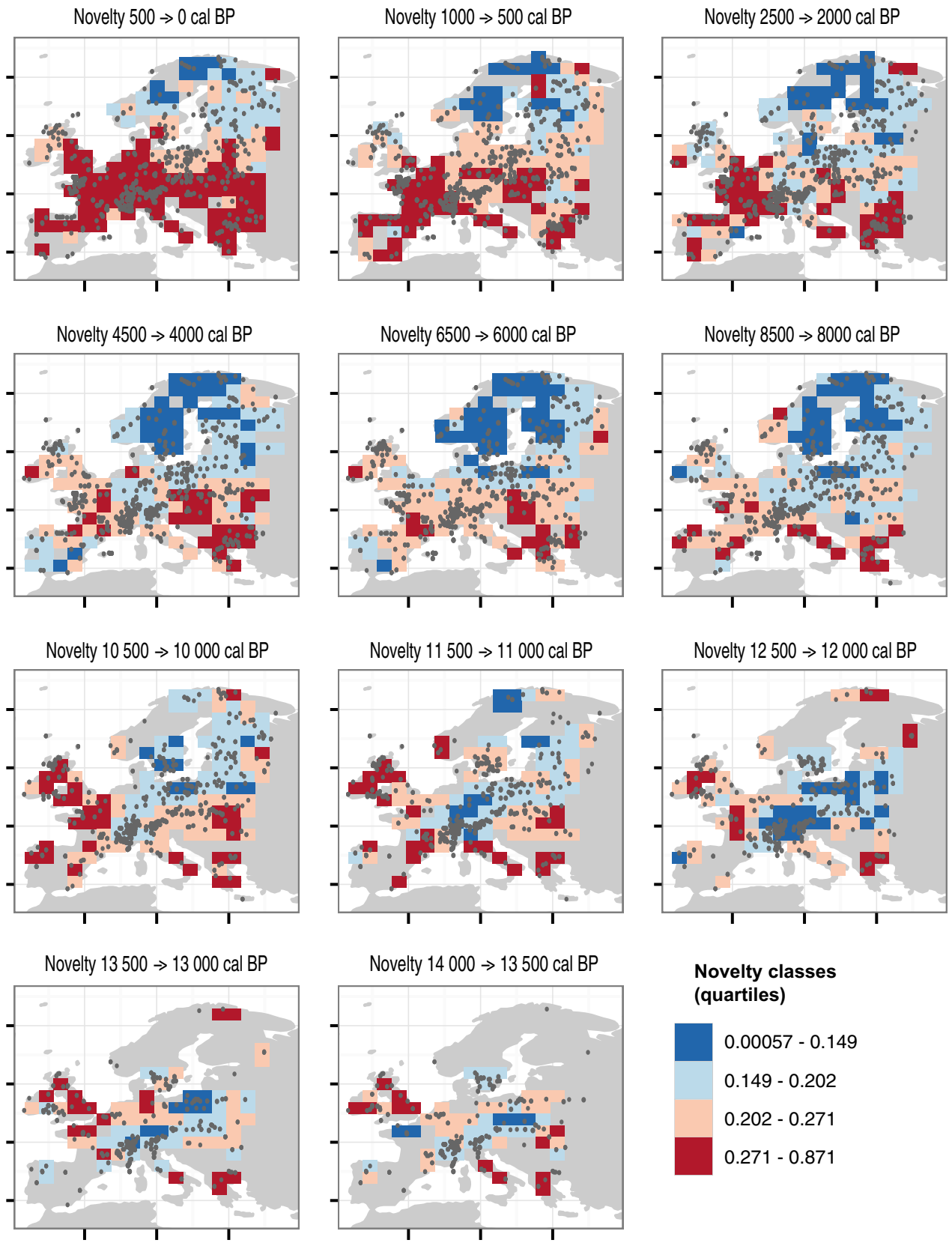
The spatial distribution of RoC and novelty scores (Figs 3 and 4) shows stable vegetation composition in northern Europe vs. continuous change further south for the last 9000 years. Similarities between the two assessments of compositional change are also seen for the Younger Dryas. In contrast, early-Holocene novelty is relatively low in central Europe while RoC values are high.

