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Running headline: Long-term population dynamics

Summary (maximum 350 words):

1. Population dynamics is a field rich in theory and poor in long-term observational data. Finding sources of long-term data is critical as ecosystems around the globe continue to change in ways that current theories and models have failed to predict. Here we show how long-term ecological data can improve our understanding about palaeo-population change in response to external environmental factors, antecedent conditions and community diversity.

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2. We examined a radiometrically-dated sediment core from the Didachara Mire in the mountains of south-western Georgia (Caucasus) and analysed multiple biological proxies (pollen, fern spores, non-pollen palynomorphs, charcoal, diatoms, chrysophyte cysts, midges, mites and testate amoebae). Numerical techniques, including multivariate ordination, rarefaction, independent splitting and trait analysis, were used to assess the major drivers of changes in community diversity and population stability. Integrated multi-proxy analyses are very rare in the Caucasus, making this a unique record of long-term ecological change in a global biodiversity hotspot.
 3. *Synthesis.* Population changes in the terrestrial community coincided primarily with external environmental changes, while populations within the peatland community were affected by both internal and external drivers at different times. In general, our observations accord with theoretical predictions that population increases lead to greater stability and declines lead to instability. Random variation and interspecific competition explain population dynamics that diverged from predictions. Population change and diversity trends were positively correlated in all taxonomic groups, suggesting that population-level instability is greater in more diverse communities, even though diverse communities are themselves more stable. There is a continuing need to confront population theory with long-term data to test the predictive success of theoretical frameworks, thereby improving their ability to predict future change.

Key words: chironomids, diatoms, diversity, Georgia, palaeoecology and land-use history, pollen, population dynamics, testate amoebae

Introduction

Improving knowledge of ecological processes is increasingly important as anthropogenic impacts affect global ecosystems in potentially irreversible ways (Parmesan 2006; Cahill et al. 2013; Kubisch et al. 2014). In a changing environment, extinction risk is an ever-present concern (Crone 2016). Population theory predicts that extinction risk is reduced in populations that are stable or increasing (Channell & Lomolino 2000). Growing populations are considered more resilient to environmental change and demographic disruptions than shrinking ones (Lande 1993; Hamilton et al. 2009). In reality, however, populations and communities change in ways that current theory cannot always predict (Moritz & Agudo 2013; Zhang et al. 2015).

The potential for observational data to shed light on long-term population dynamics is widely appreciated (Moritz & Agudo 2013; Pedrotti et al. 2014; Jackson & Blois 2015) but less often achieved (Birks et al. 2012; Horreo et al. 2016). Examples of population dynamics that do not conform to population theory are of interest as they may potentially reveal circumstances in which environmental factors, species interactions or antecedent conditions override the demographic effects of population growth and stability (Tilman 1996; Kuparinen et al. 2014; Ogle et al. 2015; Reyer et al. 2015).

Critical comparison of long-term ecological changes with independent climatic records (e.g. ice cores, speleothems) could help resolve questions about extrinsic and intrinsic factors affecting ecosystems (Ammann et al. 2000; Jeffers et al. 2011, 2015; Lavoie et al. 2013; Seddon et al. 2015). In theory, synchronous changes are likely to reflect extrinsic drivers, while asynchronous changes may reflect intrinsic processes (Lavoie et al. 2013). The extent to which this actually occurs is influenced by a population's growth rate, environmental

sensitivity, phenotypic plasticity, genetic variability and other factors (Oliver et al. 2015; Ogle et al. 2015).

Population dynamics and species diversity are closely intertwined. At the community level, high-diversity ecosystems tend to be more stable and resilient to environmental changes than less diverse systems (Tilman & Downing 1994; Cardinale et al. 2012; cf. May 1972). At the population level, on the other hand, empirical data and modelling suggest that individual populations in diverse communities should experience greater instability than those in less diverse communities (Tilman 1996; Loreau & de Mazancourt 2013). Little scientific attention has been devoted to examining this relationship temporally using palaeo-data. Knowledge of the factors that drive diversity on centennial to millennial scales is limited geographically, temporally and taxonomically (Feurdean et al. 2013; Birks et al. 2016a,b).

In this paper, we use high-quality palaeoecological data from a peatland to address the following questions:

1. Do palaeo-population dynamics correspond temporally to environmental changes (extrinsic vs intrinsic) and, if so, does this relationship differ for different groups of organisms?
2. To what extent do palaeo-population changes conform to the predictions of population theory, especially in relation to diversity?

Materials and Methods

Research Design

We adopted a palaeoecological approach to address our research questions. Biological fossils from various taxonomic groups were analysed at comparable sampling intervals in a single core to provide a long temporal sequence of palaeoecological changes in a peatland ecosystem. Palaeo-population dynamics were reconstructed based on fossil accumulation rates (Flenley 2003; Jeffers et al. 2015). We used statistical techniques that detect major changes in population size and stability for each taxonomic entity without the need for analogue-based bias corrections (Walker & Wilson 1978; Walker & Pittelkow 1981; Birks et al. 2012). Population changes were compared to independent climatic records (regional-scale conditions) and changes in sediment composition within the site (local-scale conditions). Based on ecological theory, we predicted that populations achieve greater stability following an increase in population size (Lande 1993; Hamilton et al. 2009), and that taxonomic groups of higher diversity (richness) exhibit greater community-level stability and population-level instability compared to low-diversity groups (Tilman 1996; Loreau & de Mazancourt 2013; Gross et al. 2014).

