Combining short-term manipulative experiments with long-term palaeoecological investigations at high resolution to assess the response of *Sphagnum* peatlands to drought, fire and warming

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SUMMARY

Northern hemisphere peatlands are substantial carbon stores. However, recent climate change and human impacts (e.g., drainage and atmospheric nutrient deposition) may trigger the emission of their stored carbon to the atmosphere. Biodiversity losses are also an important consequence of those changes. Therefore, there is a need to recognise these processes in space and time. Global change experiments are often conducted to improve our understanding of the potential responses of various ecosystems to global warming and drought. Most of the experiments carried out in peatlands are focused on carbon balance and nitrogen deposition. Nevertheless, it is still unclear how fast peatlands respond to temperature changes and water-table lowering in the continental climate setting. This is important because continental regions account for a significant proportion of all northern hemisphere peatlands. A combination of short-term and long-term approaches in a single research project is especially helpful because it facilitates the correct interpretation of experimental data. Here we describe the CLIMPEAT project - a manipulative field experiment in a *Sphagnum*-dominated peatland supported by a high-resolution multi-proxy palaeoecological study. The design of the field experiment (e.g., treatments), methodology and biogeographical setting are presented. We suggest it is beneficial to support field experiments with an investigation of past environmental changes in the studied ecosystem, as human impacts during the past 300 years have already caused substantial changes in ecosystem functioning which may condition the response in experimental studies.

KEY WORDS: climate change, global change experiment, long-term ecology, temperature, wetlands

INTRODUCTION

Northern hemisphere peatlands contain about one-third of the world's soil carbon (C) stock in an area accounting for only 3–5 % of the global land surface (Gorham 1991, Turunen *et al*. 2002, Frolking & Roulet 2007). *Sphagnum* peatlands are now recognised as valuable pools of sequestered carbon, and their response to predicted climate change scenarios is relevant for potential feedbacks in the global C cycle (Belyea & Malmer 2004, Rydin & Jeglum 2006, Vasander & Kettunen 2006, Yu 2006). The key to C accumulation in peatlands is not high gross primary production (GPP), but low decomposition rates. Indeed, the highest C sequestration rates are observed in ombrotrophic bogs, which have low GPP. Therefore, high research priority should be given to investigating how the constraints on decomposition in these environments are sensitive to climate (Davidson *et al.* 2006, Bragazza *et al.* 2009). One scenario is that accelerated decomposition of stored organic matter (Gavazov *et al*. 2015) results in increased releases of greenhouse gases (GHGs) (CO_2, CH_4 and N_2O) to the atmosphere (Turetsky *et al*. 2015, Wang *et al*. 2015). *Sphagnum*-dominated peatlands are primarily situated in boreal and subarctic areas (Katz 1975, Rydin & Jeglum 2006) and, according to IPCC climate projections, they may experience large climate changes in the coming century, making the identification and quantification of potential feedbacks from these high-latitude ecosystems

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essential for future climate modelling (IPCC 2014).

In Europe, peatlands have been significantly affected by peat exploitation and/or drainage for agriculture and forestry (Joosten & Clarke 2002, Chapman *et al.* 2003), and the preservation of the remaining semi-natural sites or the restoration of damaged peatlands is now a priority for European Union (EU) countries (Raeymaekers 2000). In addition to direct human impacts, peatlands are currently exposed to indirect human impacts such as climate change and atmospheric nitrogen deposition, which will affect their structure (e.g., vegetation and soil microbial communities) and functioning (e.g., C balance), and possibly invalidate previous findings under steady-state climate settings (Joosten & Clarke 2002). Indeed, peatlands that are currently recovering from past damage (e.g., through spontaneous regeneration or as a result of restoration) may fail to recover fully (de Jong *et al.* 2010, Samaritani *et al.* 2010). As shifts in vegetation are slow, and even the presence of keystone species such as *Sphagnum* spp. does not necessarily indicate the full recovery of a C-sequestering function (Francez 2000), other bioindicators such as testate amoebae (Protists) are being considered as early indicators of ecosystem dynamics and functioning (Buttler *et al.* 1996, Davis & Wilkinson 2004, Laggoun-Défarge *et al.* 2008).

Ombrotrophic peatlands, in particular, are also excellent archives of palaeohydrological changes (Charman 2007, Chambers *et al.* 2012, Gałka *et al.* 2013). This makes them important candidates for reconstructing past climate changes (de Jong *et al.* 2010). Reconstruction of palaeohydrology and C balance (e.g., by inferring gas fluxes and decomposition) coupled with field experiments in the same system is expected to provide strong constraints on modelling of biosphere–atmosphere feedbacks.

Relationships between peatlands and climate are presently being tested experimentally in several parts of the world (Jassey *et al.* 2013, Robroek *et al.* 2013, Limpens *et al.* 2014, Dieleman *et al.* 2015a, Dieleman *et al.* 2015b). Research questions cover a wide range of topics, from biogeochemistry and microbial ecology to vegetation science. However, it is still unclear how peatlands respond to increased temperatures and droughts in a continental climate setting and, since continental regions account for a significant proportion of all northern hemisphere peatlands (e.g., much of Russia and North America), how this will affect global C cycling. These questions can, therefore, be considered as research priorities to strengthen the value of peatlands as indicators of past, present and future global change and to better understand the peatland ecosystem/biodiversity response to climate warming.

The CLIMPEAT project (Linje Mire, Poland) operates within a network of several ongoing passive warming manipulation projects (e.g., PEATWARM - French Jura, CliMireSiber - Russian Western Siberia, PEATBOG - England, UK) arranged along an oceanic–continental climate gradient. Data from continental peatlands are important to fill the gap in a global view, and it is expected that the data will be extrapolated to larger scale in the future. However, it should be noted that each site is located in a different biogeographical setting and all sites are complementary to each other along the geographical transect. The CLIMPEAT project is an exceptional integration of experts aiming to study the responses of temperate peatlands to global change. We hypothesised that peatlands located in transitional climatic zones are particularly sensitive to changing climate. The underlying idea is to determine to what extent climate change will modify peatland functioning in central-eastern Europe. Furthermore, the patterns of the identified proxies are used to reconstruct climate changes during the past 2,000 years.