#### Long-term emergence of novelty relative to past baseline conditions

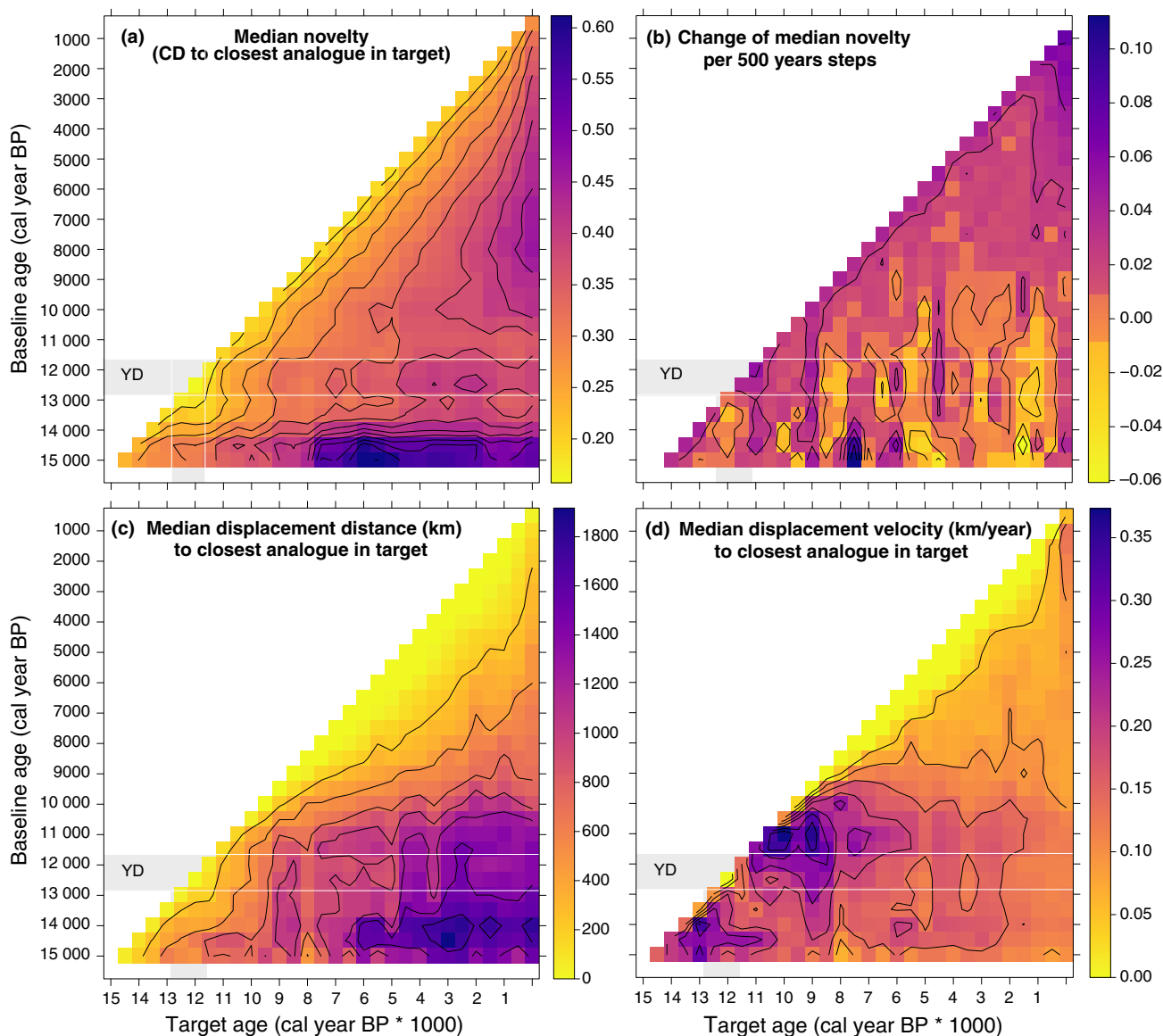
To illustrate the emergence of novelty from the virtual perspective of an observer living in the past, we summarized the



**Figure 3** Gridded maps illustrating for selected baseline time slices the spatial patterns of rates of vegetation change (RoC) for consecutive time slices (baseline age → target age).