Study Site

Our study site is a poor fen, Didachara Mire, located near the upper forest limit in the Lesser Caucasus (or Caucasus Minor) Mountains of Georgia (41°41'02"N, 42°29'49"E; see Fig. S1 in Supporting Information). It sits at the foot of Mt Tsvinta (2423 m) on the NW flank of the Arsiani Range at an elevation of 2000 m a.s.l. The peatland forms part of the headwaters of the Acharistskali River, a tributary of the Chorokhi (Çoruh) River. Geologically, the Arsiani Range is composed of Upper Miocene–Lower Pliocene volcanic and sedimentary units of the Goderdzi Suite (Gudjabidze 2003; Lebedev et al. 2012), which contain important fossil

deposits (Shatilova et al. 2011). Differential erosion of the Goderdzi Suite, along with landslides, slumping and remnants of Pleistocene glaciation, has created a complex terrain (Maruashvili 1971). Didachara is thought to have originated as a glacial lake (Margalitadze 1982).

Didachara is an optimal site for studying environmental change as it is situated at the intersection between two global biodiversity hotspots (Caucasus and Irano-Turanian: Mittermeier et al. 2005), two distinct vegetation belts (Colchic mixed-coniferous forests and subalpine vegetation: Nakhutsrishvili 2013), and two major climatic zones (maritime and continental: Javakhishvili 1964; see Fig. S1). The peatland occupies a small, closed basin (Fig. S2). Its predominant vegetation is a relatively species-rich *Sphagnum*–*Carex* association (*S. subsecundum*, *S. centrale*, *S. teres*, *C. muricata*, *C. canescens*, *C. inflata*, *C. irrigua*), with patches of *Drosera anglica*, *D. intermedia*, *Comarum palustre*, *Menyanthes trifoliata* and *Alisma plantago-aquatica*. The slopes around and below the peatland have coniferous forests dominated by *Picea orientalis* and *Abies nordmanniana*, as well as krummholz formations of *Fagus orientalis*, *Sorbus boissieri* and *Salix caprea* (Margalitadze 1982; nomenclature after Gagnidze 2005). Subalpine meadows of the West Lesser Caucasian type (Nakhutsrishvili 2013) extend from the site's elevation to the highest elevations of the nearby mountains (2452 m).

Margalitadze (1982) previously reconstructed the Holocene vegetation history of the site on the basis of undated pollen assemblages in two sediment cores. The present study greatly improves on that earlier reconstruction and is among the first of its kind in the Caucasus region to integrate dated palaeoecological data from various proxies (de Klerk et al. 2009; Moiseenko et al. 2012).

Field and Laboratory Methods

In August 2003, three parallel sediment cores were collected from the centre of the peatland using a Streif-Livingstone corer (Fig. S2; Merkt & Streif 1970). Core C, the most complete sequence, was selected for detailed multi-proxy palaeoecological analyses, loss-on-ignition and radiocarbon dating. In the laboratory, samples were taken at regular intervals to extract fossilised pollen, spores and non-pollen palynomorphs (0–910 cm), midges and mites (2–798 cm), diatoms and chrysophytes (610–810 cm) and testate amoebae (70–630 cm); these depth ranges were selected based on preliminary analyses and sediment characteristics. Statistically valid numbers of diatoms were only recovered in lake sediments. Testate amoebae were mostly found in peat.

Pollen and spores provide information on past vegetation change at regional and local scales, which is itself a reflection of climatic, edaphic and ecological factors. Pollen was prepared in 92 samples using standard methods, including 10% KOH, concentrated HF and acetolysis treatments (Moore et al. 1991). *Lycopodium* marker spores were added to calculate pollen concentrations (grains cm⁻³) and hence pollen accumulation rates (grains cm⁻² yr⁻¹). Pollen and spore identification was performed at 400× magnification following published guides (Punt 1976 ff.; Reille 1999). At least 320 terrestrial pollen grains were identified per sample (mean: 555). Aquatic pollen, spores and non-pollen palynomorphs indicative of peatland conditions were also quantified. We used microscopic charcoal particles (10–500 µm diameter) to reconstruct regional fire history (MacDonald et al. 1991; Tinner et al. 1998; Colombaroli et al. 2008). Particles were counted on pollen slides at 250× magnification (Finsinger and Tinner 2005).

Chironomids are sensitive indicators of changing freshwater environments, including temperature variations (Walker 2001). Chironomids and other invertebrate remains (biting midges and oribatid mites) were quantified in 48 samples. Sediment samples were processed following standard techniques (Walker 2001; Brooks et al. 2007). Wet sediments (1–3 g) were initially washed through a 100- μm mesh sieve. Invertebrate remains were sorted and picked out from the sieve residue in a Bogorov counting tray under a stereomicroscope at 25–40 \times magnification and mounted on microscope slides using Euparal[®]. Chironomids were identified at 200–400 \times magnification following Brooks et al. (2007) and Andersen et al. (2013a). Ceratopogonidae (biting midges) were separated into morphotypes following Walker (2001). Only chironomids were used for analyses requiring percentage data (e.g. zonation, ordination). Accumulation rates for all invertebrate taxa were calculated by wet sediment weight (remains $\text{g WW}^{-1} \text{yr}^{-1}$). At least 55 remains were identified per sample (mean: 700).

In freshwater environments, diatoms and chrysophytes may be used to trace changes in nutrient status, salinity and pH (Smol et al. 2001). Diatoms and chrysophyte cysts were enumerated in 23 lake sediment samples. Samples were digested in H_2O_2 and HCl, and mounted in Naphrax following Renberg (1990). Above a depth of 735 cm at least 250 diatom frustules were identified per sample, but below this depth 110–215 valves were counted per sample due to low concentrations (mean valve count for the core: 435). Diatom accumulation rates were not estimated.

