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**Evaluating restoration success of rewetted peatlands:
Recovery potential, temporal dynamics and comparison of
monitoring approaches**

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Summary

Ecological restoration has great potential for counteracting global losses in biodiversity and ecosystem functioning caused by unsustainable human land use. It aims at assisting the recovery of degraded ecosystems. Many restoration projects focus on peatlands, because of the significance of these ecosystems for adaptation and mitigation of climate change. Intact peatlands provide important ecosystem services like storage of water and carbon, and offer habitats for rare and endangered species, while they are highly threatened by drainage, peat extraction and afforestation. Peatland restoration supports biodiversity and ecosystem functions by creating near-natural habitat conditions, mostly through rewetting. While most meta-analyses report an incomplete short-term recovery of restored ecosystems, their long-term dynamics remain largely unknown. Peatland recovery is commonly monitored shortly after restoration, but peatlands develop slowly and initial trends may not continue. Moreover, restored peatlands are expected to provide multiple ecosystem services. This makes their assessment and evaluation of success challenging and requires novel monitoring approaches.

Thus, the **goals of this thesis** are (1) to contribute to the scientific understanding of peatland recovery and its temporal dynamics, and (2) to improve monitoring indicators and analytical methods. For this purpose, I established a chronosequence of 18 years after rewetting in 14 peatlands in a mountainous region in Central Germany comparing three drained, 19 restored and one near-natural peatland transect. Peatlands in the study region had been previously drained and afforested, and from 1998 onwards were rewetted by damming, filling of drainage ditches and removing of trees. For monitoring several ecosystem properties (i.e. water table, peat decomposition, water holding capacity, nutrient level) and characteristic peatland biodiversity (plants, dragonflies and butterflies) were assessed. I also set up a field experiment on phytometer plants in seven restored peatlands and an associated greenhouse experiment.

In the **first article** of the PhD thesis, temporal trends of plant, dragonfly and butterfly diversity were analysed and related to restored habitat conditions. It showed that, rewetting improved habitat conditions, vegetation structure and species diversity. Plants and dragonflies benefitted most from rewetting, while no specialized butterfly species were found within two decades after rewetting, and also generalists increased only temporarily. This is most likely due to poor regional connectivity of the (restored) peatlands. Dragonflies colonized immediately, once suitable bog pools were present in restored sites. Plants more slowly developed towards reference conditions, and mostly depended on undegraded peat with a

high water holding capacity. These findings suggest, that recovery is not complete after 18 years and that the three species groups are complementary indicators for restored peatlands.

The **second article** studied the responses of three characteristic peatland plants (*Drosera rotundifolia*, *Eriophorum vaginatum*, *Vaccinium oxycoccos*) to restored environmental conditions by measuring various fitness traits in two phytometer experiments. While all three species are indicators for intact peatlands, their responses to rewetting were species-specific. *E. vaginatum* performed best, since all individuals survived under field conditions. The development of *D. rotundifolia* and *V. oxycoccos* was less successful, but also those species locally found suitable habitat conditions. These results highlight that local site limitation occurs, but also point at dispersal limitation. Among all measured fitness traits, many growth traits were partly redundant, and survival provided the most conclusive results for species adapted to stressful habitats. Generally, the most suitable fitness trait depends on the growth form of the respective species.

The **third article** analyses the simultaneous recovery of multiple peatland properties with time since restoration using different multifunctionality approaches. As a reference, an optimum level was defined as the mean of the eleven highest values, while the intact peatland was excluded from the analysis. Nine out of 13 studied properties as well as the combined index significantly improved with time since restoration. Most important changes were observed within the first five years, inside the rewetted ditches, and at low or intermediate levels of functioning. A simultaneous recovery of multiple properties at high levels of functioning was not observed. These results highlight, that heavily degraded peatlands show considerable improvements in the first years after restoration, while they cannot fully recover within two decades.

The **general discussion** compares the main findings in order to derive overall conclusions and recommendations for future monitoring and peatland management. New approaches like the use of phytometers or multifunctionality approaches are promising, but differ in their degree of comprehensiveness and explanatory power and therefore need to be carefully selected according to project goals. Indicators (ecosystem properties, taxonomic groups, species traits) differ in their response to the same treatment and therefore have to be thoroughly chosen. Restored peatlands need to be surveyed even longer than two decades in order to understand if full recovery is possible. Finally, additional management measures (dam reinforcement, repeated tree removal, improved connectivity, species introduction) should be further explored in order to advance peatland restoration to its best.

Zusammenfassung

Ökologische Renaturierung kann durch ungeeignete Landnutzung verursachten globalen Verlusten an Biodiversität und Ökosystemfunktionen entgegenwirken. Ihr Ziel ist es die Regeneration degradierter Ökosysteme zu unterstützen. Moore stehen dabei aufgrund ihrer großen Bedeutung für den Klimaschutz häufig im Fokus von Renaturierungsprogrammen. Intakte Moore stellen wertvolle Ökosystemdienstleistungen zur Verfügung. Sie dienen beispielsweise als Wasserrückhalt, Kohlenstoffspeicher und Lebensraum für seltene und gefährdete Arten. Gleichzeitig sind sie bedroht durch Entwässerung, Torfentnahme und Aufforstung. Moorrenaturierung soll die Biodiversität und Funktionen dieser Ökosysteme fördern, indem durch Wiedervernässung naturnahe Habitatbedingungen geschaffen werden. Mehrere Meta-Analysen berichten von einer unvollständigen Regeneration renaturierter Ökosysteme über kurze Zeiträume. Über die langfristige Entwicklung renaturierter Moore ist jedoch noch wenig bekannt. Obwohl sie sich nur langsam erholen und anfängliche Trends sich manchmal nicht fortsetzen, finden Erfolgskontrollen meist kurz nach Maßnahmenumsetzung statt. Außerdem wird meist erwartet, dass Moore gleichzeitig mehrere Ökosystemdienstleistungen erbringen. Dies stellt eine zusätzliche Herausforderung für Erfolgskontrollen dar und erfordert neue Monitoringansätze.

Diese Dissertation soll (1) zum wissenschaftlichem Verständnis der Regeneration von Mooren und ihrer zeitlichen Entwicklung beitragen und (2) Indikatoren der Erfolgskontrolle sowie Auswertungsmethoden verbessern. Dazu wurden 14 Moore im Fichtelgebirge und Steinwald ausgewählt und anhand einer unechten Zeitreihe drei entwässerte, 19 renaturierte und ein naturnaher Bereich miteinander verglichen. Die Moore des Untersuchungsgebietes waren zuvor entwässert und aufgeforstet worden. Ab 1998 wurden sie mit Hilfe von Dämmen, Grabenverfüllung und Baumentnahme wiedervernässt. Als Bestandteil der Erfolgskontrolle wurden verschiedene Ökosystemeigenschaften (Wasserstand, Torfzersetzung, Wasserhaltekapazität, Nährstoffe) und die moortypische Biodiversität (Pflanzen, Libellen und Tagfalter) erfasst. Zusätzlich wurden in sieben Mooren ein Freiland- und ein Gewächshausexperiment mit Phytometern angelegt.

Der **erste Artikel** dieser Dissertation analysiert die zeitlichen Entwicklung der Pflanzen-, Libellen- und Tagfalterdiversität und setzt sie in Bezug zu abiotischen Bedingungen. Er zeigt, dass eine Wiedervernässung moortypische Lebensräume, Vegetationsstruktur und Artenvielfalt verbessern konnte. Pflanzen und Libellen profitierten dabei am meisten, während moorspezifische Tagfalter zwei Jahrzehnte nach der Renaturierung nicht nachgewiesen werden konnten; auch Generalisten nahmen nur vorübergehend zu. Der

Grund hierfür liegt vermutlich in einer schlechten regionalen Vernetzung der (renaturierten) Moore. Libellen besiedelten die renaturierten Moore dagegen unmittelbar, sobald geeignete Gewässer verfügbar waren. Pflanzen näherten sich dem Zielzustand langsamer an. Dabei ist ihre Wiederansiedlung in erster Linie von intakten Torfen mit einer hohen Wasserhaltekapazität abhängig. Diese Ergebnisse zeigen, dass sich Moore innerhalb von 18 Jahren nicht vollständig regenerieren und, dass die drei untersuchten Artengruppen komplementäre Indikatoren darstellen.

Der **zweite Artikel** untersucht in zwei Phytometer-Experimenten die Reaktion dreier moortypischer Pflanzenarten (*Drosera rotundifolia*, *Eriophorum vaginatum*, *Vaccinium oxycoccos*) auf renaturierte Habitatbedingungen. Die Ausprägung ihrer Wuchseigenschaften wurde dabei als Indikator ihrer Fitness vermessen. Während alle drei Arten Zeiger intakter Moore sind, reagierten sie unterschiedlich auf die Wiedervernässung. *E. vaginatum* entwickelte sich am besten, da im Freilandversuch alle Individuen überlebten. *D. rotundifolia* und *V. oxycoccos* waren weniger erfolgreich, aber auch diese Arten fanden lokal geeignete Bedingungen vor. Dies deutet auf eine lokale Standortlimitierung in den renaturierten Mooren hin. Ein Abgleich dieser Ergebnisse mit natürlichem Vorkommen der Arten lässt aber auch eine Ausbreitungslimitierung vermuten. Die Korrelation aller gemessenen Pflanzeigenschaften zeigte, dass viele Wachstumsgrößen redundant sind. Für wenig stresstolerante Arten lieferte das Überleben der Pflanzen die schlüssigsten Ergebnisse. Im Allgemeinen entscheidet die Wuchsform der jeweiligen Art darüber, welche Eigenschaften am besten ihre Fitness beschreiben.

Der **dritte Artikel** untersucht die gleichzeitige Regeneration zahlreicher Mooreigenschaften seit der Renaturierung anhand verschiedener Ansätze zur Berechnung von Multifunktionalität. Als Referenz bzw. Optimum diente das Mittel der elf höchsten gemessenen Werte; das naturnahe Moor wurde dahingegen von der Analyse ausgeschlossen. Neun von 13 Mooreigenschaften sowie ihr kombinierter Index verbesserten sich signifikant seit Beginn der Renaturierung. Dabei geschahen die größten Veränderungen in den ersten fünf Jahren, innerhalb der wiedervernässten Gräben und bei einem niedrigen bis mittleren Funktionalitätslevel. Diese Ergebnisse heben hervor, dass sich stark degradierte Moore in den ersten fünf Jahren nach der Renaturierung entscheidend verbessern, aber sich auch innerhalb von zwei Jahrzehnten nicht vollständig regenerieren.

Die **übergeordnete Diskussion** vergleicht die wichtigsten Ergebnisse der drei Artikel miteinander, um allgemeine Schlussfolgerungen sowie Empfehlungen für künftiges Monitoring und Management ableiten zu können. Neue Ansätze wie die Verwendung von Phytometern oder Multifunktionalitätsberechnungen sind vielversprechend, unterscheiden

sich aber stark in ihrem Anwendungsbereich und insbesondere im Grad der Vollständigkeit sowie ihrem Erklärungswert. Deshalb muss ihr Nutzen entsprechend der jeweiligen Projektziele abgewogen werden. Auch einzelne Indikatoren (Ökosystemeigenschaften, Artengruppen, Wuchseigenschaften von Pflanzen) können unterschiedlich auf die gleiche Veränderung reagieren und sind daher ebenso sorgfältig auszuwählen. Renaturierte Moore sollten zukünftig mehr als zwei Jahrzehnte beobachtet werden, um zu verstehen, ob eine vollständige Regeneration möglich ist. Um die Renaturierungspraxis nicht nur im Untersuchungsgebiet maximal voranzutreiben, sollten zudem verschiedene Maßnahmen (Verstärkung der Dämme, wiederholte Baumentnahmen, Verbesserung der Vernetzung, Wiederansiedlung von Arten) weiter untersucht werden.