Much progress has been made towards understanding the responses of peatland ecosystems to global change using either field observations along gradients or mesocosm experiments (Francez 2000, Knorr *et al.* 2008, Granath *et al.* 2010, Limpens *et al.* 2011, Bragazza *et al.* 2013, Jassey *et al.* 2015). However, no previous peatland studies have effectively combined palaeoecological approaches with *in situ* manipulation of temperature and water-table change. We regard it as important to compare palaeoecological and field experimental results using the same/similar proxies like testate amoebae, vegetation and non-pollen palynomorphs (e.g., fungi and algae). The aim of this article is to present the idea of the experimental setup of a field experiment where both warming and water-table depth have been manipulated, and to discuss the concept of integrating the experiment with palaeoecology.

LINJE EXPERIMENTAL SITE

Linje Mire is located in Northern Poland, near the city Bydgoszcz (Figure 1) (coordinates: 53° 11' 15" N, 18° 18' 34" E). The study site is located on a moraine plateau formed 20,000 years BP during the Poznań Phase of Weichselian glaciation (Niewiarowski 1959) and lies on the border between a moraine hill in the western part and a sandur with a dune system in the eastern part (Hałas *et al.* 2008). The mire is located at 91 m a.s.l. and the depth of biogenic deposits reaches 11.9 m in the southern part of the

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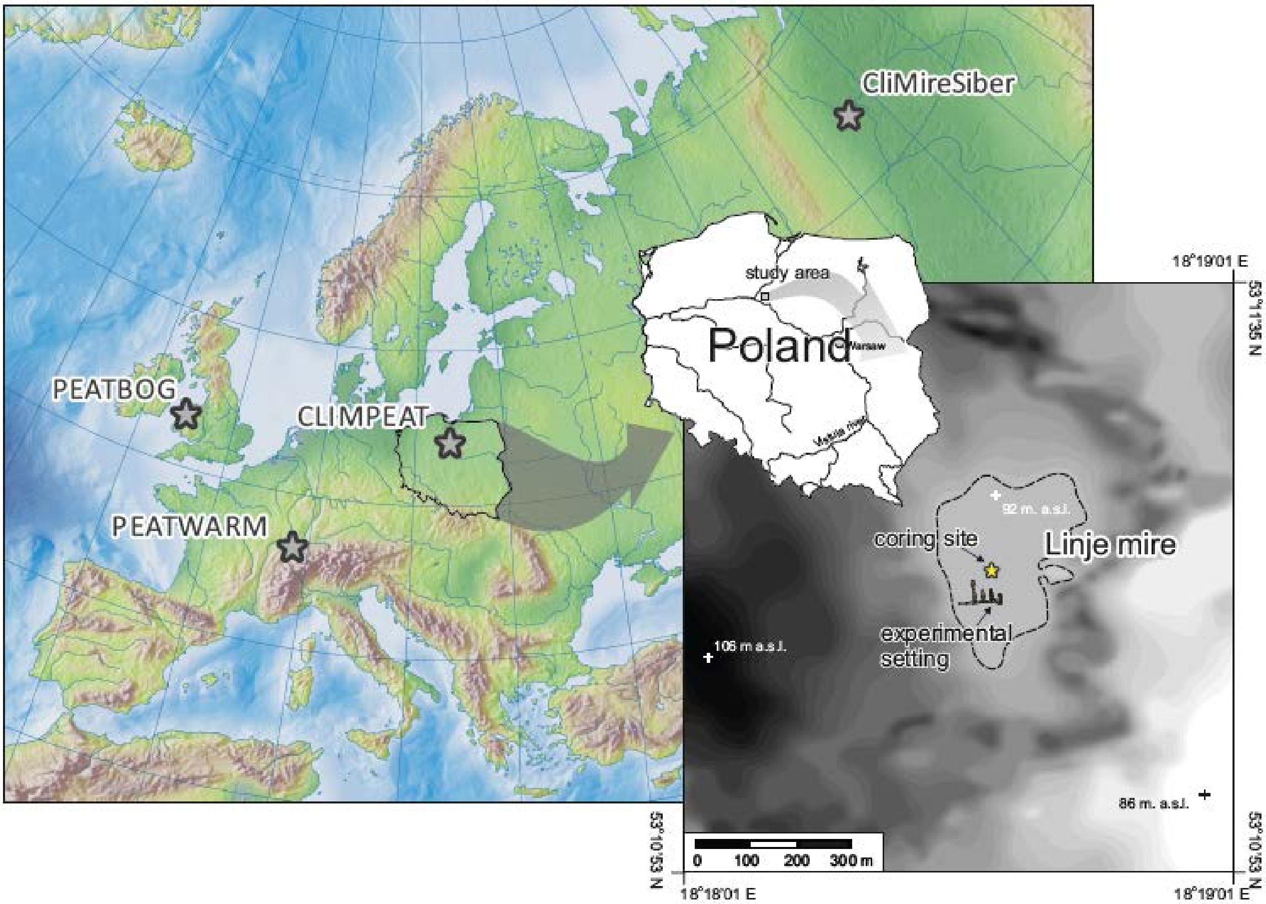

Figure 1. Location of the Linje Mire experimental and palaeoecological sampling site. The sites of similar experiments in France (PEATWARM), England (PEATBOG) and Russia (CliMireSiber) are also indicated.

mire (Kloss & Żurek 2005). Linje Mire is surrounded by mixed forest dominated by *Pinus sylvestris*, *Betula pendula*, *Quercus robur* and *Picea abies*, and is classified as a poor fen, while ombrotrophic vegetation is present in the centre of the mire (Kucharski & Kloss 2005). This site is the only lowland area in Poland with the glacial relict species *Betula nana*.