Testate amoebae are considered sensitive to changes in surface wetness and acidity in peatlands (Payne 2011; Payne 2014; Jassey et al. 2014; Lamentowicz et al. 2015). Testate amoebae were analysed in 58 samples. Preparation followed Mazei et al. (2011) and involved soaking and sieving of 1 cm^3 peat samples at 0.5 mm, settling for 24 hours and staining with

erythrosine for microscopic examination. This method avoids physical damage to tests and loss of small specimens (Payne 2009; Avel & Pensa 2013). Identifications were made using taxonomic guides (e.g. Mazei & Tsyganov 2006) to the highest level of taxonomic precision in order to capture important morphological traits (Fournier et al. 2012; Lamentowicz et al. 2015). Accumulation rates were determined by counting all tests in the prepared samples, with a statistically acceptable minimum of 50 testate amoebae per sample (Payne and Mitchell 2009) (mean count: 815).

Sediment organic content was estimated using loss-on-ignition at temperature steps of 550 and 950 °C (Heiri et al. 2001). Eleven samples of wood and other identifiable macrofossils were submitted for AMS radiocarbon dating. Radiocarbon dates were calibrated using the IntCal13 calibration curve (Reimer et al. 2013) and a calendar age of -53 BP (2003 AD – collection year) assigned to the core top. We produced an age–depth model (Fig. S3) using Bacon 2.2 (Blaauw & Christen 2011), a Bayesian approach that considers prior information on sedimentation rates. Stratigraphic diagrams showing the relative abundance of each taxon by sample depth and modelled age were produced using Tilia 2.0.32 (Grimm 2013).

Numerical Analyses

To analyse palaeo-community interactions and factors influencing ecosystem development, we used assemblage zones and multivariate ordination scores as the basis for comparison (Ammann et al. 2000). Assemblage zones were determined through binary splitting, the number of zones being assessed statistically by the broken stick model (Bennett 1996). Non-metric multidimensional scaling (NMDS) with Bray-Curtis dissimilarity measure was applied to each of the five proxy datasets (upland pollen, wetland pollen and spores, chironomids, diatoms and chrysophytes, and testate amoebae). NMDS was selected over other techniques because it makes no assumptions about response models and is therefore applicable to

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datasets of different variances. Data were square-root transformed prior to analysis in PAST (Hammer 2015).

The study of past diversity is useful for understanding present diversity patterns and making future predictions (Rull 2012). However, diversity indices are as diverse and problematic as diversity itself (Mendes et al. 2008; Giesecke et al. 2014), especially in palaeoecological studies (Smol 1981; Birks et al. 2016a). For this study, community-level richness was estimated using constant-sum rarefaction, implemented through the “vegan” package in R (Oksanen et al. 2015; R Core Team 2015). Rarefaction of accumulation-rate data was also performed where applicable, following van der Knaap (2009), to avoid problems of interdependence in percentage data.

To assess whether individual palaeo-populations have changed in consistent ways, we used independent splitting, a valuable and underutilised tool for analysing multi-proxy data (Lotter et al. 1995; Birks & Birks 2006; Birks et al. 2012). Independent splitting treats each palaeoecological taxon independently, which is only possible when accumulation-rate data and a robust age-depth model are available. Changes in accumulation-rate data through time are divided (split) into sections with homogenous mean and standard deviation statistics. These statistics are used to assess relative changes in palaeo-population size and stability, without the need for quantitative population estimates (Walker & Wilson 1978).

Independent splitting was implemented in Psimpoll (Bennett 2005). Pollen taxa with <10 occurrences were excluded, as were testate amoeba, midge and mite taxa with <5 occurrences. At each statistically significant population change (Walker & Wilson 1978), we observed whether stability increased or decreased according to the ratio of mean to standard deviation (m/sd: Walker & Pittelkow 1981). Results were compared to the null model of Blaauw et al. (2010), with 450 random proxy walks of 200 samples at population sizes of 500

and 2000 (representative of local proxies and terrestrial pollen respectively: Blaauw et al. 2010). Observed population changes in fossil data were also compared to species traits by associating fossil taxa with traits from representative or similar species (Kleyer et al. 2008; Fournier et al. 2015).

Results

Palaeoecological data from Didachara show significant long-term variations in all the taxonomic groups analysed at decadal to multicentennial scale (Fig. 1). A total of 208 terrestrial pollen taxa, 32 wetland taxa (local pollen and non-pollen palynomorphs), 52 diatom taxa and chrysophyte cysts, 61 testate amoeba taxa, 28 midge taxa and oribatid mites were identified (Fig. S4). In interpreting the data, an important distinction must be made between the larger spatial scale represented by upland pollen compared to the other proxies which represent communities within the site itself. Pollen from major pollen-producing trees in mountainous areas is readily transported upslope by wind (Kvavadze 1993). Upland pollen therefore comprises a mixed signal derived from source plants at varying distances from the site (typically 1–10 km: Markgraf 1980; Mariani et al. 2016). Other proxies (wetland plants, diatoms, testate amoebae, midges and mites) are largely derived from local, *in situ* populations. Hence upland pollen provides a terrestrial community background against which to interpret local changes in the lake/peatland community. In the following section, major palaeoecological transitions are interpreted with reference to environmental conditions.