GENERAL INTRODUCTION

Restoring degraded ecosystems

Ecological restoration is no longer an option but a necessity in a world, that has undergone considerable changes with far-reaching consequences for the natural and human environment (JONES et al. 2018). Humans have transformed landscapes and ecosystems by favouring productive ecosystem attributes, such as exploitation of natural resources, while ignoring or accepting the associated trade-offs of ecosystem resilience and degradation (KAREIVA et al. 2007). SANDERSON et al. (2002) estimated that 83% of the global land surface have experienced direct human influence. The consequences are losses of certain ecosystem attributes, whose significance is not directly visible but can be crucial for maintaining vital ecosystem functions like climate regulation, freshwater provision or even food production (FOLEY et al. 2005). Also, unsustainable human land use has caused marked biodiversity losses (SALA et al. 2000), so that currently species extinctions occur faster than ever before and many more threatened biodiversity is likely to vanish in near future (PIMM et al. 1995).

Degraded ecosystems are losing their functionality in many aspects. Ecosystem processes like primary production, nutrient and carbon cycles or decomposition are altered, and also ecosystem services, that directly or indirectly benefit humans are affected (MEYER et al. 2015). At the same time, degraded ecosystems are not capable of providing habitat for specialized and often threatened species. Though, biodiversity is not only valuable in its own right, but also an important driver of ecosystem functions, as shown by the field of biodiversity-ecosystem functioning (BEF) research (CARDINALE et al. 2012, GAMFELDT et al. 2013, BYRNES et al. 2014). However, current changes and processes are threatening biodiversity. Many species suffer from a lack of suitable habitats due to unsustainable land-use changes (KERR & DEGUISE 2004). Furthermore, increasing fragmentation, i.e. smaller and more isolated habitats, limits dispersal and negatively affects population dynamics (FAHRIG 2001, TUCKER et al. 2018). These developments highlight the crucial need not only for conserving remaining habitats and species, but for actively reversing anthropogenic changes by restoring the degraded ecosystems in order to halt losses in biodiversity and ecosystem functions.

Ecological restoration is most commonly defined as “the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed” (SOCIETY FOR ECOLOGICAL RESTORATION INTERNATIONAL 2004). Its major goal is to bring an ecosystem on a trajectory of recovery, while focusing on key ecosystem attributes, i.e. suitable physical conditions, plant

and animal species composition, structural diversity, ecosystem functionality, the absence of threats by contamination or invasive species, and external exchanges like connectivity and processes at the landscape scale (MCDONALD et al. 2016). As people have become aware of ongoing global changes, restoration projects have been increasingly implemented in nature conservation practice; they are supported by policy commitments and large public investments (e.g. ZHANG et al. 2000). The success of these projects depends on the capacity to effectively and efficiently implement restoration measures, while the science of restoration is relatively young and many questions remain open. For answering them, restoration practice and science should benefit from each other. While research can take advantage of the large number of accomplished restoration projects and use them as experiments that can inform ecological theory (HOLL et al. 2003), practitioners can learn from their results and translate them into future restoration actions.

Several meta-analyses have studied the overall potential of ecosystem restoration by summing up numerous case studies in order to understand overall processes. REY BENAYAS et al. (2009) were the first to globally evaluate the effectiveness of restoration actions with respect to ecosystem services and biodiversity. MORENO-MATEOS et al. (2017) estimated the degree of ecosystem recovery, while differentiating between biomes and degrading factors. Most recently JONES et al. (2018) analysed the benefits of active vs passive restoration – in the latter case allowing an ecosystem to recover without human intervention, but ceasing negative effects. Their conclusions are similar, as they all state an incomplete recovery compared to intact reference systems or – as MORENO-MATEOS et al. (2017) called it – a ‘recovery debt’ (Fig. 1). They highlight the importance of conservation as a key strategy and criticize restoration as a compensation tool for new habitat destruction, while they clearly show that significant improvements can be achieved. However, they fail to differentiate between trial-and-error approaches and projects based on ecological hypothesis testing. So finally and maybe most importantly, this research shows that for progressing we need to understand the underlying drivers of this incomplete recovery, that can be global, but also ecosystem-specific and dependent on time-scales. Since to date there is no universal recipe for ecosystem restoration, monitoring of past (un)successful projects is crucial for understanding and improving future efforts (GEIST & HAWKINS 2016).

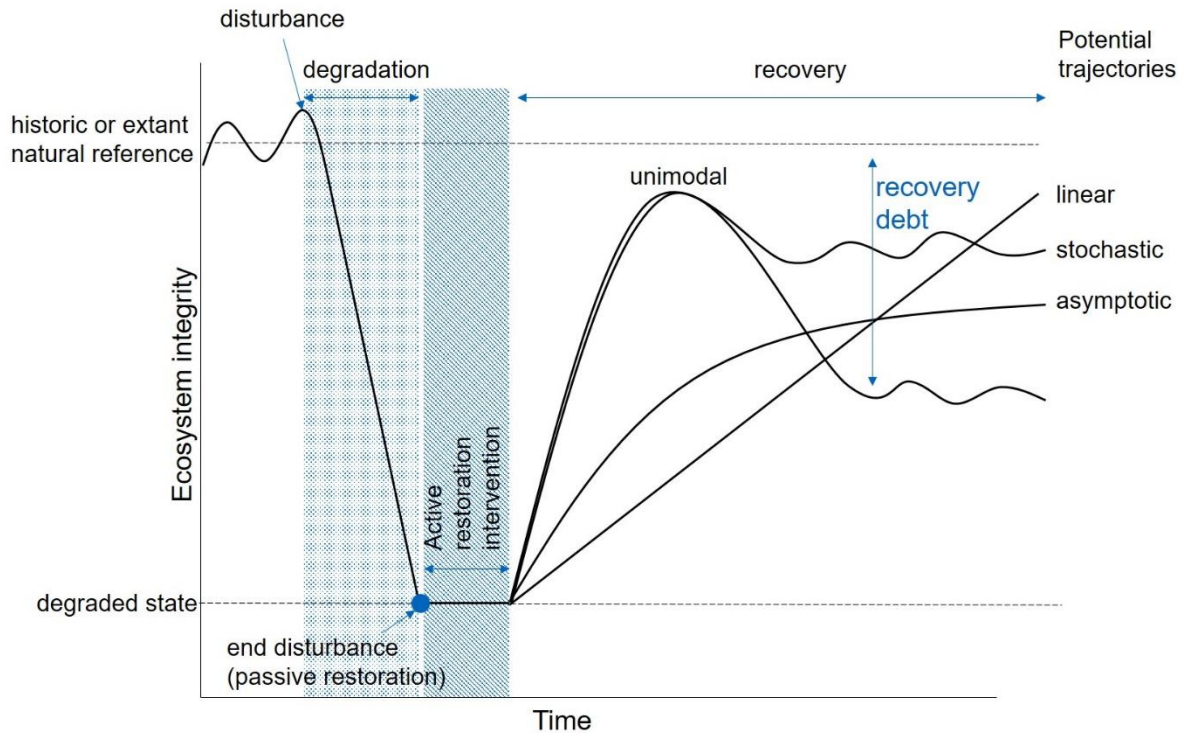


Fig. 1: Degradation and restoration of ecosystem integrity with time. Restoration can be passive after the end of human disturbance or include active intervention measures (e.g. rewetting). After restoration multiple recovery trajectories are possible. Figure modified after JONES et al. (2018) with elements of BULLOCK et al. (2011) and MORENO-MATEOS et al. (2017).

Challenges in monitoring restoration success

The extensive literature on ecological monitoring (see LINDENMAYER & LIKENS 2010) stresses its crucial role for verifying the effectiveness of restoration efforts and advancing future project success. Monitoring is used in a large variety of contexts ranging from curiosity-driven over mandated to question-driven approaches (LINDENMAYER & LIKENS 2010). Yet, it is certainly not only a management activity, but an important basis for scientific research. Against this background, the need for thorough theory-driven evaluations becomes even more evident. However, evaluating restoration is not straightforward and has caused intense discussions on (i) what characterizes restoration success, and (ii) when and (iii) how best to measure it (WORTLEY et al. 2013).

Objectives and references of restoration

Above all else, the definition of success first depends on goals and references (Fig. 2) that are realistic and verifiable (PALMER et al. 2005, LINDENMAYER & LIKENS 2010), while acknowledging the fact that they might be conflicting (BULLOCK et al. 2011). Practitioners do monitoring for management reasons and can focus on the goals set beforehand, whereas

scientists search for a more fundamental ecological understanding that requires to more comprehensively assess ecosystem integrity. For doing so, most commonly, restoration ecologists have compared restored sites to (historic) natural reference systems (e.g. KLIMKOWSKA et al. 2007, HEDBERG et al. 2013), and restoration guidelines also recommend this approach to practitioners (e.g. SOCIETY FOR ECOLOGICAL RESTORATION INTERNATIONAL 2004, McDONALD et al. 2016). However, target states based on the comparison to reference conditions might be too narrow for some types of restoration in a changing world (HIGGS et al. 2018), and are certainly not feasible in the absence of suitable natural references, as for example in novel ecosystems or extensively degraded landscapes. Therefore, multiple potential outcomes should be targeted and *processes* should be favoured over *structures* in attempts to evaluate restoration success (HIGGS et al. 2014).

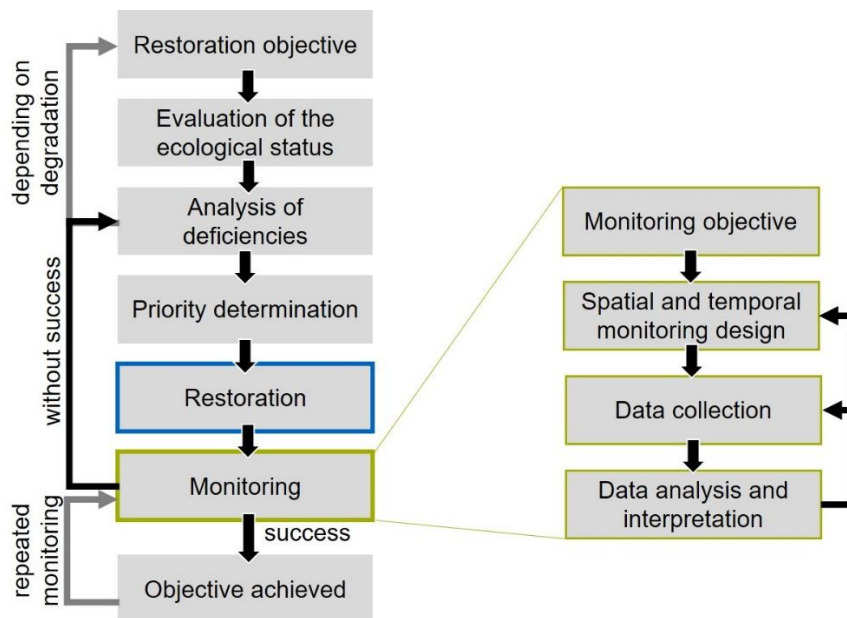


Fig. 2: The process of restoration and its monitoring includes a step-by-step procedure from stating restoration objectives to their achievement. A well-designed monitoring is the prerequisite for judging restoration success. Figure modified after PANDER & GEIST (2013) and SIDDIG et al. (2016).