The peatland is part of a protected area - the Linje Mire Nature Reserve. Linje Mire itself covers 5.95 ha of the 12.7 ha total area of the reserve (Słowińska *et al.* 2010). Since 2008, the peatland has been listed in the EU Natura 2000 habitat area. The mire lies in the contact zone between oceanic and continental air masses, and thus experiences transitional climate conditions. The mean annual air temperature of the area is 7.5–8.0 °C and total annual precipitation is 500–550 mm (Hałas *et al.* 2008).

Linje Mire and other mires in the area were drained in the past. According to historical data (Boińska & Boiński 2004), drainage ditches were established in the vicinity of the nearby villages Gzin and Linie during the second half of 19th century, causing water from Linje Mire to flow out to the south (Słowińska *et al.* 2010). Drainage was subsequently stopped and the peatland has been under protection since AD 1901, but drainage ditches are still visible on its surface (Boińska & Boiński 2004). This site was chosen for the experimental study because the local climate and hydrology are well understood and the micrometeorological conditions and hydrology of Linje Mire have been monitored since AD 2006 (Słowińska *et al.* 2010), including monitoring of hydrological bioindicators (testate amoebae) since 2010 (Marcisz *et al.* 2014).

RESEARCH CONCEPT

In this research we use Linje Mire as a model ecosystem to assess the vulnerability of peatlands in northern Poland to climate change, applying a manipulative experiment that simulates an increase in temperature and drought *in situ*. The underlying idea is to determine to what extent climate warming in combination with drought modifies peatland

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functioning in the middle of the oceanic–continental climate gradient. The Polish bog is a geographic link between other sites in Europe, which will allow assessment of how peatlands in different oceanic–continental climate settings respond to climate change. In particular, we want to investigate how climate change can affect the C-sink function of peatland ecosystems. The general aims of the project are to evaluate the effects of warming and drought on (1) above-ground and below-ground C flux balances, especially *via* ecosystem respiration; (2) biodiversity and microbial activities on *Sphagnum* and in the peat; (3) the structure of plant communities and primary production; and (4) the dynamics of labile and recalcitrant organic matter (OM) in the peat.

Among the approaches used, some are entirely new for this part of Europe. In contrast to previous projects, in this experiment we manipulate not only temperature but also water-table level. Thus, we simulate long-lasting heatwaves. The experimental heating system "Open-Top Chambers" (OTCs), based on a standardised ITEX protocol (Shaver *et al.* 2000), is used for the first time in a Polish peatland ecosystem (Figure 2). This enables comparison with similar experiments elsewhere, in particular in France (PEATWARM project), England (PEATBOG project) and Russia (CliMireSiber project) (Figure 1). A novel aspect of our research is the combination of several complementary disciplines, including palaeoecology, to obtain an optimal view of the complex ecosystem processes in relation to global change. We benefit not only from the foreign study sites but also from one in northern Poland (Rzecin mire, WETMAN project) where carbon sequestration is currently being monitored.

EXPERIMENT

The CLIMPEAT field design is an idea that came from a long-established cooperation between Polish and Swiss partners. The design is partly based on the former field experiment PEATWARM that took place in the French Jura Mountains (Jassey *et al.* 2013). An important added value of this study is that, together with warming (OTC), hydrological manipulation has been applied. This was achieved by modification of the peatland microtopography to artificially create microhabitats such as hollows and hummocks on 1 m^2 plots. We selected 28 plots within the bog with homogeneous plant species assemblages, with a good balance (50 % vascular plants *versus* 50 % mosses) between *Sphagnum* mosses and vascular plants, and comparable water-

Figure 2. Linje Mire experimental site with open-top chambers passive heating system (photo Jan Barabach).

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table depths. Three water-table manipulations (Figure 3B) were randomly assigned to plots and combined with warming (OTC), yielding six treatments - wet plots with and without OTC, dry plots with and without OTC, and intermediate control plots with and without OTC (Figure 4). In addition, intact control plots with and without OTC were installed as in the other projects PEATWARM, PEATBOG and CliMireSiber. For each wet plot, we cut and removed four peat blocks of 50×50×30 cm, then excavated a further 10 cm of peat and replaced the peat blocks in the same order but in a 10 cm lower position. The excavated peat from wet plots was then added to dry plots, following the same procedure except that the peat blocks were raised by 10 cm. In intermediate control plots, the four peat blocks were cut and replaced immediately in their original positions to enable the effect of cutting to be disentangled from that of water-table manipulation when compared to the control plots on intact (uncut) surfaces. All cut plots (1 m^2) were bordered with a plastic sheet of 15 cm height, in order to maintain the structure of the moss carpet. The control plots on intact (uncut) surfaces served also for the comparison across experiments, for example with PEATWARM, where OTC (only) has been used without cutting the peat for water-table manipulation.

Each plot was equipped with air temperature and humidity sensors above the vegetation canopy (HOBO U23 pro v2 with external data logger, Onset Computer Corporation, USA), a soil temperature and moisture sensor (Decagon 5TM connected to a Campbell central data logger), and four of them with a leaf wetness sensor (Decagon Devices) (Figure 4C). Figure 5 shows an example of the warming effect of OTC at the Linje site; which varied with the season and solar radiation. On 05 May 2013, when the strongest warming effect was observed, the difference between OTC and ambient (CTL) plots reached 4.1 °C during daytime. However, a cooling effect of OTC was also observed in the late afternoon and at night. Air humidity responded to air temperature, and vapour pressure deficit was much higher in the OTC plots than in the control plots during daytime. A set of radiation sensors was also attached to the meteorological data logger. These