**Figure 4** Gridded maps illustrating for selected baseline time slices the spatial patterns of novelty emergence for consecutive time slices (baseline age -> target age).



**Figure 5** Summary heat maps showing, for each past ‘baseline dataset’ (*y*-axis), (a) the median degree of novelty, (b) the change in median novelty per 500 years step (to highlight negligible changes, values around the zero (+5% and –5% of the total range) were grouped together), (c) the median displacement distance (km), and (d) the median displacement velocity (as  $\text{km year}^{-1}$ ) to the closest counterpart in the ‘target dataset’ (*x*-axis). Grey-shaded area marks the Younger Dryas (YD).

novelty scores using the median value for each baseline-to-target couplet (Fig. 5a). For every baseline, the development of novelty in its contingent futures can be followed moving along the *x*-axis. Hence, the squares along the diagonal represent the median novelty for a single 500-year time-step from the baseline, as plotted in Fig. 2d.

Median novelty to the nearest counterpart in target bins often increases as time from baseline increases (Fig. 5a). However, for some baselines median novelty decreases, in other words novelty ‘cycled backward’. Hence, novelty does not increase as a constant, linear function of time from baseline conditions, and different trajectories can be discerned depending on the composition of baseline pollen assemblages. Contour lines (Fig. 5a), separating median novelty values at equal intervals, are sometimes packed together as a result of steeper

increases of median novelty indicating more rapidly reshuffling of communities that were present in the baseline sets. Conversely, when median novelty levels off, contour lines are stretched further apart. For example, early-Holocene baseline landscapes found similarly close counterparts in mid-to-late-Holocene targets, and several late-glacial baselines had more dissimilar counterparts in the mid-Holocene than in late-Holocene targets. These novelty-emergence trends are mirrored by the proportion of sites experiencing a relatively high across-site turnover that is broadly comparable to present-day vegetation turnover between biomes (see Appendix S1).

To highlight the changes of novelty through time, Fig. 5b shows the rate of novelty change between consecutive target systems. For most baselines younger than 7000 cal BP, median novelty continuously increased and jumped when



compared to target sets younger than 1000 cal BP. For earlier baselines, the trajectory of novelty development is more variable, including distinct jumps at 11 000 and 9000 cal BP, strongest backwards cycling centred around 1000 cal BP, and levelling off or decreasing novelty during the late-Holocene.

The median displacement distance to the closest analogues in target sets (Fig. 5c) generally increases as a function of time and the highest median displacement distances (> 1200 km) are found when considering late-glacial and early-Holocene baselines and late-Holocene targets. Lowest median displacement distances (< 200 km) lasted longer for mid- and late-Holocene baselines than for most late-glacial baselines, and the highest median displacement velocities (ca. 0.3 km year<sup>-1</sup>) are displayed for early-Holocene baselines (Fig. 5d). Varying site density (Fig. 2f) has no influence on the displacement–distance trends (Appendix S1).

Median displacement velocities between closest analogues at the two endpoints of the baseline–target couplets, show opposite long-term trends (Fig. 5d). Long-term velocity decreases for late-glacial and early-Holocene baseline assemblages, indicating that the fastest shifts occurred shortly after baseline conditions, whereas later shifts were slower. By contrast, mid- and late-Holocene baseline assemblages experienced gradually increasing velocities, because closest analogues were found initially closer to the site. An increase in displacement velocities characterizes all late-Holocene baselines younger than 4000 cal BP when compared to target sets of the past 1000 years, indicating that an acceleration of displacement velocities occurred.

## DISCUSSION

Until now, analyses of novelty emergence have been limited to short time periods from past baselines to the present (Hobbs *et al.* 2009; Radeloff *et al.* 2015). Here, we sampled the fossil pollen record over a *c.* 15 ka time scale to investigate how novelty was related to RoC at time lags of 500 years, and reconstruct the longer term emergence of novelty in different snapshots of the contingent futures for several baselines in the past. Our results provide new insights into several key aspects of novelty development in relation to environmental changes. We show that (1) the largest rise in RoC at the beginning of the Holocene was not associated with rising novelty because the spread of plants mitigated the effects of short-term rates of environmental changes on novelty emergence, (2) novelty rose fast with human land-use, and land-use change had a greater effect than post-glacial climatic changes, (3) although novelty generally increases as a function of time, its temporal emergence followed baseline-specific trajectories, and (4) emergence of novelty accelerated due to the contribution of anthropogenic land-cover changes.