Time scale of restoration assessment

Another challenge in ecological monitoring addresses its time frame (Fig. 3). For judging restoration success, we need to have sufficiently long monitoring periods, that capture the moment of maximum recovery. Nevertheless, many authors report, that most studies are carried out too short after restoration activities (HOLL et al. 2003, WORTLEY et al. 2013, KOLLMANN et al. 2016), mostly due to limited funding and a ‘culture of short-termism’ (LINDENMAYER & LIKENS 2010). This can have far-reaching consequences, as it might give a false picture of restoration success. For example, JONES et al. (2018) discuss, that the incomplete recovery of restored ecosystems shown in their study could be due to an

insufficient amount of time. Moreover, for a scientific understanding the ecological processes and dynamics induced by restoration, we also need repeated measurements; particularly because ecosystem recovery is not always a linear process.

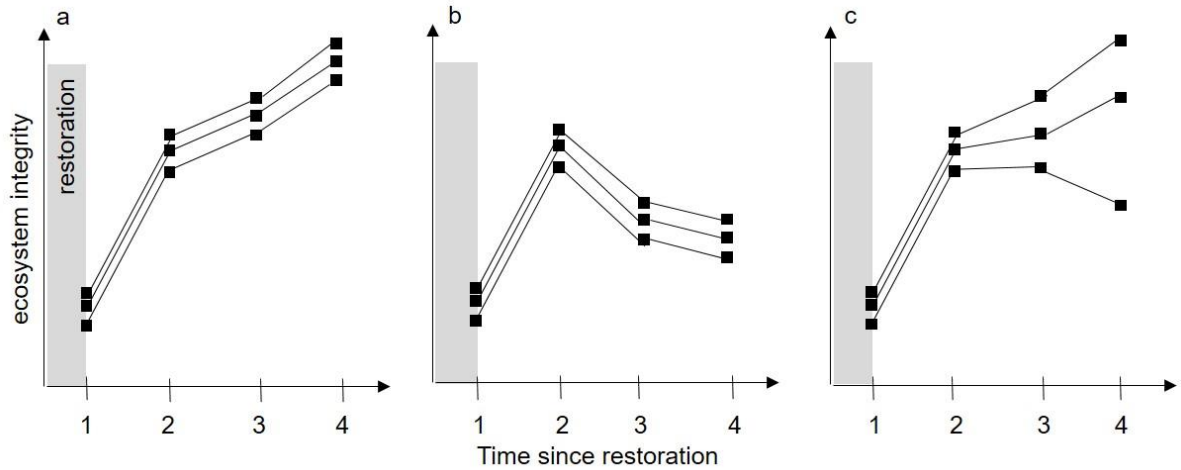


Fig. 3: Restoration trajectories can be different resulting in varying levels of success. Repeated observations of several sites reveal, if the degraded systems all develop towards the restoration target (a) continue degradation after initial recovery (b), or differ in restoration response (c). Figure modified after SUDING (2011).

While there is a lack of empirical research on general recovery patterns (JONES et al. 2018), ecological theory on this topic is abundant. For example, BULLOCK et al. (2011) propose different trajectories of restored biodiversity against time, which can develop in an asymptotic, linear, unimodal or stochastic way (Fig. 1). MATTHEWS & SPYREAS (2010) and SUDING (2011) highlight the importance of spatio-temporal comparisons of restored and reference conditions, as (a) several restored sites may all converge towards target conditions, (b) all deviate from the target, or (c) unintentionally diverge among each other (Fig. 3). In the first case restoration can be considered successful, while the third one suggests differences in (a) biotic conditions like nutrient loads or dispersal limitation at least in some sites. In the second case the system seems to be in a ‘stable alternative state’ (BEISNER et al., 2003). This can be associated to what STANDISH et al. (2014) called ‘unhelpful resilience’ meaning that an ecosystem returns to a degraded state, because of a threshold that cannot be passed by restoration (ANDRADE et al. 2015). Consequently, monitoring needs to reflect these dynamics by covering sufficiently long time scales with repeated measurements. However, these dynamics are highly ecosystem- and species-specific, e.g. at least as long as the generation time of dominant organisms (LINDENMAYER & LIKENS 2010), highlighting the need for ecosystem-specific studies of recovery trajectories.

Indicators for restoration success

A third highly debated field in monitoring ecological restoration concerns the selection of indicators for most adequately describing the response of an ecosystem to restoration actions; like addressed by reviews of RUIZ-JAEN & AIDE (2005), WORTLEY et al. (2013) and KOLLMANN et al. (2016). While the first two suggested to test for ecosystem attributes as stated by the Primer of the SOCIETY FOR ECOLOGICAL RESTORATION INTERNATIONAL (2004), they found that none of the previously published articles had included all of them. Studies had rather focused on diversity, vegetation structure and ecological processes, with ecosystem functions becoming only recently more important (KOLLMANN et al. 2016). Diversity measures in these reviews included richness, functional and genetic diversity of several taxonomic groups, i.e. plants, vertebrates, invertebrates, microbes and fungi. Structural attributes covered plant growth, vegetation height and cover, biomass, wood density, basal area and litter structure (cover, biomass, number of layers). Processes cover, nutrient cycling, carbon dynamics, productivity, decomposition, soil development, but also dispersal, reproductive success, pollination and other trophic interactions. This large range of potential indicators emphasises even more, that their careful selection at the onset of a project is important, especially when resources or time are limited and not everything can be assessed. Most importantly, the selection of indicators should be driven by the context, and their suitability largely depends on well-thought-out questions (LINDENMAYER & LIKENS 2010, SIDDIG et al. 2016).

Generally, there seems to be a trade-off between the comprehensive assessment of a restored ecosystem and the power of an approach to explain the underlying drivers of change (Fig. 4). Indicators, including terms like 'bioindicators', 'umbrella', 'keystone' or 'flagship species', ecosystem engineers or foundation species (SIMBERLOFF 1998, SIDDIG et al. 2016), have a long tradition in conservation biology. Indicator species integrate or predict the conditions of their environment via their current status or trend in diversity, abundance or fitness (BURGER 2006), and thus are used as a proxy for other biota or environmental change (LINDENMAYER & LIKENS 2011). They are frequently monitored, because their survey is easier, more efficient and cost-effective, while being reliable and meaningful (SIDDIG et al. 2016). However, a single population, species or taxonomic group rarely reflects the complexity of the environment (LINDENMAYER & LIKENS 2011), while the integration of multiple (a)biotic components leads to a more holistic understanding of a restored ecosystem (GEIST 2011). Ecological or environmental indices summarise a broad number of species or properties, and usually express it as a final single value. They are well-known for monitoring water quality (THIEBAUT et al. 2002), but are also useful indicators for other ecosystems, as they are simple,

fast and easy to perform. Furthermore, they capture the complexity of an ecosystem, as they include many different properties (Fig. 4). However, underlying trends of indices might become invisible, when their components move to different directions (MUELLER et al. 2014).

All the above-mentioned indices and their components (i.e. species or properties) are based on observations of the current status of an ecosystem. Thus, many different factors, including those not related to restoration activities, can potentially influence them, making it difficult to disentangle the drivers responsible for a specific observation. Therefore, for an easier interpretation it can be helpful to formulate testable hypotheses and use manipulative experiments to systematically test them (DIETRICH et al. 2013). Experimental approaches reduce confounding effects by minimizing differences among replicates and by controlling the factor of interest (e.g. water, light, plant age; GIBSON 2002), thus having a great potential for understanding the underlying drivers of specific restoration outcomes or single targets (Fig. 4), especially when used as complementary to observational field surveys.

Restoration target	Trade-off in monitoring		Thesis
Ecosystem integrity		Observational	integrative indices Article 3
Multiple targets		Observational	indicator species Article 1+2
Single target		Experimental	Direct measurement of single attributes (species, properties) Article 1+3
			Article 2

Fig. 4: Monitoring approaches depend on restoration targets, that can range from single targets (e.g. re-establishment of one species, carbon storage etc.) to a fully functional ecosystem. While integrative indices can comprehensively inform about ecosystem integrity, they are usually too general for understanding the underlying drivers of incomplete recovery. Observing a suite of single properties or indicator species can point at ongoing processes. Indicator species (e.g. keystone or umbrella species, SIMBERLOFF 1998) represent other species and ecosystem properties. Experimental approaches can help to understand the underlying causes of processes.

Monitoring approaches used in this thesis

For addressing the above-mentioned challenges of monitoring ecological restoration, the present thesis employs novel and complementary approaches, including (i) a unique chronosequence, (ii) the combination of both plant and animal species as collective indicators for ecological restoration, (iii) phytometers and (iv) a new multifunctionality approach.

Chronosequence for measuring long-term restoration success (Article 1 and 3)

While it is generally agreed, that the best source of evidence for analysing ecosystem changes are long-term time series, that are sufficiently repeated in space and time (WALKER et al. 2010), there is often a lack of resources for sufficiently long studies. Chronosequences using a space-for-time substitution are a common alternative, as they allow researchers to sample a large dataset within a short time period (BANET & TREXLER 2013), particularly in slowly developing ecosystems like forests or peatlands (ANDERSEN et al. 2017). This approach is valid under the assumption that the spatial relationship between an environmental driver and a response can be used as a proxy for the temporal relationship (BANET & TREXLER 2013). This implies the presence of ecological succession (WORTLEY et al. 2013). While there has been some debate about the validity of this approach (WALKER et al. 2010), it can substantially advance our understanding of ecological processes. In restoration ecology, this approach is particularly promising for cases, where restoration measures have been carried out in the past, but initially have not been accompanied by (scientific) monitoring. Furthermore, restoration activities usually trigger ecological succession.

In articles 1 and 3 of this thesis, I make use of a chronosequence approach for tracking recovery trajectories of biodiversity and ecosystem functions within a region, where restoration measures had been regularly undertaken by practitioners over almost 20 years with similar methods, but without a large-scale systematic assessment.

Animals as part of assessing biodiversity recovery after restoration (Article 1)

While ecologists equally use invertebrates and vegetation (SIDDIG et al. 2016), restoration ecologists have traditionally focused on abiotic and vegetation-based properties as a goal and as a monitoring criteria, while animals and trophic interactions have been studied to a lesser extent (CRISTESCU et al. 2013, FRASER et al. 2015, KOLLMANN et al. 2016). This is related to the assumption, that if habitat quality and vegetation structure recover, the fauna will spontaneously follow (PALMER et al. 1997). At the same time, vascular plants are easier

to assess and show less seasonal variation in most regions (RUIZ-JAEN & AIDE 2005). However, it has been shown that the correlation between flora and fauna recovery is not always true, but that insect communities do not recover to the same extent as plant communities (BABIN-FENSKE & ANAND 2010). FRASER et al. (2015) called for an increased integration of animal species into ecological monitoring, since animals are a significant part of ecosystem recovery, given their role as decomposers, herbivores and predators strongly affecting plant diversity and ecosystem functioning (FRASER et al. 2015).

Article 1 of this thesis follows this recommendation by comparing recovery trajectories of vegetation structure and plant diversity to those of butterflies and dragonflies, and their habitat requirements.

Phytometers for understanding site limitation of restored ecosystems (Article 2)

Plants are most frequently used for monitoring restored ecosystems, because they integrate site conditions over relatively long time periods (ELLENBERG et al. 2001). This potential is used in so-called phytometer experiments, that have a long tradition in agricultural sciences (DIETRICH et al. 2013), while the idea of using phytometers for evaluating restoration success is rather recent (DIETRICH et al. 2013). Phytometers are standardized plants, that are experimentally transplanted to indicate differences between sites via growth, mortality and fitness (ANTONOVICS & PRIMACK 1982). Therefore, they combine the advantages of plants as indicators and of experimental approaches, that can be useful for understanding underlying drivers of restoration success, as mentioned above. More specifically, their experimental addition to restored sites allows to discriminate between site limitation, i.e. abiotic constraints on species establishment (e.g. nutrients, water, light) and dispersal limitation, i.e. constraints imposed by dispersal and (re)colonization potential of the respective species (EMSENS et al. 2018). The differences in performance are best assessed by measuring plant traits related to survival, growth and reproduction (VIOLLE et al. 2007). The list of traits, that can potentially indicate within-species differences is long and various traits have been used in transplant experiments.