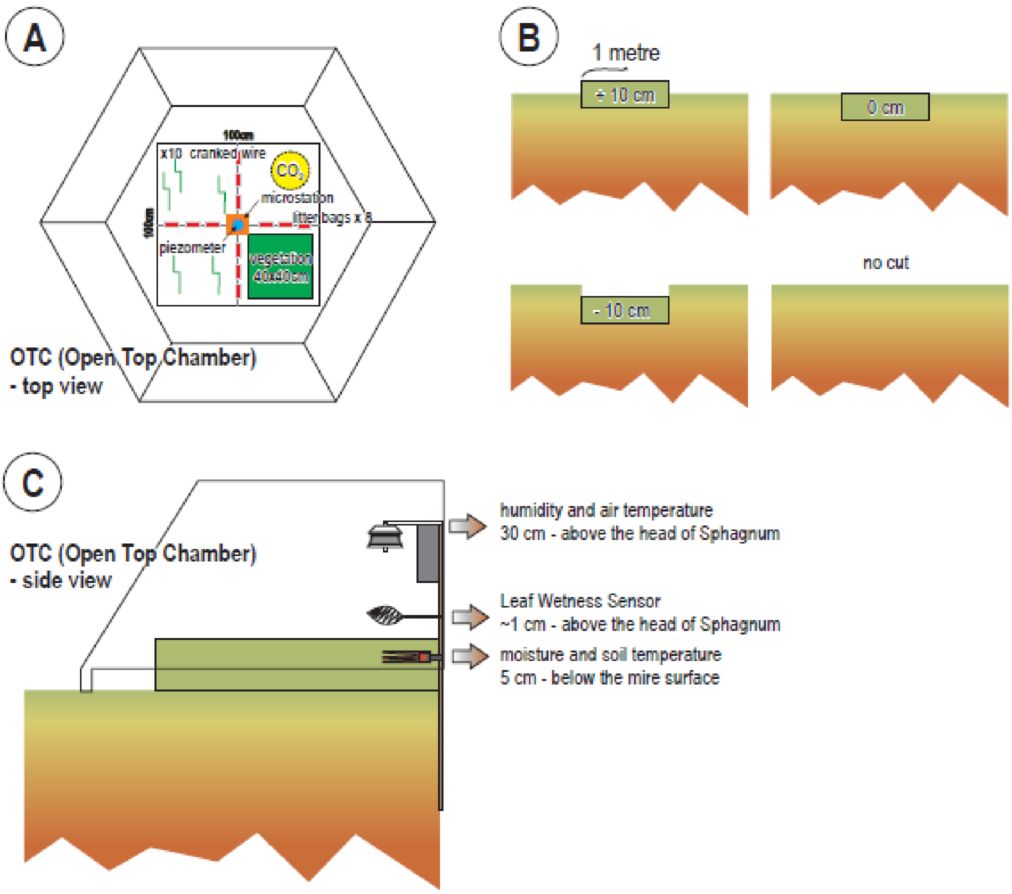

Figure 3. Experimental plot with descriptions of: (A) within-plot space subdivision for the various measurements and sampling; (B) water level manipulation treatments; and (C) environmental monitoring within each plot.

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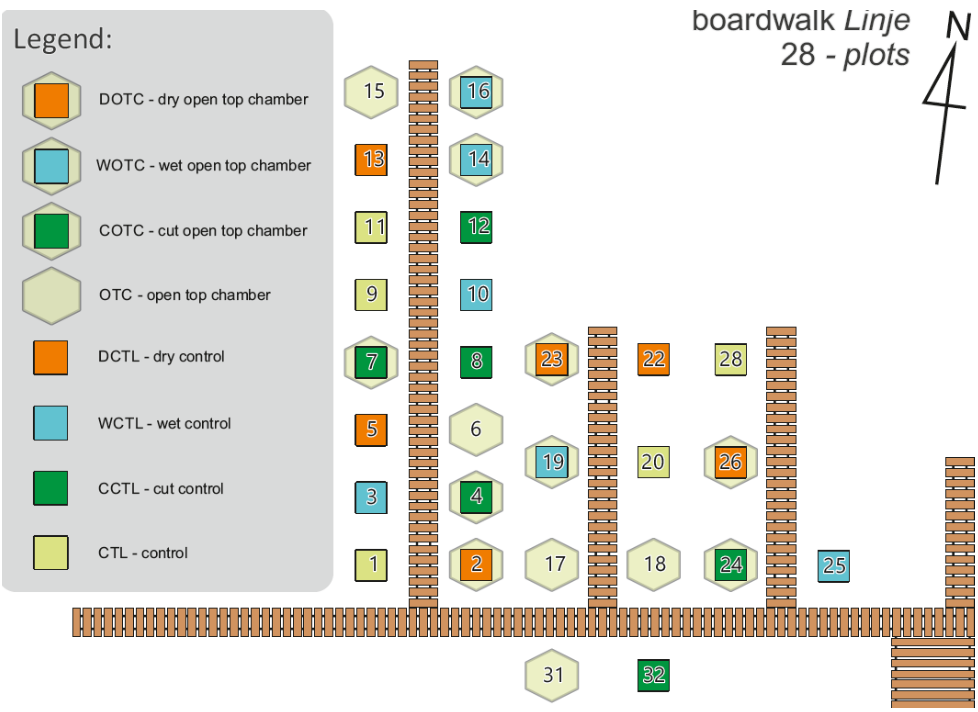

Figure 4. Plan of the experimental site with plots and treatments (OTCs and water-level manipulation): wet–OTC, wet-control, dry-OTC, dry-control, intermediate-control-OTC, intermediate-control, intact-OTC, intact-control.