We considered the emergence of novelty as a pervasive and continuous process (Radeloff *et al.* 2015) and avoided categorizing novelty as a binary variable (e.g. ‘novel’ vs. ‘non-novel’). Nevertheless, using the 75th and 95th percentiles of all  $CD_{ij,min}$  distances for all baselines and all target sets as thresholds to determine the abundance of genuinely novel counterparts (Appendix S1) yields the same patterns as the median degree of novelty (Fig. 5a). Therefore, median novelty

is a representative estimate of baseline assemblages experiencing genuinely novel conditions, i.e. shifts in vegetation composition in the order of magnitude of present-day turnover between vegetation types or biomes. Other thresholds would lead to correspondingly larger or more restricted estimates of the area of novel ecosystems, but the spatiotemporal patterns of novelty (Figs 4 and 5) would remain unchanged.

## SHORT-TERM EMERGENCE OF NOVELTY IN RELATION TO RATES OF VEGETATION CHANGE

At the scales considered here, we found a strong association between novelty and RoC, both temporally (Figs 2b and c) and spatially (Figs 3 and 4). High rates of environmental changes have been advocated as a potential cause of higher novelty based on the assumptions that (1) favourable climatic conditions may shift across the landscape faster than species disperse into new areas of suitable climate space (Jackson & Overpeck 2000; Ohlemüller *et al.* 2006), and that (2) land-use pressure induced habitat transformation, habitat fragmentation and spread of alien invasive species may promote the reshuffling of species into novel ecosystems (Radeloff *et al.* 2015). While we did not estimate post-glacial velocities of climatic change (Ordonez & Williams 2013) or anthropogenic-induced rates of environmental change, highest rates of environmental change occurred when RoC scores were high (Fig. 2c): (1) during the late-glacial and the early-Holocene, which were characterized by pronounced and frequent changes in vegetation composition (Birks & Ammann 2000; Giesecke *et al.* 2011) and in climatic conditions (Fig. 2b), and (2) during historical times, with the increase in human populations and accompanying land-use (Huntley 1990; Seddon *et al.* 2015). However, the magnitude of the responses varied, as novelty was generally lower than RoC scores (Fig. 2c and d and legends to Figs 3 and 4). Based on linear mixed models, climate change is a stronger predictor for within-site variation in RoC, while the novelty response displays a larger between-site variance (see Appendix S1). These patterns suggest that novelty and RoC may differ in the degree at which they respond to environmental changes, and that across-site novelty varies at a slower pace than the location-specific vegetation changes. The underlying causes of lower novelty might be best illustrated considering the early-Holocene time period, when the association between RoC and novelty was weakest (Fig. 2c and d) and changes in RoC and novelty had a significant positive relationship with  $\delta^{18}\text{O}$  changes (see Appendix S1). This period was marked by highest geographical distances to closest analogues (Fig. 2e) and by high rates of spread of early-successional plants, such as *Pinus*, *Betula*, *Ulmus* and *Corylus* (Feurdean *et al.* 2013). Therefore, we interpret the low early-Holocene emergence of novelty as the consequence of the rapid post-glacial range shifts of taxa. The vegetation composition changed rapidly at most locations, as shown by the highest within-site variance in the linear mixed-effect models for RoC pre-8ka BP (see Appendix S1). Hence, the high rates of spread meant that replacement by low-novelty counterparts occurred across the landscape, thereby reducing the novelty. This finding is at odds with the assumption that favourable climatic conditions can shift across the

landscape faster than species disperse into new areas of suitable climate space (Jackson & Overpeck 2000; Ohlemüller *et al.* 2006).