Terrestrial community development since 13,000 cal. BP

The earliest **upland palaeovegetation** zone (*Poaceae-Artemisia*; Fig. 1) indicates a largely treeless landscape of grassy steppe, with moderate burning and deposition of minerogenic sediments, typical of Lateglacial environments across the region (Wick et al. 2003; Messenger et al. 2013, 2017). Increasing temperature and precipitation at the beginning of the Holocene (approx. 11,700 cal. BP; Fig. 2) allowed the lake to fill, meadow and marsh vegetation to expand (*Poaceae-Potentilla* zone), and fire to increase as fuel limitations decreased. Meadow vegetation was replaced by deciduous woodland species (*Ulmus-Fraxinus* zone) around 9900 cal. BP, likely favoured by a decreased impact of fire (limit zones 2-3). Today *Ulmus* and *Fraxinus* rarely occur at the upper forest limit, only achieving dominance in low–middle elevation forests (Ketskhoeli 1971). Neither tree is a major pollen producer (Connor 2011), so it seems certain that they were canopy dominants in Early Holocene vegetation around Didachara, facilitated by increased temperatures and a lack of competition. *Fraxinus* was probably outcompeted by the cold- and shade-tolerant *Fagus orientalis* as it expanded its range around 8200 cal. BP (*Fagus-Ulmus* zone). Mixed coniferous-deciduous forests followed around 6300 cal. BP, with *Picea orientalis* and *Abies nordmanniana* increasingly important (*Picea-Abies* zone). This association is typical of the mountain forests of Colchis (Western Caucasus) today (Nakhutsrishvili 2013), although the timing of its Holocene establishment varies from place to place (Connor & Kvavadze 2008). Fire activity in the *Picea-Abies* zone peaked at ca. 4000, 3000 and 1800 cal. BP, indicating disturbances in the forest. A brief episode of deforestation followed at 950 cal. BP (*Poaceae-Fagus* zone), mainly affecting coniferous forest and accompanied by an increase in anthropogenic pollen indicators (Behre 1986). Human populations increased in the highlands during the mediaeval period (Burney & Lang 1971), with widespread ecological impacts (Connor 2011). Since 300

cal. BP coniferous forests have returned. *Abies* populations have not recovered as successfully as *Picea*, being more sensitive to human activities (Connor 2011).

Overall, significant changes in the terrestrial community's structure (assemblage zone boundaries) are closely associated with regional-scale climatic changes recorded in isotopic records (Fig. 2).

Lake/peatland community development since 13,000 cal. BP

Within Didachara's **aquatic and wetland vegetation**, sedges (Cyperaceae) were dominant from 13,000 to 9900 cal. BP (Fig. 1), suggesting a shallow or fluctuating water-table. Spores of dung-inhabiting fungi (i.e. *Cercophora* and *Sporormiella*) suggest herbivores were present, perhaps visiting the site as a waterhole. Around 9900 cal. BP, as *Ulmus-Fraxinus* woodlands expanded, *Pediastrum* algae indicate rising lake levels (*Pediastrum*-Cyperaceae zone).

Increasing numbers of fern spores after 8000 and particularly after 6300 cal. BP indicate that open water was being encroached upon by wetland vegetation and the wetland surface was increasingly shaded by trees. *Sphagnum* and *Menyanthes trifoliata* appear at 4000 cal. BP (fern-*Sphagnum* zone) as a peatland formed in the former lake basin (Fig. 1). The return of a fern-Cyperaceae association from 1400–800 cal. BP suggests a drying phase, as has been inferred for this period from sites further east (Connor 2011). Higher moisture levels returned more recently (Cyperaceae-*Sphagnum* zone).

Diatom and chrysophyte palaeo-assemblages are recorded from 11200–7700 cal. BP. An initial succession of benthic taxa (e.g. epiphytic *Gomphonema olivaceum* and epipellic *Fragilariforma nitzschoides*) suggests an initially low lake level, corresponding to the final stages of steppe vegetation in the surrounding landscape. A peak in chrysophyte cysts constitutes the next phase (10,960–10,800 cal. BP), perhaps influenced by increased nutrient inputs as the lake filled (Smol 1985), a supposition corroborated by rapid fluctuations in

mineral content (Fig. 1). *Aulacoseira nygaardii*, a species typical of oligotrophic lakes, peaks shortly after (10,800–10,640 cal. BP), followed by a largely benthic diatom community including aerophilic species (*Orthoseira roeseana*) and indicative of nutrient enriched, shallow water with limited thermal stratification (*Pinnularia-Orthoseira* zone). After 9970 cal. BP, tycho-planktonic *Aulacoseira nygaardii* again becomes dominant, with short-lived peaks in *Pinnularia microstauron* and chrysophytes around 9300 and 8600 cal. BP. This *Aulacoseira-Pinnularia* zone indicates a higher lake level and corresponds to the Cyperaceae-*Pediastrum* zone in the wetland vegetation and the expansion of *Ulmus-Fraxinus* woods around the study site.