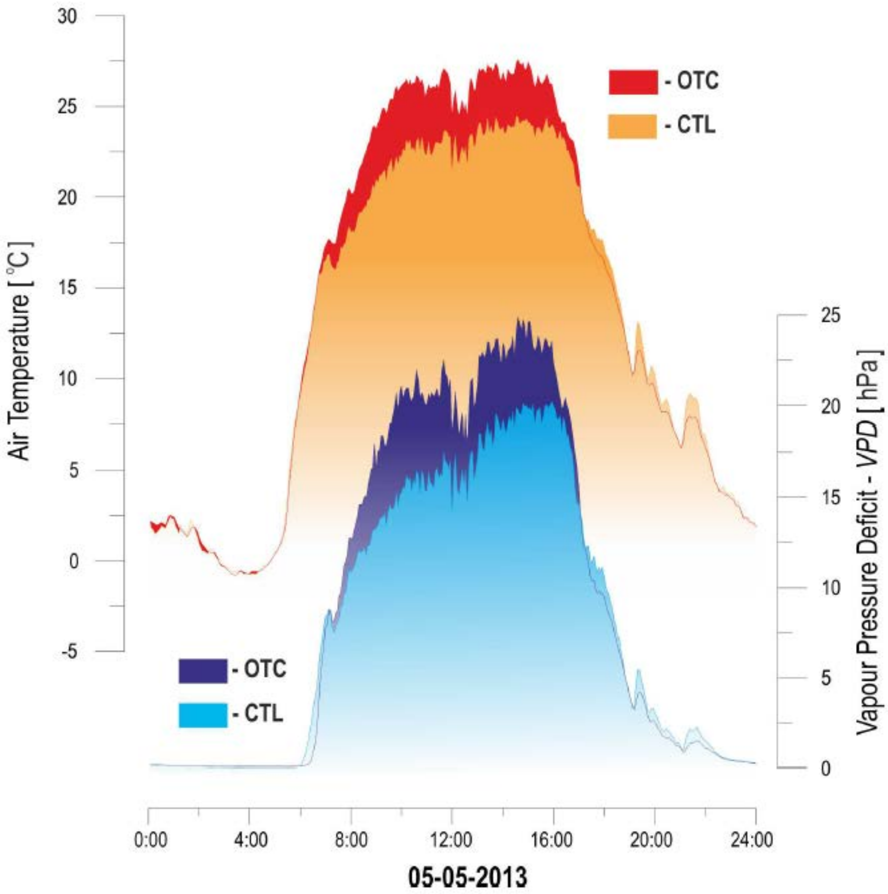

Figure 5. Daily course of averaged air temperature and vapour pressure deficit (*VPD*) 30 cm above the mire surface in OTCs and CTLs plots on 05 May 2013 – exemplary day with the strongest OTC effect.

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sensors were installed at a height of ~ 1.5 m above the surface. Three pairs of sensors were applied to estimate both incoming and outgoing radiation within different spectral ranges. The following radiation types are measured: longwave radiation (spectral range 4.5–40 µm; IR02 pyrgeometer; Hukseflux Thermal Sensors, Delft, the Netherlands), shortwave radiation (spectral range 0.285–3.0 µm; LP02 pyranometer; Hukseflux Thermal Sensors, Delft, the Netherlands), and photosynthetic photon flux density (spectral range 0.410–0.655 µm; SQ-110 quantum sensor; Apogee Instruments, Logan, USA). The values collected can be used to calculate the radiation balance, as the basis for peatland active surface heat balance studies (Runkle *et al*. 2014) and the broadband normalised difference vegetation index (Huemmrich *et al*. 1999), which is the spectral parameter for estimation of the physiological status of vegetation (Chojnicki 2013).

Air temperature and humidity were measured at a height of 30 cm to capture the microclimate of the whole plot. In the centre of each plot a pipe was inserted down to 100 cm depth for water hydrochemistry analyses and for manual readings of water-table depth. The micrometeorological monitoring network that has been in place on Linje Mire since 2006 supports the experiment. Therefore, we have a good understanding of how sensitive the peatland is to micrometeorological variables (Słowińska *et al*. 2013).

Each of the experimental plots comprised four sub-plots (the four cut monoliths) devoted to different measurements (Figure 3A). One sub-plot was used for vegetation surveys following Buttler *et al*. (2015), which involved point-intercept frequency measurements with a pin at 400 points using a frame of 40×40cm (Figure 6), as well as for photographic analyses of the same 40×40 cm surface for frequency measurement on the computer screen, *Sphagnum* increment (cranked wire method) and other non-destructive plant growth measurements. Another sub-plot was used for gas exchange measurements using an infrared analyser (EGM-4, PP System) with a collar of 15 cm diameter inserted into the soil to 10 cm depth. Sampling points for microbes (both biomass and activity) were spread across three of the sub-plots (excluding the sub-plot used for vegetation survey) and marked permanently with small sticks. At each of these points, *Sphagnum fallax* was sampled and fixed in 20 ml of glutaraldehyde (2.5 %

Figure 6. Point-intercept vegetation study - fieldwork (photo Thomasz Horla, summer 2013).

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final concentration). The biomass of various microbial groups (bacteria, fungi, cyanobacteria, protists, micrometazoans) living in the *Sphagnum* moss was quantified according to (Gilbert *et al.* 1998), in order to determine the response of the structure of microbial communities to climate change. Microbial enzymatic activity was assessed according to (Jassey *et al.* 2011); enzymes associated with both easily degradable (hydrolases) and recalcitrant (oxidases) compounds were quantified. Connected to microbial activity and community structure, the rate of decomposition of various litter mixtures was studied by means of litter bags which were inserted along the trenches separating the four cut monoliths.

The boardwalk design is illustrated in Figure 7. This construction was considered to be very important in preventing any trampling of the field site during the measurement and maintenance works. The open deck of the boardwalk was positioned 70 cm above the peatland surface. Poles were made of oak, while pine wood was used for other parts. This construction is expected to last for at least ten years.

The CLIMPEAT field experimental design, including the palaeoecological approach, was applied similarly at the Mukhrino peatland in Western Siberia (Figure 8). A group of researchers from France, Switzerland and Poland set up the same experiment during expeditions in 2012 and 2013 within the INTERACT EU project (http://www.eu-interact.org), and the site was subsequently equipped with the OTCs and sensors. Comparisons between the Linje and Mukhrino sites will provide an interesting view at continental scale of the climate impact on peatland ecosystems.