For article 2 of this thesis, three peatland species were used and numerous plant traits measured in order to systematically compare plant responses. The goal was to advance the application of the phytometer approach in the field of ecological restoration.

Multifunctionality approach for assessing restored ecosystem integrity (Article 3)

Biodiversity-ecosystem function (BEF) researchers have developed approaches for simultaneously assessing (MEYER et al. 2015) and analysing several functions (BYRNES et al. 2014). These results show, that the loss of species impacts single ecosystem processes like productivity or nutrient cycling (BALVANERA et al. 2006, CARDINALE et al. 2006), authors claimed, that the relationship between diversity and ecosystem functioning might be different or even stronger, when multiple functions are considered (GAMFELDT et al. 2008). Therefore, there is a need for developing methods to assess this so-called multifunctionality, and to standardise the approach for increasing the comparability of studies (BYRNES et al. 2014).

Article 3 of this thesis identified a similar need for evaluating restored ecosystems, as trajectories of single properties might differ and not necessarily correlate with the overall ecosystem trajectory. For more comprehensively describing the ecosystem multifunctionality approaches - as recently suggested by BYRNES et al. (2014), i.e. the 'averaging approach', the 'single threshold approach' and the 'multiple threshold approach' – were modified for this purpose. Hence, instead of analysing the multifunctionality response to diversity, this study focuses on ecosystem recovery and analysed multiple properties as a function of time since restoration.

Peatlands as study ecosystems of the thesis

For this PhD thesis, restored peatlands were chosen as most suitable study systems, since restoration activities currently often focus on them with varying targets ranging from the provision of habitats for specialized and rare species over the attenuation of flood peaks to the reduction of greenhouse gas emissions (GRAND-CLEMENT et al. 2013). At the same time, their monitoring is particularly challenging, as (i) natural reference sites are scarce due to their widespread and profound degradation, (ii) they slowly recover and (iii) are supposed to fulfil multiple ecosystem functions.

Peatlands are wetland ecosystems, that are characterised by the presence of a naturally accumulated peat layer (SUCCOW & JOOSTEN 2001), for which most commonly a minimum depth of 30 cm is defined (AD-HOC-ARBEITSGRUPPE BODEN 2005). Peat is sedentarily accumulated plant and soil material consisting of at least 30% (dry mass) of dead organic matter (JOOSTEN & CLARKE 2002, AD-HOC-ARBEITSGRUPPE BODEN 2005). Following this definition, the term 'peatland' includes drained sites, where peat is no longer actively accumulating, but still present at the soil surface; and it is opposed to the term 'mire', that

describes a peatland, where peat is currently being formed (JOOSTEN & CLARKE 2002). Thus, mires are characterised by an incomplete nutrient cycle, where the production of organic matter (mainly plant material) exceeds its decay (decomposition) due to permanent waterlogged conditions and an associated lack of oxygen (JOOSTEN & CLARKE 2002). While the presence of water is crucial for the development of a mire, its origin is decisive for the two resulting peatland types. While bogs or ombrogenous mires are fed by rainwater and usually raise above the surrounding landscape, fens or geogenous mires are depend on ground water and are usually situated in depressions (Fig. 5). Differences in pH and base richness of the water determine the floristic variation between these two mire types with ombrotrophic communities in bogs and minerotrophic communities in fens (CONRADI & FRIEDMANN 2013).

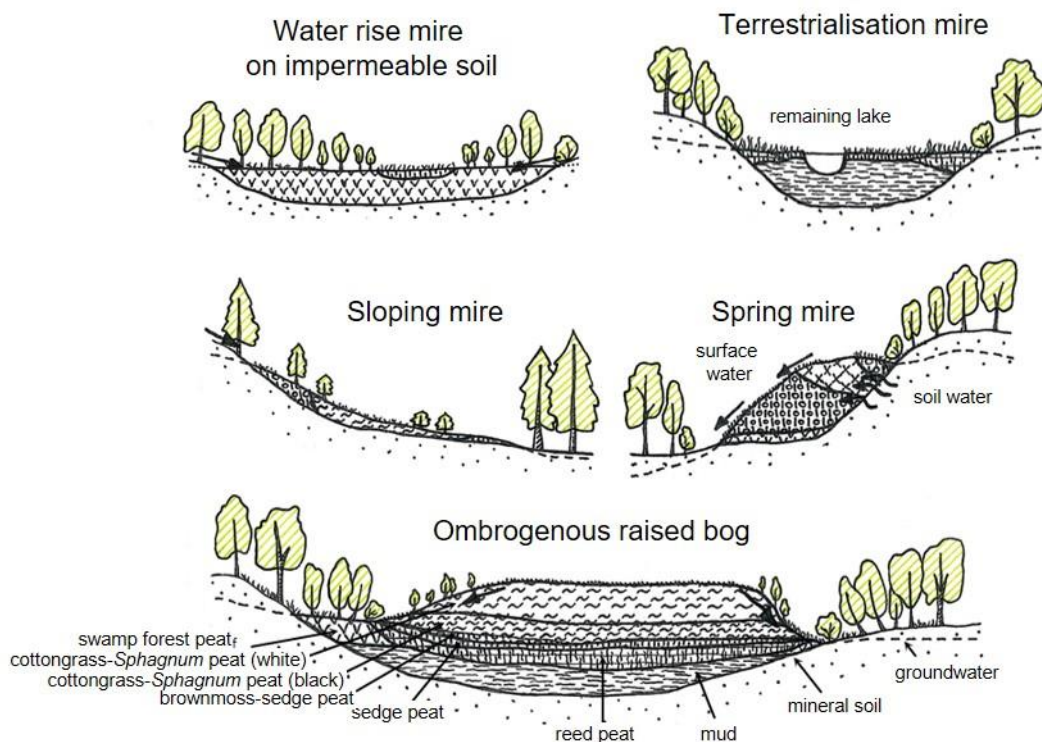


Fig. 5: Different hydrogenetic mire types depending on their topographic situation and inflow water origin, mainly its nutrient and base content. Figure modified after KOLLMANN et al. (2019)

Peatlands are amongst the most valuable ecosystems (COSTANZA et al. 1997). They provide essential functions that are beneficial to the human well-being (BONN et al. 2016); many of them related to the above-mentioned incomplete decomposition processes. The most prominent function, that has become a major political focus in the attempt to mitigate global warming, is their capacity to act as a carbon sink (QUINTY & ROCHEFORT 2003). While peatlands only cover around 3% of the global land surface (SUCCOW & JOOSTEN 2001), they store around 540 Gt of carbon, i.e. 30% of global carbon stored in plants and soil (PARISH et

al. 2008). They are also assumed to store 10% of the global freshwater resources (JOOSTEN & CLARKE 2002), thus attenuating runoff and discharge rates, and therefore reducing flooding (BONN et al. 2016). Other examples include the preservation of historic records (e.g. stratigraphical archive, pollen record, archaeological artefacts) and the use of peatland plants for medicinal purposes (e.g. *Drosera* spp., *Menyanthes* spp.; BONN et al. 2016). Many of these services are only provided by intact or marginally degraded peatlands, but sometimes sustainable use is compatible with certain functions. For example, 'paludiculture' is a type of agriculture, that conserves the peat body and reduces greenhouse gas emissions or other forms of pollution (JOOSTEN et al. 2016). However, there are some provisioning services (e.g. intensively produced timber, peat as a horticultural substrate), that require drainage and negatively affect the peat body (SCHUMANN & JOOSTEN 2008).

Another major function of peatlands is the provision of habitats for specialized species. Most of the above-mentioned ecosystem services depend on biodiversity, and conservation of biodiversity has an ethical foundation (JAX et al. 2013, MINAYEVA et al. 2016). Generally, besides water and peat, plants play a crucial role in peatlands so that these three components are considered mutually dependent (JOOSTEN 2016). The role of vegetation in peatlands is two-sided: on one side, only few specialized plant species occur under the prevalent extreme site conditions, on the other side, plants substantially determine these site conditions (MINAYEVA et al. 2016). For example, peat mosses (*Sphagnum* spp.) act as ecosystem engineers and contribute to creating acidic, nutrient-poor, cold and anoxic conditions of peatlands (VAN BREEMEN 1995). This environment creates restrictions for other living organisms and explains, why peatlands are usually species-poor compared to mineral soil ecosystems within the same region (MINAYEVA et al. 2017). At the same time peatland species are usually highly specialized and not found in other habitats, which underlines the significance of peatlands for biodiversity (JOOSTEN 2016). Most peatland species have specific strategies in order to cope with the particular conditions, e.g. aerenchyma facilitating gas exchange between roots and shoots, carnivory or mycorrhiza improving nutrient and mineral uptake, and small, thick leaves conserving water during dry summer months (MINAYEVA et al. 2016). Many invertebrates are also very specialized. They can be obligatorily ('tyrphobiontic') or predominantly associated ('tyrphophilous') to peatlands (SPITZER & DANKS 2006). Most vertebrates only use peatlands at certain life stages, but have also developed strategies for coping with the specific conditions of peatlands, e.g. amphibian and bird egg shells, that resist to the acidic environment (MINAYEVA et al. 2016).

Peatlands have suffered severe losses of biodiversity and ecological functions due to non-sustainable human use. The main causes are direct peat extraction for fuel or horticultural

substrate production, indirect changes in landscape hydrology, atmospheric nitrogen deposition and changes in land use by agriculture, forestry and urban transformation (GROOTJANS et al. 2012). As a consequence, 500,000 km² or 12% of the global mires have been altered in a way, that peat is not accumulating any more (GROOTJANS et al. 2012). In Europe, where mire losses are particularly pronounced, almost half of the peatlands have been degraded (JOOSTEN 2016), and in Germany this figure reaches almost 80% (JOOSTEN 2010). Until today, more peatland is lost than naturally expanding, so that global peat volumes are still decreasing (JOOSTEN 2016). When peatlands are drained – as necessary for peat extraction or intensive agricultural or silvicultural use – peat gets oxidised and biogeochemical processes, that were previously inhibited, set in. Thus, when peat decomposes, greenhouse gases (carbon dioxide and nitrous oxide), are released to the atmosphere, summing up to 2 Gt of CO₂ per year (PARISH et al. 2008). Moreover, anthropogenic disturbance at different spatial scales led to habitat loss, degradation and fragmentation with severe impacts for peatland biodiversity (MINAYEVA et al. 2016).

For counteracting these changes, peatland restoration activities are initiated and research on peatland restoration has emerged as an active scientific field in the past 30 years (ROCHEFORT & ANDERSEN 2017). In Europe, the EU LIFE nature programme alone invested 167.6 M€ in 80 projects between 1993 and 2015 (ANDERSEN et al. 2017), and it is complemented by many regional and local incentives. The most widely acknowledged goal of peatland restoration is the re-establishment of a self-sustaining naturally functioning mire ecosystem, including the accumulation of peat (WHEELER & SHAW 1995, QUINTY & ROCHEFORT 2003, ROCHEFORT & ANDERSEN 2017). Specific measures depend on the degree and type of degradation as well as on the ecosystem components affected (SCHUMANN & JOOSTEN 2008).