Compared to other proxies, **midge and mite** palaeo-assemblages exhibit more consistency over the period analysed (11,000 cal. BP onwards). *Limnophyes*, a chironomid often found in semi-aquatic habitats amongst mosses and macrophytes (Andersen et al. 2013b), is common in all zones except in the uppermost *Tanytarsus-Psectrocladius* zone (Fig. 1). In the earliest zone, cool conditions are inferred until 10,100 cal. BP, based on the abundance of *Krenopelopia*, *Micropsectra radialis*-type and other cold-stenothermic taxa (Pankratova 1977; Cranston & Epler 2013). This is followed by a phase with warmth-adapted taxa (e.g. *Corynoneura scutellata*-type, *Procladius*) that corresponds temporally to the *Ulmus-Fraxinus* phase in the upland vegetation. Cooler conditions returned from 8100–4000 cal. BP, as *Fagus* and coniferous trees extended their range in the area. The second zone (*Limnophyes-Corynoneura*) indicates relatively warm summers from 4000 to 1400 cal. BP. Abundant oribatid mite remains in this phase correspond to peat accumulation and the Cyperaceae-*Sphagnum* zone in the wetland vegetation. Oribatid mites are commonly associated with *Sphagnum* in the Caucasus (Murvanidze & Kvavadze 2010). The loss of warmth-adapted chironomids in the third zone (1430–170 cal. BP) could indicate cooler temperatures, although it is also possible that habitat changes in the wetland (i.e. *Sphagnum* decline)

contributed to this change. The subsequent *Tanytarsus-Psectrocladius* zone indicates a major shift in invertebrate communities: true aquatic and thermophilous chironomids increase in percentage and in absolute terms, suggesting warmer and wetter conditions. At the nearby Goderdzi Pass (2025 m), meteorological data show a significant temperature rise since records began in the 1960s (Westphal et al. 2011; Keggenhoff et al. 2014). Diatom assemblages from the Caucasus Mountains likewise record pronounced 20th-century temperature rise (Moiseenko et al. 2012).

Testate amoebae palaeo-assemblage changes are closely linked to shifts in the wetland vegetation over the period analysed (8080–500 cal. BP). The first zone (*Trinema-Pseudodifflugia*) falls within the Cyperaceae-fern wetland phase (Fig. 1). In the Eastern Mediterranean and Black Sea region, the testate amoebae identified in this zone are found in fen or swamp environments with a near-surface water-table (Payne 2011). The second zone (*Hyalosphenia-Pseudodifflugia*) is a wet transitional zone of only two samples (6670–5740 cal. BP). The *Difflugia-Centropyxis* association that replaces it is typical of minerotrophic sedge-dominated fens (Payne 2011). A major change occurs around 4100 cal. BP, when testate amoebae characteristic of poor fens and *Sphagnum*-dominated vegetation increase (e.g. *Nebela penardiana*, *Heleopera sphagni*), indicating terrestrialisation. Another transitional zone (one sample) occurs between 1950 and 1850 cal. BP with a *Trinema lineare* peak. The last three zones track wetland vegetation changes closely, with indications of greater oligotrophy during the last millennium, reflecting peatland acidification linked to climate change.

Overall, significant changes in the lake/peatland community prior to 6000 cal. BP (lake phase) are associated with changes in the terrestrial community (Fig. 2). After this time, significant changes relate to shifts within the peatland community that are largely independent of terrestrial community changes.

Palaeo-population dynamics and diversity estimates

The temporal distribution of major palaeo-population changes is shown in Fig. 2. Within the terrestrial community (upland pollen), changes are concentrated around the Pleistocene–Holocene transition. A second period of rapid population change occurred from approx. 4500 cal. BP to the present. This coincides with terrestrialisation and the increasing prevalence of *Picea orientalis* in the surrounding vegetation. Within the peatland community, the various taxonomic groups (wetland vegetation, midges and mites, and testate amoebae) exhibit very different patterns. Wetland vegetation follows the terrestrial community pattern, albeit with a stronger reaction to terrestrialisation. Midge and mite population changes are clustered during recent centuries. Testate amoebae population dynamics intensify after terrestrialisation and are dominated by population increases.

The effect of antecedent population conditions on subsequent populations is shown in Fig. 3. Population theory predicts that populations should stabilise following an increase and destabilise following a decrease. This pattern (Fig. 3a) is observed in 73% of cases among upland taxa, 70% among wetland vegetation taxa, 71% among testate amoebae, and 78% among midges and mites and these figures are relatively insensitive to the exclusion of rare taxa (in which case results are 66%, 69%, 67%, and 71%). Species that do not conform to these predictions ('unpredicted' in Fig 3a) have a different distribution of body-size traits compared to species that exhibited the predicted response (Fig. S5)..

Reconstructed richness trends are shown in Fig. 4. Each taxonomic group exhibits a different trend in richness and no group remains stable through time. The terrestrial community (upland pollen) exhibits peaks corresponding to phases in which Poaceae (grasses) are prominent. Richness in the wetland vegetation group increased substantially at the time of terrestriation. Both diatoms and chironomids show long-term declines in richness, although chironomid richness has peaked in recent decades. Richness among testate amoebae has increased gradually through the last 8000 years. Accumulation-rate diversity estimates agree with constant-sum rarefaction results, except in the case of upland pollen, which has greater accumulation-rate variability. For each taxonomic group, diversity estimates through time are positively correlated with the total number of population changes (Fig. 5).

Discussion

1. Intrinsic and extrinsic drivers of palaeo-population dynamics

In the Didachara record, significant population changes were not evenly distributed through time (Fig. 2). The most prominent changes in terrestrial populations are associated with rapid changes in precipitation, temperature and seasonality at the Pleistocene–Holocene boundary, *ca* 11,700 cal. BP (Wright et al. 2003; Wick et al. 2003; Göktürk et al. 2011; Messenger et al. 2013, 2017). Regional climatic shifts are ‘slow/large’ environmental changes that theory predicts would reduce ecosystem resilience (Seddon et al. 2011, 2015). Our observations suggest that these changes impacted upon both terrestrial and lake/peatland communities (Fig. 2). Population-level reactions were particularly strong within the terrestrial community. This is perhaps due to the larger spatial scale represented by the upland pollen proxy and its greater sensitivity to regional-scale climate change.