PALAEOECOLOGY

Knowledge of the history of any ecosystem is important for the appropriate understanding of its present state (Willis *et al.* 2010). Palaeoecology is able to reveal the historical perspective of past disturbance to an ecosystem that is under experimental study (Chambers *et al.* 1999). Indeed, long-term ecological studies provide important information on the dynamics of peatlands, past disturbance, and ecosystem resilience (Turetsky & Louis 2006, Lavoie & Pellerin 2007, Turner & Swindles 2012, Ireland *et al.* 2014).

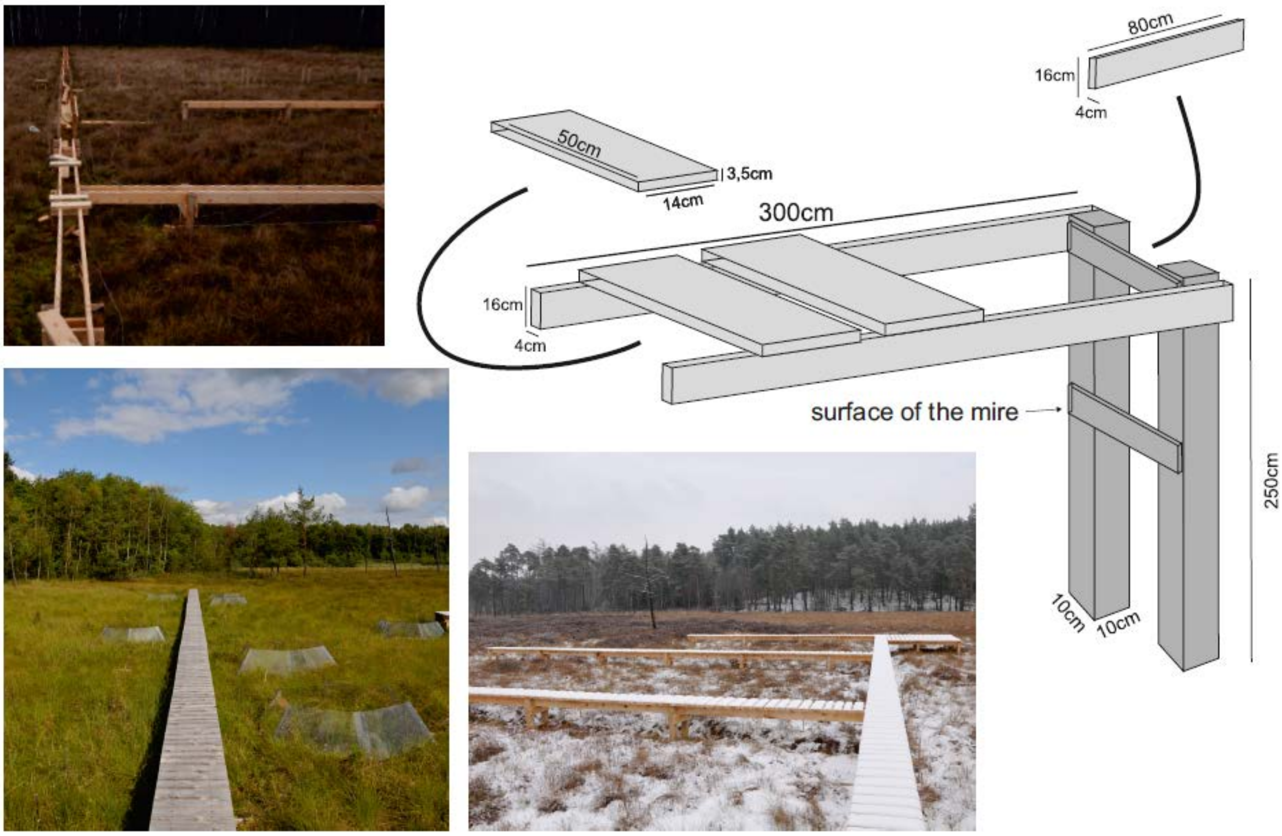

Figure 7. Design of the boardwalk at Linje Mire.

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Figure 8. Mukhrino Mire experimental site. The Linje Mire (Poland) experimental design was applied at this peatland in Western Siberia (Russia) in 2013 (photo Alexandre Buttler).

Linje is an exceptional case study in that it integrates the plot-scale experimental approach (four years) and site-scale environmental monitoring (eleven years) (Słowińska *et al.* 2010) with a high-resolution multi-proxy palaeoecological investigation (past 2,000 years). It often happens that, despite being included (as a work package/task) in interdisciplinary projects, palaeoecology is finally neglected in projects that focus on manipulative field experiments. Despite the fact that integration of ecology and palaeoecology is mentioned in several publications (Rull 2010, Willis *et al.* 2010, Willis & Bhagwat 2010, Rull & Vegas-Vilarrubia 2011, Rull 2014, Cole *et al.* 2015), such approaches are rare, especially in the case of peatland ecosystems (Chambers *et al.* 2007a, Chambers *et al.* 2007b, Chambers *et al.* 2013, Gałka *et al.* 2016, McCarroll *et al.* 2016). However, linking long-term temporal scales with short-timescale processes is especially inspirational in terms of prompting novel research questions (Fukami & Wardle 2005, Sutherland *et al.* 2013, Seddon *et al.* 2014,) relating to the complex responses of peatlands to global warming, human impact and fire activity (Marcisz *et al.* 2016).