As most peatlands in Central Europe have been degraded due to drainage (ANDERSEN et al. 2017), rewetting is the most commonly applied restoration method. It generally consists of raising and stabilising the water table close to the surface by blocking drainage ditches, in order to recover waterlogged, anoxic conditions and therefore peat accumulation. In eutrophied fen meadows, another frequent action is topsoil removal (KLIMKOWSKA et al. 2015). While often species are expected to recover or re-establish spontaneously (e.g. by re-colonizing from surrounding populations), in some cases species (mostly plants) are actively reintroduced (MINAYEVA et al. 2016). After large-scale peat cutting, sites are often too degraded for spontaneous plant recovery, and diaspores have to be introduced (e.g. ROCHEFORT et al. 2003). In this way, functions like water or carbon storage as well as specific habitat conditions, and characteristic peatland biodiversity are expected to recover. While full

recovery is rarely possible, the overall potential of peatland restoration largely depends on site-specific factors like peatland type and degradation stage (SCHUMANN & JOOSTEN 2008).

Peatland are slowly recovering 'complex adaptive systems' (GORHAM & ROCHEFORT 2003), that are capable of rapid change and reorganization in response to environmental change (DISE 2009), e.g. induced by restoration activities. Several studies reported on the recovery trajectories of restored peatlands or wetlands. Generally restoration activities like rewetting and diaspore transfer in formerly block-cut peatland (POULIN et al. 2013, ROCHEFORT et al. 2013, GONZÁLEZ & ROCHEFORT 2014) or forestry-drained peatlands (HAAPALEHTO et al. 2017) moved most sites towards the expected development trajectory within the first 10 years after restoration. However, POULIN et al. (2013) reported an incomplete recovery compared to the undisturbed references, GONZÁLEZ & ROCHEFORT (2014) found alternate restoration conditions in early phases, and HAAPALEHTO et al. (2017) recorded important within-site spatial variability. While those peatland studies only described vegetation change, MELI et al. (2014) showed for wetlands that biodiversity as well as ecosystem functions and services could be substantially improved after restoration, but vegetation recovery was again incomplete and ecosystem functions were more difficult to recover than biodiversity. Furthermore, MATTHEWS et al. (2009) and MATTHEWS & SPYREAS (2010) pointed at unexpected deviation and non-linear developments in restored wetlands. These results highlight the crucial importance of long-term repeated observations in peatlands, while no studies on peatland trajectories of more than 10 years exist until now, and a minimum of 10–30 years seems more appropriate for tracking their recovery (POULIOT et al. 2011), including possible non-linear developments.

OBJECTIVES AND OUTLINE

This thesis makes use of past peatland rewetting activities to evaluate the beneficial effects on peatland restoration and to understand their recovery dynamics. By using several observational and experimental monitoring approaches, the thesis aims at reflecting the wise selection of indicators (ecosystem properties, taxonomic groups and species) depending on the context. The Fichtelgebirge mountains in NE Bavaria were selected for this purpose, since here degraded peatlands have been restored in different years albeit with similar methods. Therefore, I could use a chronosequence approach for studying long-term developments and implement ecological experiments for assessing their suitability for monitoring. I hypothesized, that peatland recovery would be incomplete compared to an intact reference system. Peatland recovery was also expected to be slow (several decades) and non-linear, meaning that outcomes would vary depending on the monitoring period. Moreover, I anticipated considerable differences in the recovery of individual properties and species (groups), that would influence the conclusions drawn depending on the assessed indicators. Finally, I assumed that an experimental approach would considerably extend the understanding of underlying drivers of incomplete recovery, but that a careful indicator selection also has to precede this approach.

These assumptions were tested in three steps, that correspond to the three articles constituting this cumulative PhD thesis. **Article 1** analyses the trajectories of different taxonomic groups in terms of diversity (structure, richness, assemblage) and compares them among each other as well as with an intact reference (Fig. 4). It detects potential non-linear recovery curves and the role of monitoring timeframes for drawing conclusions on restoration outcomes. **Article 2** tests the potential of experimental approaches for evaluating restoration success. By using three characteristic peatland plants as phytometers, it expands the method to this specific ecosystem. It also compares a large variety of measured plant traits for advancing the approach with respect to the selection of suitable indicators of plant growth in a restoration monitoring context. **Article 3** is an integrative assessment of multiple peatland properties and draws the most comprehensive picture of the ecosystem complexity. It uses different approaches, that are inspired from multifunctionality approaches in BEF research, in order to assess to what extent peatlands can be restored and which role time plays in their recovery. It also juxtaposes trajectories of individual properties and the combined index.

STUDY REGION AND METHODS

Study region and site selection

Field data for this thesis was sampled in montane peatlands in NE Bavaria (longitude E11°44'59"–12°5'5", latitude N49°53'46"–50°5'45", altitude 660–1000 m a.s.l.) in the natural regions 'Hohes Fichtelgebirge' and 'Selb-Wunsiedler Hochfläche' (MEYNEN & SCHMITHÜSEN 1959) that are part of the continental biogeographical region (SSYMANK 1994). Geologically it belongs to the Eastern base rock mountains of Bavaria, with the highest peaks being the Schneeberg (1051 m a.s.l.) and the Ochsenkopf (1024 m a.s.l.). Peatlands within the region developed under cool and humid climatic conditions with mean annual temperatures of 5.5–6.2 °C and annual precipitations of 910–1120 mm (BAYERISCHES LANDESAMT FÜR UMWELT 2017). However, the sloping and sometimes rocky terrain and rather well-drained soils have allowed peat to form only on specific sites with clayey and therefore mostly impermeable substrate (REGER 2007). Typically, peatlands formed on slopes or saddles, and most of them can be characterized as acidic transitional bogs with varying proportions of soligenous water and some being solely fed by rainwater (ombrotrophic).

Historically intensive drainage has altered the water regime of almost all peatlands within the area. The main period of drainage and peat cuttings was in the 19th and 20th century, while one of the first drainage ditches in the relatively well-preserved Fichtelseemoor dates from 1956 (FIRBAS & ROCHOW 1956). Peatlands were mostly used for wood production; only in some larger peatlands peat was cut for fuel use. Restoration started with small manual ditch blockings in the beginning of the 1990s, rewetting on a larger scale in 1998. Trees, mainly spruce (*Picea abies*) were removed along former drainage ditches and the ditches blocked by wooden dams, or (partially) filled with peat from the direct surrounding. This resulted in the creation of small pools, that should benefit a characteristic peatland fauna, mainly amphibians and dragonflies. After restoration, sites were mostly left to natural succession (Fig. 9) and generally no plants introduced. Only locally, tree species (*Betula pubescens*, *Pinus mugo* ssp. *rotundata*) were planted, and regenerating *Picea abies* removed by forest authorities.

For the PhD project I selected 14 characteristic peatlands within the region, that are comparable in terms of bedrock, landform, hydrological conditions and past peat formation as well as (former) land use and restoration method, but have been restored in different years between 1998 and 2015 (Fig. 6 & Table 1). This allowed me to assess their succession in a space-for-time substitution (chronosequence). In order to increase the available time span, data was sampled in two subsequent years (2015, 2016). Some sites were subsequently

restored in several years and therefore divided in sub-sites. The full time series included: degraded (non-restored) sites, sites that were restored 0, 1, 2, 3, 4, 5, 7, 8, 9, 13, 15, 16, 17 or 18 years before sampling, and a near-natural reference site.

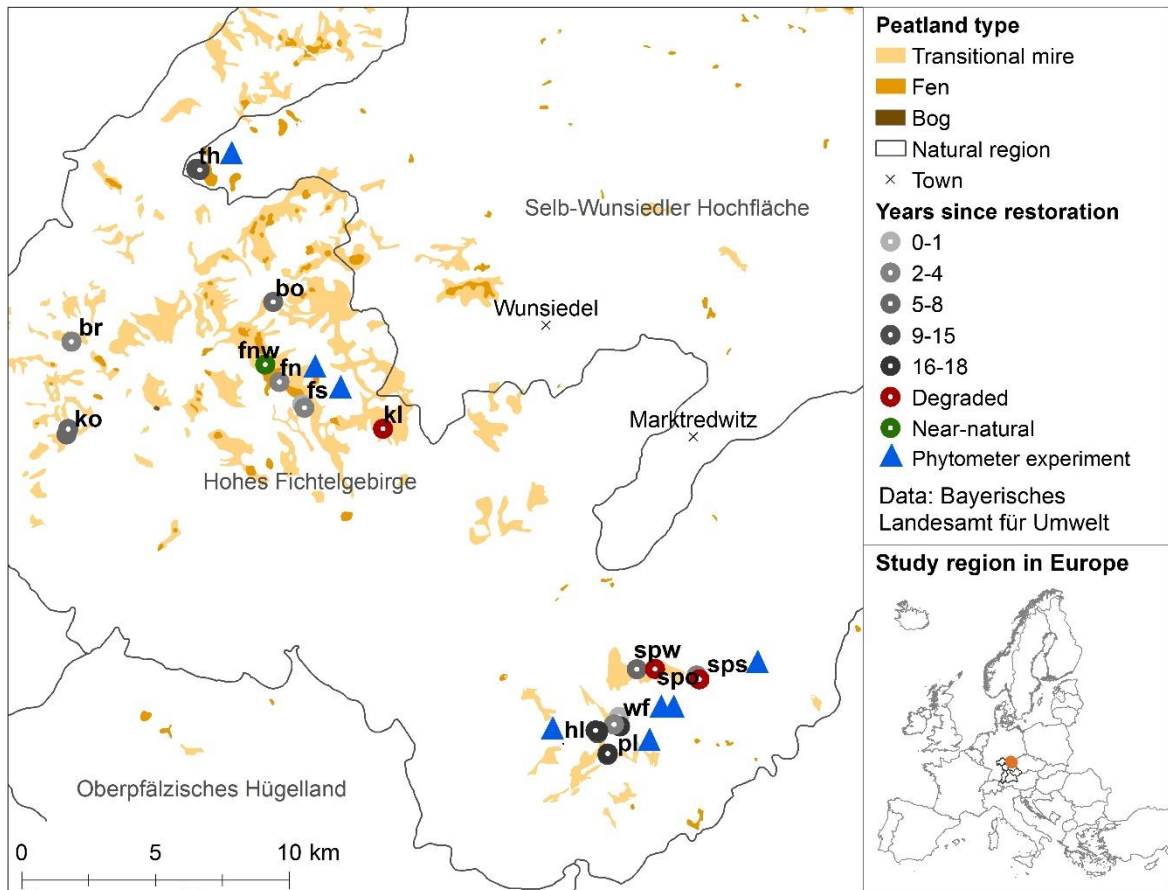


Fig. 6: Overview of the selected study sites within the natural regions (after MEYNEN & SCHMITHÜSEN 1959) 'Hohes Fichtelgebirge' and 'Selb-Wunsiedler Hochfläche'. For abbreviations see Table 1.

STUDY REGION AND METHODS

Table 1: Overview of the selected study sites and sampling effort. For sites that were subsequently restored, only years considered in this study are displayed (oral communication by land owners and public forest management authorities).