The close correspondence between terrestrial population changes and regional climatic trends supports the idea that environmental changes are primary drivers of long-term community development and population dynamics (Jackson & Blois 2015; Crone 2016). However, climate change acting on one or more species may have initiated an ecological cascade via biotic interactions with other species. Simulations and empirical evidence show that biotic interactions (such as competition) may override climatic controls on species abundance (Brooker 2006; Miller et al. 2008).

Terrestrialisation (or ‘macrosuccession’: van der Valk 2012) had major impacts on lake/peatland population dynamics. Populations of midges, mites, testate amoebae and other wetland taxa increased at the transition from shallow lake to peatland, 4500–4000 cal. BP (Fig. 2). Chironomid population dynamics subsequently tracked temperature changes and testate amoebae population dynamics followed increasing oligotrophy (Fig. S6). Community dynamics also changed during the mid-late Holocene, with lake/peatland community shifts generally occurring out-of-phase with terrestrial shifts (Fig. 2). This would be expected if intrinsic dynamics (such as terrestrialisation) overtook extrinsic factors (such as climate) in their importance for ecosystem functioning (Seddon et al. 2014, 2015; Jeffers et al. 2015).

Terrestrialisation was related primarily to intrinsic processes of organic matter accumulation within the peatland. Its timing, however, was influenced by extrinsic climatic warming, indicated by increases in thermophilous chironomid assemblages at Didachara (Fig. S6), as well as isotopically and palynologically inferred temperatures across the region (Wick et al. 2003; Connor 2011). Terrestrialisation was therefore intrinsically driven and climatically mediated, a finding that agrees with research into peatland systems elsewhere (Belyea & Baird 2006; Lavoie et al. 2013).

As in other parts of Eurasia (Seddon et al. 2015), we suggest that ‘slow/large’ processes diminished in the Caucasus during the mid-Holocene (Fig. 2) and that greater resilience developed in the peatland community (i.e. macrophytes, testate amoebae and invertebrates). This resilience weakened around 1000 cal. BP as anthropogenic deforestation impacted on the terrestrial community, creating feedbacks onto water table depth (via tree removal), macrophyte cover (sunlight availability) and trophic status (acidification). Responses across various trophic levels in and around the site are evidence of a trophic cascade triggered by deforestation (Ireland & Booth 2012).

2. Antecedent conditions

A key question in ecology is whether populations, distributions or ranges change in predictable ways (Brooker 2006). Population dynamics theory predicts that growing populations should subsequently achieve stability, while declining populations will experience greater instability (Channell & Lomolino 2000). If this were true in every instance, a great number of ecological problems could be instantly solved. Allee effects and other concepts are used to describe exceptions to this theory (Kuparinen et al. 2014; Oliver et al. 2015).

Two-thirds of our observations support the key theoretical predictions of population theory (Fig. 3a). The observations are remarkably uniform given that they derive from mostly unrelated taxonomic groups. Random walk simulations produce similar results to the fossil data (Fig. 3a), casting doubt on whether the observed differences in palaeo-population response are real or artefactual. The null model has no inherent consideration of species interaction or environmental forcings (Blaauw et al. 2010), factors expected to influence palaeo-population dynamics at Didachara. While our results support the predictions of

population theory, they call for caution in attaching ecological explanations to patterns that may be caused by random variation.

Certain fossil observations fall beyond the bounds of the random simulations (asterisked in Fig. 3a). This is particularly true for testate amoebae and wetland pollen, taxonomic groups at Didachara whose histories are closely intertwined. This raises the possibility that community-level interaction influences population dynamics, although taphonomy, life history, niche specialisation, environmental change and interspecific interaction may be equally important.

Several limitations apply to our palaeo-population analyses. Although population splits are significant, stability changes in the fossil data were not significantly different to those generated by the null model. Generation and response times of testate amoebae and chironomids are many times faster than terrestrial trees. Sampling intervals for short-lived taxa may be inadequate to detect rapid changes in population size and stability. Even generation times of terrestrial trees vary by several orders of magnitude (Walker & Chen 1987).

It is unlikely that any feasible sampling interval can adequately represent all palaeo-population changes for every taxon. It may be necessary to model empirical data using Bayesian statistics (Clark & Bjørnstad 2004) to target particular taxa or groups. Such datasets could be used to identify taxa whose histories exhibit early warning signals of ecosystem change (Scheffer et al. 2009). Independent splitting results hint at population instability predicting subsequent population decline among longer-lived taxa (Fig. S7), but sampling intervals may be inadequate to address this using the current dataset.

While there is considerable replication within the Didachara record (337 palaeo-population changes), they solely relate to a single core from a single site and are dominated by terrestrial pollen changes. We encourage replication in other palaeo-records to determine the

generalisability of these findings. Questions also remain regarding the degree to which population dynamics can be overridden by random variation, competition and environmental change.

We used trait analysis to gain further insight into population dynamics that diverged from theoretical predictions. Tall canopy trees are disproportionately represented among taxa that conflict with theory – they increased and subsequently experienced greater variability (Fig. S5). Competition between canopy dominants seems the most likely explanation for this pattern (Bennett 1986), as *Picea orientalis*, *Abies nordmanniana*, *Pinus kochiana* and *Fagus orientalis* all inhabit the same bioclimatic niche (Nakhutsrishvili 2013).