In the CLIMPEAT project, the palaeoecological work package provided an important temporal perspective on past disturbance of the peatland Linje Mire (Marcisz *et al.* 2015) where it appears that *Sphagnum* cover has been transformed, mainly through drainage *ca*. 100 years ago (Figure 9A). The CliMireSiber site located in Western Siberia also changed its path of development *ca*. 100 years ago (Lamentowicz *et al.* 2015) (Figure 9B); however, this was most probably a natural shift connected with climate change or the development of bog microforms. Indeed, the two sites possess contrasting development histories with different levels of direct (Linje) and indirect (Mukhrino) disturbance. Linje has experienced increasing anthropic disturbance since the Middle Ages, when landscape openness was increasing through deforestation. At a later stage, Linje was also affected by eutrophication resulting from the development of agriculture and industry in the surroundings. In conjunction with the industrial dust deposition, Linje was drained and peat was extracted from its northern part. Thus, the CLIMPEAT experiment is taking place in a secondary succession (with *Sphagnum fallax* as the dominant moss species) towards recovery from anthropic disturbances (Figure 9A). The Mukhrino site in Siberia appears to be pristine in terms of direct human impact on hydrology and vegetation, experiencing its first human impacts through atmospheric dust input only during the last century (Fiałkiewicz-Kozieł *et al.* under review). Thus, its development was mainly driven by climatic and

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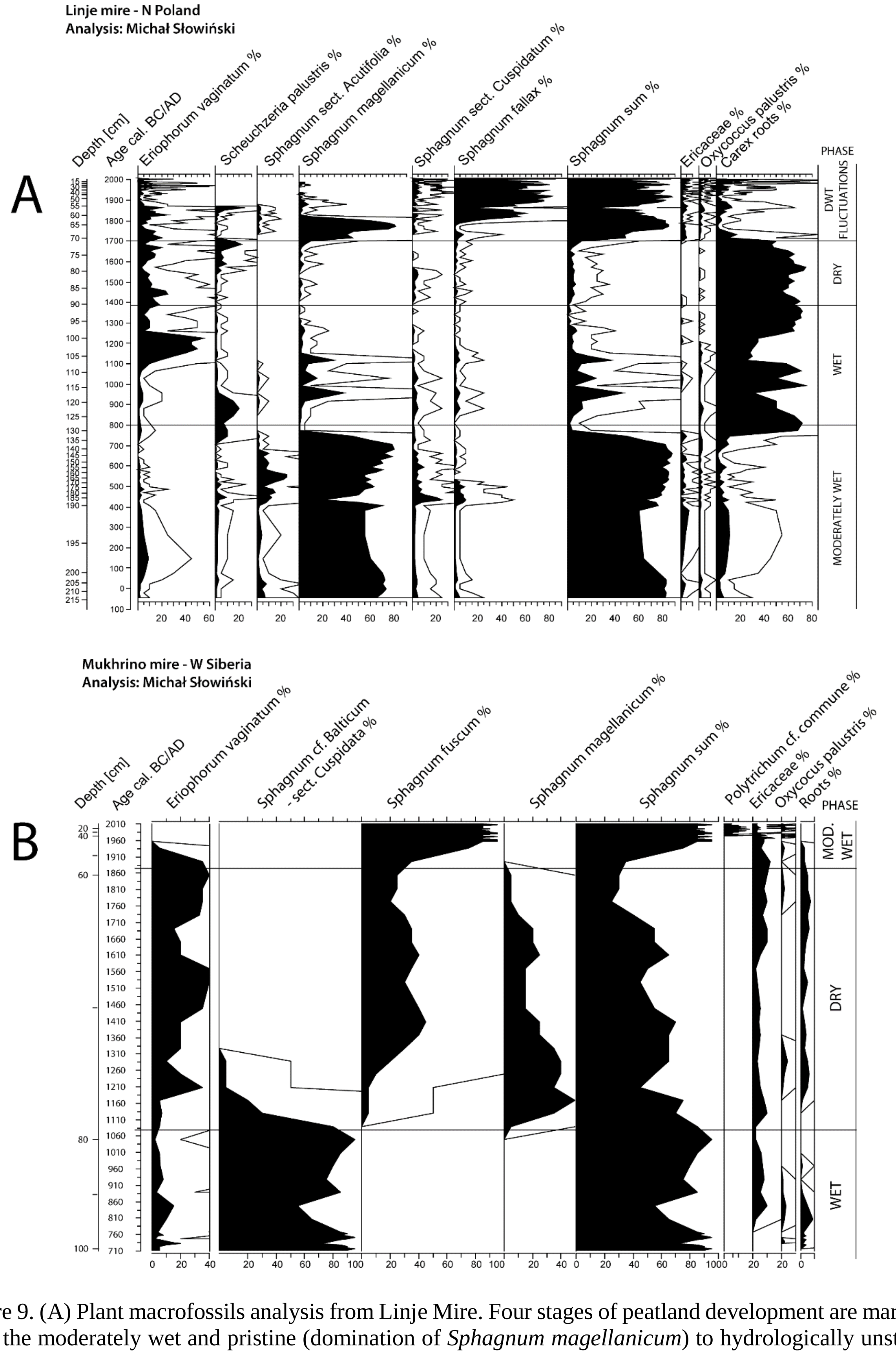

Figure 9. (A) Plant macrofossils analysis from Linje Mire. Four stages of peatland development are marked, from the moderately wet and pristine (domination of *Sphagnum magellanicum*) to hydrologically unstable modern peatland (domination of *Sphagnum fallax*) (modified from Marcisz *et al*. 2015). (B) Plant macrofossils analysis from Mukhrino mire. Three stages of peatland development are marked, from wet (domination of *Sphagnum cf. Baltcum*) to moderately wet modern peatland (domination of *Sphagnum fuscum*) (modified from Lamentowicz *et al.* 2015).

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autogenic processes and, therefore, the experiment is taking place in almost-pristine conditions (Figure 9B). Despite these contextual differences, both experiments operate in real life, reflecting conditions that are typical for peatlands under long-term significant (Linje Mire) and short-term insignificant (Mukhrino Mire) human impact. Ecosystems in pristine (or close to pristine) condition can respond differently to experimental manipulations than systems that have been under anthropic influence/stress for hundreds of years. However, the effects of the intensity of past human impact on the results of manipulative experiments in peatlands have not been well studied and need more attention in the future.