Site name	Code (Fig. 6)	Peatland type	Size (ha)	Height (m a.s.l.)	Coordinates	Restoration year	Fauna		Plants		Phytometer
							Plot number	Study year	Transects	Study year	Transects
Backöfele	bo	sloping mire	6	1000	4489914 5545819	2008	5	2016	1	2016	0
Brunnschlag	br	sloping spring mire	3	750	4482554 5544249	2011	4	2016	1	2016	0
Fichtelseemoor NW	fnw	bog (ancient lake mire) & sloping mires	9	770	4490345 5542756	reference	1	2016	1	2016	1
Fichtelseemoor S	fs		5	740	4491229 5541877	2014	2	2015	2	2015 2016	1
Fichtelseemoor NO	fn		5	780	4489765 5543398	2011	2	2016	1	2015	0
Fuchslöh/ Wolfsloh	wf	sloping mire	23	820	4502861 5530065	1998, 2012, 2015	10	2015	3	2015 2015 2015	2
Hahnenfalzlohe	hl	sloping mire	8	830	4502172 5529699	1998, 2000, 2002	4	2015	3	2015 2016	1
Hopfenwinkel	sps	sloping mire (saddle)	6	760	4506032 5531692	2011, degraded	4	2016 2015	2	2015 2015	1 0
Kalkloh	kl	degraded sloping mire	2	650	4494175 5541038	degraded	1	2016	1	2016	0
Königsheide	ko	sloping mire	48	800	4482321 5541132	2008 2011	17	2016	2	2016	0
Palmlohe	pl	sloping mire	3	820	4502525 5528887	1998 2000	5	2015	2	2015 2016	1
Spitzerberg Ost	spo	degraded sloping spring mire	8	710	4504368 5532046	degraded, 2011	2	2015+16	1	2015	0
Spitzerberg West	spw	sloping spring mire	3	710	4503661 5532009	2011	7	2016	1	2016	0
Torfmoorhölle	th	sloping mire (saddle)	26	670	4487306 5550554	2007	16	2015	2	2015 2016	1

Study design and data sampling

In total seven datasets were generated for this thesis including five field observations, one field experiment and one greenhouse experiment (Fig. 7). They were sampled in a complementary way, so that they could be combined for several articles. For example, the abiotic environment could be used in all three articles.

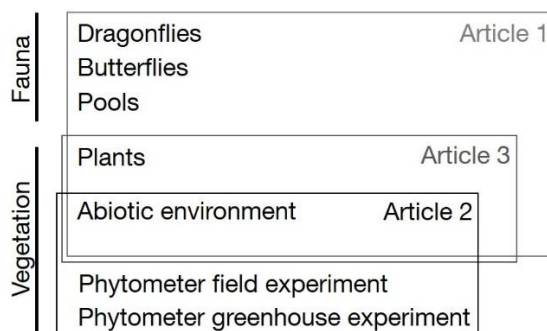


Fig. 7: Overview of the datasets and their use in the three articles of this thesis.

Fauna and pools

At each site, dragonflies (Odonata) as well as butterflies (Lepidoptera) were assessed. Therefore, the 14 peatland sites were divided into plots containing potential dragonfly and butterfly habitats, i.e. the open areas of the peatland excluding afforested parts. Two collectors walked along a path linking all plots and crossing all ponds. They stopped at every pond and every plot for 10–15 min for catching butterflies and dragonflies with butterfly nets and released them after identification. All sites were sampled three times (in June, July and August) on warm and windless days (>17 °C) between 9:30 and 17:00.

For characterizing dragonfly habitats, pool quality and quantity was assessed in September 2016. At each site the number of ponds was counted and mapped. At each water-filled pond, pond area was visually estimated and pond depth measured in about 1 m distance from the bank. I measured temperature, pH and conductivity using a field pH and conductivity meter (PCE-PHD 1). Cover of floating vegetation was estimated on the pond surface and riparian vegetation in a perimeter of 3 m around the pond, again following the scale of Londo (1976). The number of sunny spots counted in a perimeter of 3 m around the ponds. Shading was recorded on a scale ranging from 1 ('full sun') to 5 ('full shade'; WÖRLEIN 1992).

For characterizing butterfly habitats, presence and abundance of butterfly host plants was assessed. Their cover was estimated following the scale of LONDO (1976). Recorded host

plants were *Vaccinium myrtillus*, *V. oxycoccus*, *V. uliginosum* and *V. vitis-idaea*, as caterpillars of the specialized butterflies feed on them (Kuhn & Burbach 1998).

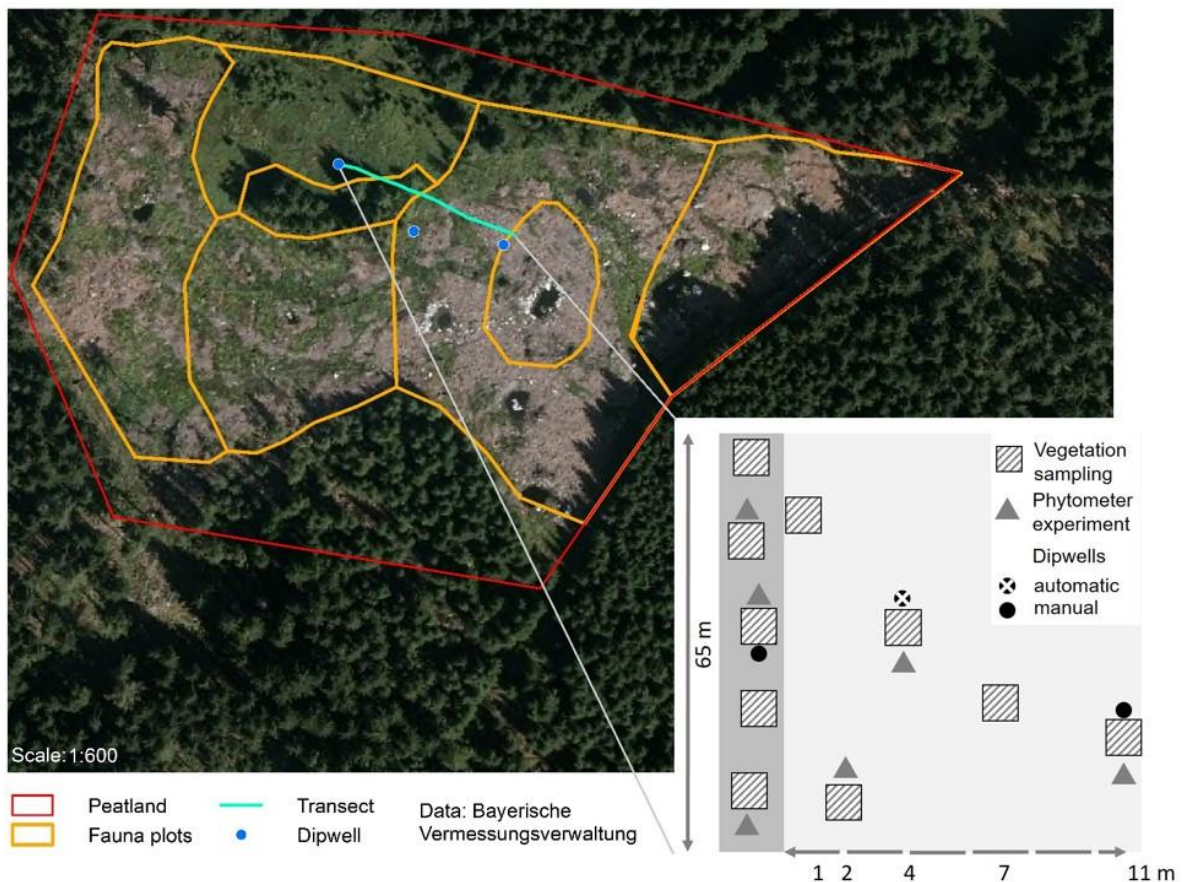


Fig. 8: Sampling design demonstrated at one example site (spw, see also Table 1).

Vegetation and abiotic environment

For the vegetation surveys I randomly established 23 transects of 65 m parallel to former drainage ditches in the 14 study sites. In larger peatlands and sites, that were subsequently restored in different years, I selected ≤ 3 transects, while I selected only one in the five smallest peatlands. The distance between transects was at least 50 m. Transects within sites were independent, as they were separated by woodland strips, that effectively isolated plant and animal populations. Along each transect I randomly placed 10 plots (0.5 m²), i.e. five plots ('ditch') within the former drainage ditch and five plots ('field') at 1, 2, 4, 7 and 11 m distance (Fig. 8). At each plot, vascular plants and bryophytes were identified at species level and vegetation cover visually estimated following the scale of LONDO (1976) between June and August 2015 or 2016.

For characterizing the abiotic environment, I recorded water level, shading by trees and peat characteristics (moisture, decomposition, water holding capacity, pH, conductivity, nutrient content). Water level was recorded manually as well as automatically at each

transect. The 'manual' dipwells were placed at one randomly chosen 'ditch' plot and at the 11-m 'field' plots (Fig. 8) and water level recorded once per month from April to September 2016. The 'automatic' data loggers (Schlumberger Mini-DIVER®) were placed at 'field' plots in 4-m distance (Fig. 8). They automatically recorded water levels every 12 hours.

Shading, i.e. light conditions below canopy, were measured at 1.5 m above ground level using a Solariscope (SOL 300, Ing.-Büro Behling, Wedemark), which analyses hemispherical photographs and models various shading indicators. I chose the total site factor (TSF) as the most appropriate measure for our purposes. It is defined as the proportion of direct (DSF) and diffuse (ISF) solar radiation and expressed as a percentage of the radiation received above the canopy (RICH 1990). The degree of peat decomposition was estimated following the scale of POST (1924). Peat moisture was measured as the mean value of three measurements per subplot (Soil Moisture Meter HH2).

In order to determine water holding capacity, pH, conductivity and nutrient content in the laboratory, mixed samples (3x 100 ml) of the upper 5 cm were taken with a soil corer at every plot in August 2015 and 2016. The maximum water holding capacity was defined as the amount of water absorbed by 100 g of dry peat. The peat samples were placed in filters and 200 ml of distilled water poured over them to determine the saturated 'fresh mass'. 'Dry mass' was obtained after oven drying at 65 °C for >72 h. The pH was measured in 5 g peat (dry mass) stirred up in 100 ml distilled water. Nutrient concentrations (anions and cations) were obtained using ion chromatography (Dionex ICS-1600, Thermo Fisher Scientific Inc.).

Phytometer experiments

Three specialist bog species were selected, that are naturally occurring in the study area and were commercially available, as phytometers, i.e. *Drosera rotundifolia* L., *Eriophorum vaginatum* L. and *Vaccinium oxycoccos* L (STROBL et al. 2018b, Fig. 10).

Drosera rotundifolia (Droseraceae) is a carnivorous hemicryptophyte (NORDBAKKEN et al. 2004), that overwinters as a resting bud, the so-called hibernaculum (THOREN et al. 2003). Its leaves are spirally arranged in a basal rosette of 3–6 cm and covered in mucilage in order to trap and digest prey (NORDBAKKEN et al. 2004). The seeds are wind- or water-dispersed. It usually grows on *Sphagnum* mats, but can also be found on bare sand or peat (THOREN et al. 2003). It is classified as 'vulnerable' (category 3) on the German and Bavarian Red List of vascular plants (LUDWIG & SCHNITTLER 1996, BAYERISCHES STAATSMINISTERIUM FÜR UMWELT, GESUNDHEIT UND VERBRAUCHERSCHUTZ 2005).

Eriophorum vaginatum (Cyperaceae) is a tussock-forming hemicryptophyte sedge (BENNINGTON et al. 2012) with mature tussocks of 300–600 tillers (FETCHER & SHAVER 1982). Individual tillers generally live <8 years, while tussocks reproduce vegetatively and can persist more than 100 years. Mature tussock size largely varies between regions and ranges from around 15 to 50 cm (BENNINGTON et al. 2012). It is dominant in many plant communities of moist arctic tundra and is known to quickly and successfully colonize bare peat (FETCHER & SHAVER 1982). Its flowers are wind-pollinated and the seeds wind-dispersed. In Germany it is not threatened or specifically protected.

Vaccinium oxycoccos (Ericaceae) is an evergreen chamaephyte with thread-like, woody, flexible stems up to 80 cm long and ascending flowering branches (JACQUEMART 1997). Its leaves are about 5–7 mm long, 2–3 mm wide and evergreen with a thick wax layer. The plant produces red berries (8–10 mm, cranberries), that contain 3–11 seeds and often stay on the plant during winter. Flowers are insect-pollinated and fruits are dispersed by water, birds or mammals. It usually occurs in the wetter parts of peatlands and often grows in *Sphagnum* carpets. The species is listed as ‘vulnerable’ in the Bavarian and German Red List (LUDWIG & SCHNITTLER 1996, BAYERISCHES STAATSMINISTERIUM FÜR UMWELT, GESUNDHEIT UND VERBRAUCHERSCHUTZ 2005).