It is difficult to say if rates of spread will mitigate the emergence of novelty in the future. Our estimates of early-Holocene median displacement velocities (*c.* 0.35 km year<sup>-1</sup>; Fig. 5e) are consistent with predicted mean climate velocities for the temperate broadleaf and mixed forests biome (Loarie *et al.* 2009) and with climate-displacement estimates for the past century (Ordonez *et al.* 2016). However, it is possible that such high rates of spread were limited to the particular environmental conditions encountered during the early-Holocene. At that time, landscapes were fairly open and dominated by early-successional pioneer taxa spreading fast as a result of their life-history strategies (fast growth, large seed production, good dispersal), and greater stress tolerance to large amplitude temperature change and drought (Bhagwat & Willis 2008). Competition was probably low, and even later-successional taxa with heavy seeds like *Quercus* reached high rates of spread (Giesecke 2016).

The median novelty for recent target sets exceeds the background of post-glacial novelty (Fig. 2). Over the Middle Ages and the Industrial Revolution, land-cover changes associated with booming human population and agriculture became major determinants for vegetation changes, particularly in Southern and Central Europe (Kaplan *et al.* 2009; Gaillard *et al.* 2010). Pasture grassland and arable or disturbed land increased, which led to a decrease in forest cover (Fyfe *et al.* 2015). Moreover, cultural landscapes became ever more characterized by forest-management practices, and by introduced or cultivated trees for wood and food production (Conedera *et al.* 2004). The finding of strongest novelty rise for these target sets thus demonstrates that in Europe the effects of land-use were more important than post-glacial climatic changes for the emergence of novelty at a time lag of 500 years.

We found lower novelty, thus more persistent analogy with their future closest counterparts, for late-Holocene Fennoscandian sites than for Central and Southern European sites (Fig. 4). These spatial patterns are at odds with vegetation-modelling results (Reu *et al.* 2014), which predict higher biological novelty in eastern Scandinavia based only on the effects of abiotic factors. By contrast, our findings are consistent with prior results that inferred lower novelty in Fennoscandia based on the effects of abiotic factors plus human population for historical to modern (AD 1900–2000) and for modern to projected (AD 2000–2050) baseline-to-target couplets (Radeloff *et al.* 2015). Hence, our results support the view that land-use adds complexity to the modelling of future biological novelty that should be accounted for in analyses of the probability of future effects of climate forcing and land-use change scenarios (Ordonez *et al.* 2014). Yet, at these short-term time lags, most baseline sites did not encounter genuinely novel assemblages (see Appendix S1).

### Long-term emergence of novelty

To our knowledge, this study is the first to separately analyse the long-term emergence of novelty for a large set of pre-historical and historical baselines. Our data show that novelty

often increases as a function of time from the virtual perspective of an observer living in the past (Fig. 5a), and thereby confirms earlier theoretical considerations (Jackson 2006, 2013) that were based on the evidence of the rather recent emergence of some modern ecosystems, and the occurrence in the past of no-modern analogue vegetation assemblages (Overpeck *et al.* 1992; Jackson & Williams 2004). However, we found that the emergence of novelty followed different, baseline-specific trajectories (Fig. 5a), confirming the view that it is only meaningful to talk about levels of novelty relative to a specific temporal baseline (Radeloff *et al.* 2015).

We found that novelty did not develop as a constant, linear function of time from past baseline conditions (Fig. 5b), which would imply a gradually changing world with steadily accumulating changes (Jackson 2013): evidence of novelty jumps occurring several millennia after baselines at times of rapid environmental changes indicate an accelerated reshuffling of vegetation composition across sites. The most distinct of all novelty jumps occurred around 8000 cal BP for Bølling baseline conditions (Fig. 5b). At that time, most of the open pine- and birch-dominated woodlands that characterized the Bølling landscapes of Western and Central Europe had gone. Further, European forest cover was overall at its Holocene maximum, although regional variability accounts for slightly shifted timing of maximum forest cover (Fyfe *et al.* 2015). In Central Europe, both *Fagus* and *Abies* expanded and compositional changes occurred probably in response to shifting climatic modes around 8200 cal BP (Tinner & Lotter 2006). While this requires further investigation, it offers an example of how terrestrial ecosystems respond to non-linear environmental changes.