Low-growing taxa are most frequent among species whose populations have decreased, which reflects the replacement of low-statured Late-glacial steppes and Early Holocene meadows by taller forest vegetation. Species that do not follow the predictions of population dynamics theory, however, tend to be taller (Fig. S5). Additional height may confer competitive advantages (Brooker 2006), particularly in an increasingly forested environment.

Peatland taxa exhibit similar size-related tendencies (Fig. S5). Testate amoebae with smaller apertures are more prevalent among the populations that conflict with theoretical predictions (Fig. 3), including abundant taxa such as *Diffugia* and *Hyalosphenia* species. Our results suggest that organism size affects population dynamics (Brooker 2006; Pelletier et al. 2007) and that biotic interactions such as competition may play a stronger role in ecosystem dynamics than is generally acknowledged (Jeffers et al. 2015). Wider application of independent splitting to other suitable palaeoecological records is likely to uncover consistent ecological responses for taxa whose lifecycles are too long or cryptic to monitor using alternative methods.

3. Diversity and stability

Ecological theory states that greater diversity lends stability to communities (Cardinale et al. 2012; Tilman et al. 2014; cf. May 1972). Upland pollen has the highest overall richness in rarefaction results (Fig. 4). Over the long term, upland pollen tends to exhibit relatively gradual transitions between different assemblages (Fig. S6). Chironomids have the lowest overall richness and exhibit more pronounced fluctuations in assemblages (Fig. S6), although fewer significant shifts in assemblage structure (Fig. 2). Seen through ordination results, our observations suggest that more diverse communities are inclined towards greater long-term stability, but seen through numbers of statistically significant assemblage shifts, the inverse is true, raising questions about how best to assess long-term stability (see also Loreau & de Mazancourt 2012). Life histories are also critical: it may be expected that upland vegetation composed of long-lived trees may have a greater degree of ecological inertia than short-lived chironomid communities (Smith 1965; Von Holle et al. 2003).

Richness in the various taxonomic groups has not remained stable through time (Fig. 4). Peaks in richness in the terrestrial community are associated with periods in which grasses (Poaceae) played a prominent role (zones 2 and 6; see Fig. 1). The lowest richness is associated with forested periods (5 and 7) because of the dominance of competitive, late-successional tree species (e.g. *Fagus* and *Picea*; Nakhutsrishvili 2013). The grassland zones have greater palynological evenness, a characteristic that has been shown to correspond to greater habitat diversity (Feurdean et al. 2013; Matthias et al. 2015). These zones were also more affected by fires (Fig. 1), which are a key disturbance agent contributing to greater landscape diversity and taxonomic richness in Europe (Giesecke et al. 2012; Colombaroli et al. 2013) and the Caucasus (Connor 2011).

Within the peatland community, long-term changes in diversity are apparent in all taxonomic groups. Richness among wetland vegetation indicators rises abruptly around 4000 cal. BP, coinciding with the onset of terrestrialisation, which likely created a diversity of habitat patches of peatland surface and open water. Diatom richness was highest in the zone with predominantly benthic species (*Pinnularia-Orthoseira* zone) and corresponds to more minerotrophic conditions and the absence of competing *Pediastrum*. Among midges (chironomids) and mites, the greatest richness occurs in the most recent zone (*Tanytarsus-Psectrocladius*), which is likely related to increased temperatures and greater effective moisture. For testate amoebae, constant-sum and accumulation-rate rarefaction results are in close agreement, indicating a steady rise in richness through the last 8000 years that tracks the inferred expansion of oligotrophic conditions (Figs 4 and S6).

Population-level instability is apparently linked to higher community diversity, as suggested by positive correlations between diversity estimates and population changes (Fig. 5). Correlations are strongest for testate amoebae (r^2 : 0.38) and wetland vegetation (r^2 : 0.29). These long-term observations appear to support theoretical predictions and previous empirical observations from shorter-term ecological studies (Tilman 1996; Loreau & de Mazancourt 2013; Gross et al. 2014). Highly diverse systems experience greater population-level variation after a disturbance due to interspecific competition. The effects of this competition on overall community structure and biomass are to lend stability, either because there is a greater probability that disturbance-resistant species will be present compared to a low-diversity system (Tilman 1996) or because species responses to disturbance occur at different times and rates (Loreau & de Mazancourt 2013).

Surprisingly, random walk simulations produce comparable relationships between richness and population change (Fig. 5). The relationship is stronger (r^2 : 0.16) for a simulated population size of 500 compared to 2000 (r^2 : 0.05), replicating correlations observed in the fossil communities. In communities with a low overall population, increases in richness are likely to be accompanied by significant changes in population sizes as new species migrate into the community. This effect is diluted in larger, more diverse communities in which many populations are already present and interspecific interactions may be more critical.

Our results, while representing conditional support for the richness and stability relationships observed in short-term studies, suggest that there is greater scope for testing ecological theories using long-term ecological data, model simulations and alternative indices of diversity and stability.

Conclusions

Population dynamics theory makes important predictions that are notoriously difficult to test using short-term datasets. We analysed palaeoecological data from a peatland ecosystem to provide a long-term perspective on population dynamics. In accordance with predictions, populations of taxa that lived within the peatland tended to respond concurrently to internal changes, especially terrestrialisation. This pattern was not consistent through time, however, with both peatland and terrestrial taxa being impacted by external environmental changes such as major climatic shifts and human impacts at various times. The data show that antecedent population increases led to future population stability in two-thirds of cases.