The field experiment was conducted in eight out of the 23 transects (Table 1) and integrated within the vegetation sampling design. The experiment was established at the three first ‘ditch’ plots and at the 2, 4 and 11 m-distance ‘field’ plot, resulting in six experimental plots per transect (Fig. 8). In May 2015 the plots were prepared by removing all naturally present vascular plants within a triangle with 45-cm-long sides, in order to reduce the effects of competition at the time of planting. Only the upper layer of 2–3 cm of moss was removed, as the transition between living *Sphagnum* spp. and subjacent peat was gradual in most cases. One individual of each of the three phytometer species (*D. rotundifolia*, *E. vaginatum*, *V. oxycoccos*) was planted in the corners of the triangular plots at a distance of 25 cm from each other and 10 cm away from the edges of the plot. Possible competing vegetation (such as herbaceous plants and *Sphagnum* spp.) was removed from the plots every other month in April–October.

A greenhouse experiment with two treatments, i.e. ‘peat provenances’ and water level was established. Therefore, in May 2015 peat was collected from the eight phytometer field sites and brought to the greenhouse. All individuals of the three species were planted in separate pots with different diameters according to the size of the species (5 cm for *D. rotundifolia*, 15 cm for *E. vaginatum*, 19 cm for *V. oxycoccos*). The peat obtained from the eight field sites was used as substrate, i.e. the ‘peat provenance’ treatment. Then, three

different species, but in substrate of same 'peat provenance', were placed in a tray to apply the 'water treatment'. Trays were flooded with rain water at either 3 or 8 cm below pot level, imitating belowground water levels in the study sites. Each block (peat provenance x water level) was repeated twice, leading to a total of 32 trays and 96 pots. A constant water level was assured by watering 2-3 times a week depending on weather conditions. The experiment was kept in a greenhouse with a constant temperature of about 10 °C during winter and transferred to a half-open greenhouse with wire mesh walls in summer, allowing for more natural variation of temperature. Light was not manipulated in the greenhouse and corresponded to natural conditions in Freising. The trays were randomly placed on four tables and their position was changed once per month.

Species classification

For data analyses, species were grouped as generalists or specialists. Plants were categorized as specialists of Bavarian montane peatlands following QUINGER & SIUDA (2009) and can mainly be attributed to Oxycocco-Sphagnetea communities (Oberdorfer et al. 2001). Odonata and Lepidoptera specialists were defined according to KUHN & BURBACH (1998). This definition resulted in a total of 11 specialist vascular plant species (*Agrostis canina*, *Andromeda polifolia*, *Carex canescens*, *C. echinata*, *C. nigra*, *C. rostrata*, *Drosera rotundifolia*, *Empetrum nigrum*, *Eriophorum angustifolium*, *E. vaginatum* and *V. oxycoccus*) and nine bryophytes (*Calliargon cordifolium*, *C. stramineum*, *Calypogeia sphagnicola*, *Sphagnum angustifolium*, *S. capillifolium*, *S. cuspidatum*, *S. fallax*, *S. magellanicum* and *Warnstorfia exannulata*).

Dragonfly specialists were defined as the two potentially occurring tyrphobiotic (*Aeshna subarctica* ssp. *elisabethae* and *Somatochlora arctica*) and nine tyrphophilous Odonata species (*Aeshna juncea*, *Coenagrion hastulatum*, *Lestes virens*, *Leucorrhinia dubia*, *L. pectoralis*, *L. rubicunda*, *Libellula quadrimaculata*, *Somatochlora alpestris* and *Sympetrum danae*). Three butterfly specialists were defined (*Boloria aquilonaris*, *Colias palaeno* and *Plebejus optilete*). Nomenclature follows Buttler & Hand (2008) for vascular plants, KOPERSKI et al. (2000) for bryophytes and SCHAEFER et al. (2000) for Odonata and Lepidoptera (Supporting information of STROBL et al. 2019, Table S1).



Fig. 9: Degradation and restoration of montane peatlands. Pictures show (a) a drained and afforested peatland before restoration, (b) largely bare peat after tree removal and freshly created pools less than one year after damming of drainage ditches, (c) colonization of graminoids around six years after rewetting, (d) dead trees and spreading *Eriophorum vaginatum* and *Vaccinium uliginosum* eight years after rewetting, (e) *Sphagnum* overgrowing pools behind dams around 14 years after rewetting, and (f) colourful *Sphagnum* mats colonized by *Drosera rotundifolia* and *Vaccinium oxycoccos* in a largely undisturbed peatland.



Fig. 10: The three characteristic peatland species, that were used for the phytometer experiments, in their natural environment. Pictures show (a) the rosette and (b) fruit stand of *Drosera rotundifolia*, (c) shoots and (d) fruit stands of *Eriophorum vaginatum*, and (e) flowers and (f) fruits of *Vaccinium oxycoccos*.

MANUSCRIPT OVERVIEW

The thesis contains three articles, for which the publication status, the contribution of all authors, a brief summary and a graphical abstract are given:

ARTICLE 1: Positive trends in plant, dragonfly and butterfly diversity of rewetted montane peatlands

Strobl, K., Moning, C., Kollmann, J. (2019): Positive trends in plant, dragonfly and butterfly diversity of rewetted montane peatlands. *Restoration Ecology*, in press, doi: 10.1111/rec.12957

Author contributions

KS and JK conceived and designed the study. **KS** sampled vegetation and habitat characteristics. CM designed and supervised the mapping of dragonflies, butterflies and ponds. JK and **KS** discussed the data analysis and manuscript structure. **KS** analysed the data and wrote a first draft. JK and CM corrected the manuscript.

Summary

The first article analyzes long-term trends in diversity of different peatland-specific taxonomic groups (plants, dragonflies, butterflies) in terms of diversity (structure, richness, assemblage). Previous research has shown, that drainage and afforestation cause extensive habitat degradation and species losses in peatlands. Restoration efforts usually aim at reversing these damages and supporting peatland biodiversity by creating suitable habitat conditions, often focusing on stable high water tables. However, the expected colonization by characteristic species can take decades or even fail. Monitoring programs need to detect these developments in order to adapt management strategies, if necessary. For choosing suitable monitoring time scales, intervals and indicators, we need to know, if initial trends are continued on the long term, and if results differ among taxonomic groups. Therefore, this study aims at comparing the recovery of plant, dragonfly and butterfly diversity about two decades after rewetting of montane peatlands in central Germany. We compared diversity and species composition of 19 restored sites with three drained peatlands and one near-natural reference site in a chronosequence approach. Peatland rewetting improved habitat conditions, vegetation structure and species diversity, while there were marked differences among taxa. Plant and dragonfly diversity benefitted most from restoration, while no peatland-specific butterflies were observed in the rewetted sites (Fig. 11). More specifically, characteristic peatland plants increased when peat was intact, while dragonflies colonized rapidly freshly created ponds. Plant species reached around 50% of similarity to reference conditions after 18 years. However, plant specialist richness was only temporarily higher compared to degraded conditions and slightly decreased after more than 7 years, and plant assemblage rather slowly approached reference conditions. Dragonflies respond markedly to early-successional stages, at least partly due to newly created bog pools, while plants

integrate long-term changes in site conditions and peatland plant specialists are positively correlated with peat accumulation. Butterflies were unsuitable indicators in our study, while they could be useful in regions with a more abundant peatland butterfly community. These findings demonstrate that peatland restoration improves habitat conditions and thus benefits characteristic diversity, but recovery is still incomplete after two decades. Also, developments were not always linear and there were species-specific responses to restoration, highlighting the importance of repeated long-term monitoring and a strategic selection of indicators.

Graphical abstract

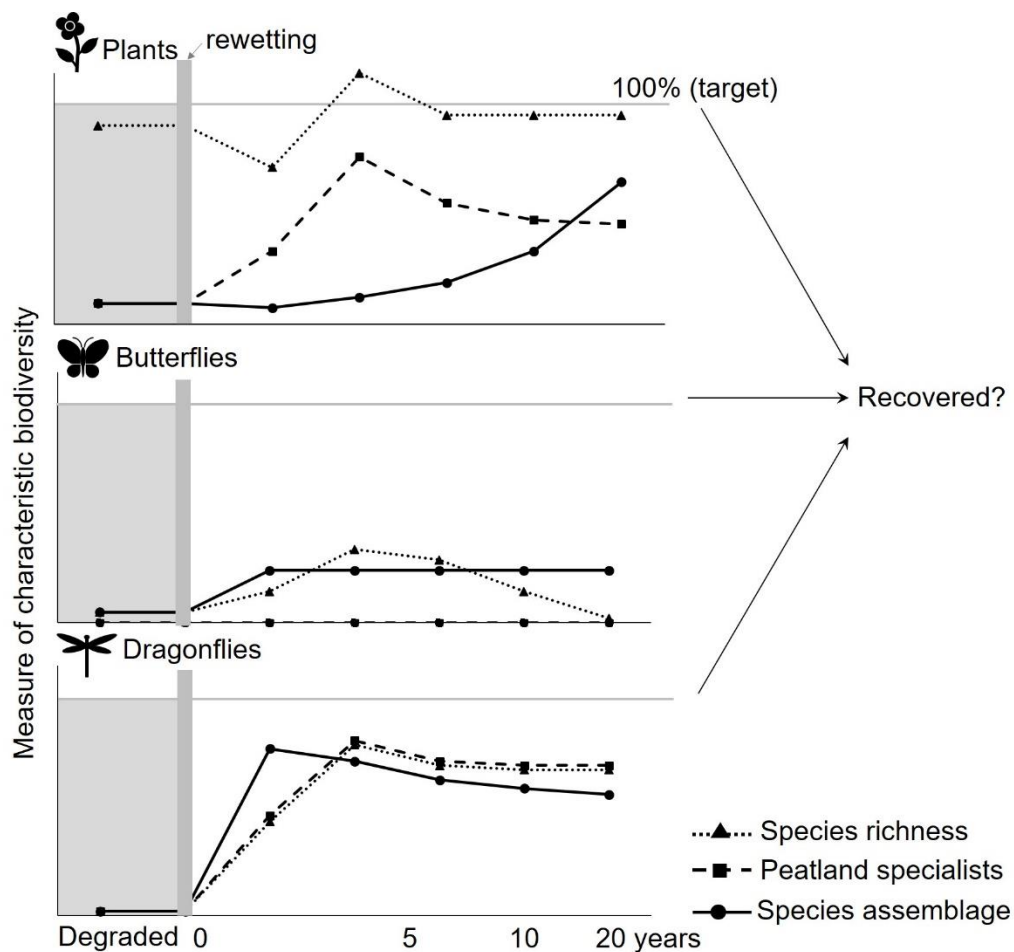


Fig. 11: Recovery of plant, butterfly and dragonfly diversity after restoration of montane peatlands. Figure modified after STROBL & KOLLMANN (2018)

ARTICLE 2: Selecting plant species and traits for phytometer experiments. The case of peatland restoration

Strobl, K., Schmidt, C., Kollmann, J. (2018): Selecting plant species and traits for phytometer experiments. The case of peatland restoration. *Ecological Indicators*, 88, 263-273, doi: 10.1016/j.ecolind.2017.12.018

Author contributions

KS, CS and JK conceived and designed the study. CS and **KS** set up the experiments. CS sampled and analysed the data of a preliminary experiment. **KS** sampled and analysed the data of the main experiment. **KS** wrote the first draft of the manuscript. **KS**, CS and JK discussed the results. CS and JK improved and edited all manuscript versions.