DISCUSSION: COMBINING LONG-TERM WITH SHORT-TERM STUDIES

Descriptive ecological datasets (calibration/training datasets) are often applied to fossil data to obtain quantitative estimates of past environmental changes in peatland and lake ecosystems (Booth *et al.* 2008, Rees *et al.* 2008, Horsák 2011). Calibration datasets are collected along different gradients in space to infer past changes, such as trophic status and water quality (Bennion *et al.* 2001, Roe *et al.* 2010, Patterson *et al.* 2012), temperature (Lotter *et al.* 1999, Brooks 2006, Finsinger *et al.* 2007) or hydrological status (Charman *et al.* 2010, Väliranta *et al.* 2012, Nevalainen *et al.* 2013, Swindles *et al.* 2014, Van Bellen *et al.* 2014). In reality, present-day analogue communities are sought out and related to the fossil communities, in order to reconstruct past environmental variables quantitatively (Juggins & Birks 2012). Most of the studies providing such calibration datasets are purely observational using “natural experiments” (altitudinal or latitudinal gradients) to explore palaeoecological changes (Seppä *et al.* 2004). However, building a robust calibration dataset is very often challenging (Heiri *et al.* 2011). Experimental approaches under controlled conditions are an appropriate way to build and test such datasets and can become a reliable basis for calibration and for considering various climatic scenarios. Ultimately, the model of peatland response to climate/land-use changes can be based on long-term studies covering, for example, the last 10,000 years. Perspectives of past changes can be used for the projection of impact of future climate change and/or to find reference conditions for restoration activities in nature protection.

Quantitative hydrological reconstructions from peatlands are usually based on testate amoebae space-for-time substitution (Charman 1997, Booth 2007, Payne *et al.* 2008, Roe *et al.* 2010, Swindles *et al.* 2014). Most of the calibration datasets were sampled from wide areas of Eurasia and North America, now also partly from Patagonia (Booth 2002, Van Bellen *et al.* 2014, Lamentowicz *et al.* 2015, Amesbury *et al.* 2016). Most transfer functions are based on environmental variables (e.g., water table) measured only once in the field. Long-term estimation of the water table or hydrochemistry is usually not available for a calibration dataset. In this situation, manipulative experiments can provide a basis for building and testing a calibration dataset. However, such strongly integrated designs do not exist, despite an important need to test proxies and long-term responses of peatland ecosystem to various disturbances.

The need for integration of ecology and palaeoecology has been mentioned in various publications (Rull 2014, Seddon *et al.* 2014). However, there is still a need for better integration of the two disciplines, as they are methodologically very close and, therefore, they allow a beneficial flow of ideas and concepts (Figure 10). Development of basic ecological concepts and the application of these concepts to environmental problems can be more effective when conducted in a complementary manner (Fukami & Wardle 2005). Monitoring and purely observational ecological studies are placed somewhere between experimental and palaeoecological studies, and they fairly complete the understanding of ecosystem dynamics. Overall, both long-term palaeoecological approaches and short-term experimental approaches provide important tools for nature conservation and management, especially in the context of global change.

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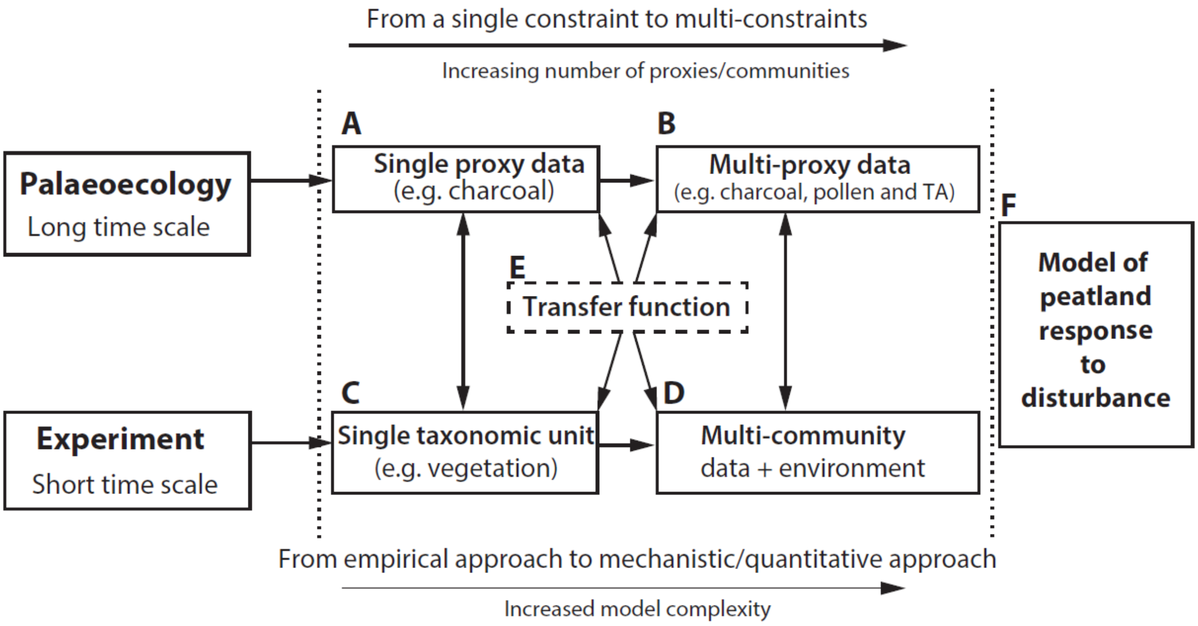

Figure 10. A concept for linking palaeoecological and experimental approaches. The diagram shows an increasing complexity of the palaeoecological information/record from one proxy to multiple proxies, paralleled by an increasing complexity in experiments on population to communities. As the number of dimensions of datasets increases, the complexity of models based on transfer functions also increases.

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