Random variation and inter-species competition emerged as likely explanations for population changes that did not conform to this theoretical prediction. This result highlights the need to integrate intracommunity interactions into population models and confront these

with null models. As predicted, taxonomic groups of higher diversity tended to have greater community-level stability and population-level instability compared to low-diversity groups, although questions remain about how to best assess community stability. Future research should aim to expand knowledge of long-term population changes beyond a single site, aiming at replication on a regional scale.

Author contributions

BA initiated and led the project; NM selected the study site; JL analysed pollen data; BA and WK described and dated the sediment; FC identified botanical macrofossils; AM analysed diatoms; BI and EI analysed chironomids; EM, YM, EADM, RJP and ML analysed and interpreted testate amoebae; DC and EG collated data; and SC undertook numerical analyses and wrote the paper with assistance from all co-authors.

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Data accessibility

Complete datasets are given in Supporting Information and available through the Neotoma Paleocology Database (Connor et al. 2017):

Geochronology <https://apps.neotomadb.org/Explorer/?datasetid=22323>

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Plant macrofossil <https://apps.neotomadb.org/Explorer/?datasetid=22324>

Chironomid <https://apps.neotomadb.org/Explorer/?datasetid=22325>

Testate amoebae <https://apps.neotomadb.org/Explorer/?datasetid=22326>

Diatom <https://apps.neotomadb.org/Explorer/?datasetid=22327>

Loss-on-ignition <https://apps.neotomadb.org/Explorer/?datasetid=22328>

Charcoal <https://apps.neotomadb.org/Explorer/?datasetid=22329>

Pollen <https://apps.neotomadb.org/Explorer/?datasetid=22330>

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FIGURE LEGENDS

Fig. 1. Major taxa from the various taxonomic groups at Didachara, southern Georgia. Data are presented in stratigraphical order in both percentages (filled curves) and accumulation rates (bars); x-axes are scaled independently for accumulation-rate data (lower scales: remains $\text{cm}^{-2} \text{yr}^{-1}$). Ages, depths, lithology and loss-on-ignition (LOI) results are given on the left side; assemblage zones are given on the right. Further details in Table S1 and Figs S3 and S4.

Fig. 2. The Lake Van palaeoclimatic record (Wick et al. 2003) compared to significant changes in taxonomic groups (ellipses) and the direction of palaeo-population changes at

Didachara (histograms). Ellipses represent significant assemblage-zone boundaries (Fig. 1); histograms represent the number of independent splits in each 500-year timeslice with a detected increase or decrease in mean accumulation rates. Diatoms were not included as accumulation rates could not be determined. Organic content (loss-on-ignition) results are shown in grey.

Fig. 3. Testing population dynamics theory with palaeo-population data. The graphs indicate the percentage of major population changes that show an increase or decrease in stability following a change in palaeo-population size. ‘Predicted’ responses accord with population dynamics theory, in contrast to ‘unpredicted’ responses. Hollow histograms show results for the more abundant taxa only (number of observations n given in parentheses). Box plots indicate random walk simulations with population sizes of 500 (representative of local proxies) and 2000 (representative of upland pollen: Blaauw et al. 2010). Asterisks denote observations that exceed 95% confidence intervals.

Fig. 4. Diversity trends in each of taxonomic groups at Didachara. Rarefaction results show estimated changes in richness for each fossil assemblage plotted by age; solid lines are smoothed constant-sum rarefaction estimates (Lowess span=0.2, with 95% confidence intervals shaded); dotted lines are smoothed accumulation-rate rarefaction estimates (after van der Knaap, 2009).

Fig. 5. Relationship between community-level richness (Fig. 4) and population-level instability (number of independent splits: Fig. 2). Timeslices as in Fig. 2. Random walk simulations (maximum richness 15) shown for comparison.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Figure S1 *Location and climatic information for the study site.*

Figure S2 *Photograph of coring the study site, Didachara Mire in the Lesser Caucasus.*

Figure S3 *Modelled age–depth relationship for Didachara Core C, with weighted mean age (solid line) and 95% confidence intervals (dotted lines). Uncalibrated ages and errors (Table S2) are given alongside modelled age distributions for each dated level (in calibrated years before present).*

Figure S4 *Complete multiproxy stratigraphic diagrams.*

Figure S5 *Organism size in relation to population response. ‘Predicted’ responses are those that align with theoretical predictions from population dynamics theory, contrasting with ‘unpredicted’ responses. Testate amoebae traits derived from Fournier et al. (2015); plant traits from Kleyer et al. (2008) – see Table S3.*

Figure S6 *Major community-level trends in each taxonomic group. Non-metric multidimensional scaling (NMDS) ordination results are grouped by relevant environmental variables; assemblage zones (Fig. 1) indicated by colours. Independent palaeoclimatic trends from the Sofular speleothem (Göktürk et al. 2011) are shown in grey in the upper panels for comparison.*

Figure S7 *Testing population dynamics theory with palaeo-population data. Histograms indicate the percentage of major population changes that a) show an increase or decrease in stability following a change in palaeo-population size; and b) show a change in population size following a change in stability. ‘Predicted’ responses accord with population dynamics*

theory, in contrast to ‘unpredicted’ responses. Hollow histograms show results for the more abundant taxa only (number of observations n given in parentheses). Results of random walk simulations are shown as box plots.

Table S1 *Detailed lithological description.*

Table S2 *Radiocarbon dates.*

Table S3 *Traits associated with fossil taxa.*

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