Our data indicate that environmental changes related to anthropogenic land-cover changes accelerated the emergence of novelty. Because novelty increased faster during the past millennium relative to baselines younger than 6000 cal BP (Fig. 5b), we interpret the jumps at 1000 cal BP as the consequence of the rapid emergence of pre-industrial and industrial cultural landscapes (Kaplan *et al.* 2009; Fyfe *et al.* 2015). As increasing median displacement velocities to closest analogues are associated with this acceleration (Fig. 5d), it shows that anthropogenic land-cover changes were spatially widespread.

Conversely, we found backwards cycling of novelty (i.e. the transition from high to less novelty) between late-glacial baselines and late-Holocene targets, and a levelling-off of novelty between early-Holocene baselines and late-Holocene targets (Fig. 5a). Jackson (2013) hypothesized the possibility of backwards cycling of novelty with glacial–interglacial cycles, based on the qualitative evidence that last glacial maximum environments and vegetation would have been more similar to those of other glacial maxima than to the interglacial periods. By contrast, because the late-Holocene vegetation composition changes and forest-cover reductions in Europe are mostly attributed to land-use intensification and forest clearance (Henne *et al.* 2013; Fyfe *et al.* 2015), our results imply that novelty cycled backwards or levelled-off due to the contribution of land-use changes. Similar observations were made comparing early-Holocene assemblages from Central Italy to modern pollen assemblages (Finsinger *et al.* 2010).

The somewhat surprising finding of backwards cycling and of non-increasing novelty from late-glacial and early-Holocene baselines to pre-industrial cultural landscapes may be partly due to the low pollen-taxonomical resolution within herbaceous plant genera, which reduces our ability to distinguish pollen assemblages produced by different species compositions (Jackson & Williams 2004). An alternative, or additional, explanation is that Europe went from a late-glacial and early-Holocene steppe-dominated continent with groves of trees to a widely deforested landscape with extensive pastures, fields, heaths, maquis, settlements and secondary forests (Birks & Tinner 2016). The steppe elements became abundant again with the clearance of the forest for agriculture and form today's ruderal flora with only minor additions of archaeophytes that came with the import of seeds from the Near East. As a result, Allerød and early-Holocene baselines have high analogy (low novelty) to past and modern remnants of the steppe and boreal forests, which persisted in Europe throughout the Holocene and were displaced at increasing distance from the source locations (Fig. 5c).

Under some scenarios, a backwards cycling might be expected to occur in the future. Although Europe is still considered the continent with the smallest fraction of its original forests remaining (Millennium Ecosystem Assessment 2005), forest cover in Europe has increased during the last century due to the abandonment of agropastoral activities in economically marginal areas and the establishment of nature reserves (European Environment Agency 2016). If the current reforestation trend will continue in spite of the growing predicted land-use pressure (Montesino Pouzols *et al.* 2014), reforested areas may be expected to buffer the rise of future novelty with respect to mid-Holocene baselines. These were characterized by highest forest cover (Fyfe *et al.* 2015) and are, among all Holocene baselines, the ones showing the highest proportion of between-vegetation-type turnover relative to their closest counterparts in modern cultural landscapes (see Appendix S1).

We found a complex relationship between the post-glacial trajectories of novelty and RoC. Whereas RoC increased at times of rapid climate change and during historical times, the rate of novelty emergence in historical times exceeded the longer term background variability (Figs 2d and 5b). The results support the notion that the search for static conservation targets in dynamic environments is likely to be elusive (Radeloff *et al.* 2015), since landscapes are inherently transitory and the emergence of novelty is inevitable (Williams & Jackson 2007) on longer term timescales. In addition, they show that unintentional and intentional human action has contributed to a faster rise of novelty earlier than was previously assumed (Radeloff *et al.* 2015).

Our approach presents an explicitly future-driven perspective of vegetation composition changes through time that provides a valuable long-term perspective on the dynamics and legacies of past ecological systems, which may help bridging the gap between palaeoecology and ecology (Willis & Birks 2006). Further evaluation of our results should be done through comparison with vegetation and climate models.

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## AUTHORSHIP

WF, TG and SB designed the experiments; ML compiled the data, WF developed and performed the RoC and novelty analyses, and the gridded maps; SB developed and performed the linear mixed-effect models. All authors analysed the results and contributed to writing the manuscript.

## DATA ACCESSIBILITY STATEMENT

Data and R scripts to replicate all the calculations for results presented in the paper are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.cg250>.

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