Summary

The second article evaluates the potential of a novel monitoring approach using phytometers for assessing peatland restoration success. Phytometers are indicator transplants that provide information on site conditions based on plant fitness, i.e. survival, growth and reproduction. Since a key attribute of successfully restored peatlands is their capacity to sustain viable populations of characteristic species, the phytometer approach seems a promising assessment method. More than descriptive approaches, they should be capable of detecting the underlying causes, when target species do not spontaneously colonize as expected. In comparison with the observation of natural populations of the respective species, they can inform about site or dispersal limitation. However, their use is comparatively new in ecological restoration and has not yet been applied to peatlands. The goal of this study is to advance the definition of standards for a more common implementation of phytometers in restoration monitoring by comparing the responses of several species and traits to environmental conditions in restored peatlands. Three characteristic peatland species (*Drosera rotundifolia*, *Eriophorum vaginatum*, *Vaccinium oxycoccos*; Fig. 10) were planted in seven restored montane peatlands in central Germany. In a simultaneous greenhouse experiment, the same species were grown on peat from the field sites and exposed to two different water levels (-3 and -8 cm below surface). We measured numerous plant traits and compared them with varying light, water and soil conditions. We saw, species-specific responses to abiotic conditions, highlighting that the use of several phytometer species increases the reliability of monitoring. Survival and growth traits were suitable to assess a wide range of habitat conditions, while reproductive traits were more time-consuming to measure. Survival provided the most conclusive results for species sensitive to stressful habitat conditions. Biomass and other size metrics of the phytometers, as well as growth and

reproductive traits were partly redundant. Thus, we suggest recording survival and biomass. Non-destructive growth measurements are useful for repeated assessments, while the choice of the most suitable size trait should generally depend on the growth form. Our study stresses the potential of phytometers for monitoring a restoration outcome, expands the method to the specific ecosystem of peatlands and highlights the importance of species and trait selection (Fig. 12).

Graphical abstract

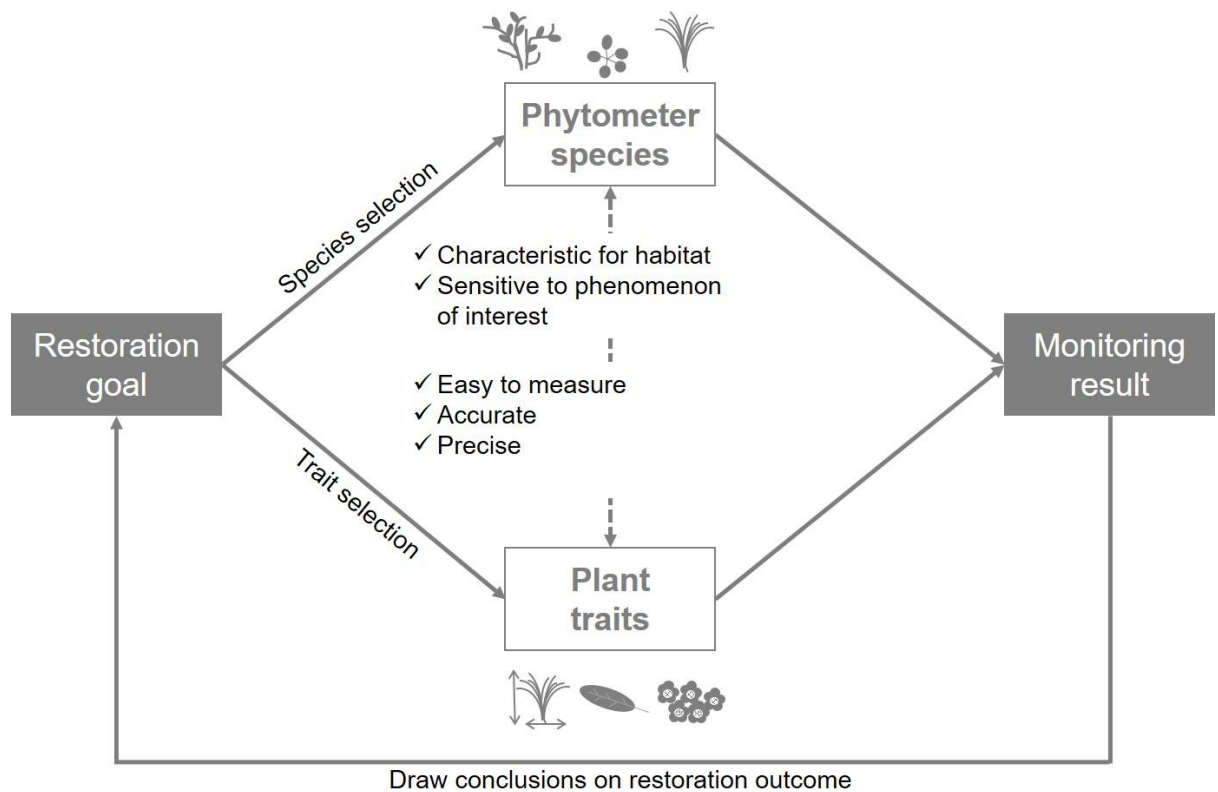


Fig. 12: Phytometer species and traits are indicators of restoration success, that have to be carefully chosen according to the restoration goal to be evaluated, since they considerably affect the monitoring outcomes.

ARTICLE 3: Integrated assessment of ecosystem recovery using a multifunctionality approach

Strobl, K.*, Teixeira, L.H.* , Kollmann, J. (in revision): Integrated assessment of peatland recovery using a multifunctionality approach. *Ecological Applications* (equal contribution)

Author contributions

KS and JK conceived the field survey. KS sampled the data. LT had the idea for the data analysis and performed it. **KS**, LT and JK discussed the data analysis and manuscript structure. **KS** and LT wrote the manuscript. JK improved and edited the manuscript.

Summary

The third article is an integrative assessment of peatland recovery based on multiple properties including characteristic plants, vegetation structure, water level, peat quality indicators and nutrient level. Since ecological restoration – as it is the case also for peatlands - often aims at the simultaneous recovery of numerous ecosystem functions and services, it can be challenging to comprehensively analyse and interpret those potentially contradicting targets. This is even more true, when numerous indicators have to be sampled or when there are no natural references. Therefore, we used different multifunctionality approaches, that were inspired from biodiversity and ecosystem function (BEF) research. In order to study peatland recovery, we analysed this multifunctionality against time since restoration. We wanted to know, to what extent restored peatlands recover and how time since restoration is controlling the simultaneous development of multiple properties. We studied rewetted drainage ditches and their direct surrounding in a chronosequence (0–18 years after restoration) and compared their recovery to an optimum value, that was defined as the mean of the seven highest values. Thus, we argue that this approach can be used for evaluating ecosystem restoration without natural references. We found, that nine out of 13 properties as well as the combined index significantly increased with time since restoration (Fig. 13). However, improvements were strongest within the restored drainage ditch and rewetting effects did not spread to the whole peatland. While we could not observe the simultaneous recovery of multiple properties at a high level of functioning, there was significant progress with time at low and intermediate levels of functioning (Fig. 13). Our results show that heavily degraded peatlands cannot fully recover within 18 years, instead restoration should rather focus on fewer or lower targets at these time scales. Some properties might also have longer time lags than others. However, even if not all properties can simultaneously be restored, a considerable improvement is possible. We believe, that multifunctionality approaches can help summarize large monitoring datasets and give an integrative picture of ecosystem

recovery. While the integrated assessment informs about the degree of ecosystem recovery, juxtaposing trajectories of individual properties helps understanding ecosystem-specific dynamics, that are crucial for deciding on potential future management.

Graphical abstract

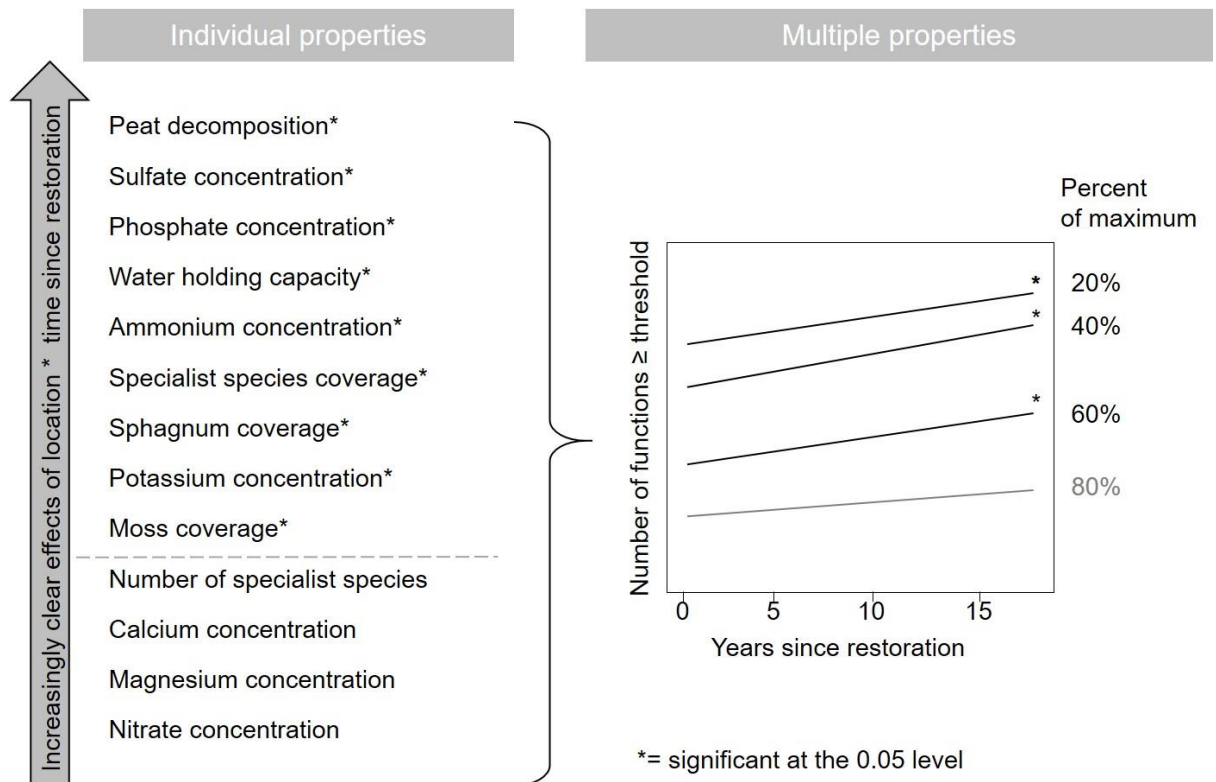


Fig. 13: Nine out of 13 properties were significantly affected by the interaction of location (inside/ outside the ditch) and time since restoration. The simultaneous analysis of multiple properties showed significant improvements with time at low and intermediate levels of functioning.

GENERAL DISCUSSION

Ecological restoration has become a major strategy for recovering biodiversity and functioning of degraded ecosystems. There is a strong focus on peatlands, because of their critical status and their great potential to store carbon and to mitigate climate change. However, their recovery is complex and slow, making it particularly difficult to adequately assess and judge their restoration success. The goal of this thesis was to improve the scientific understanding of peatland recovery potentials and dynamics as well as to reflect the wise selection of monitoring methods. For this purpose, I used several observational and experimental approaches and numerous indicators of rewetting success. This chapter of the thesis summarises the different approaches and compares the main findings based on numerous indicators in order to point out the effectiveness of rewetting measures and derive recommendations for future monitoring as well as peatland restoration management (Fig. 14).

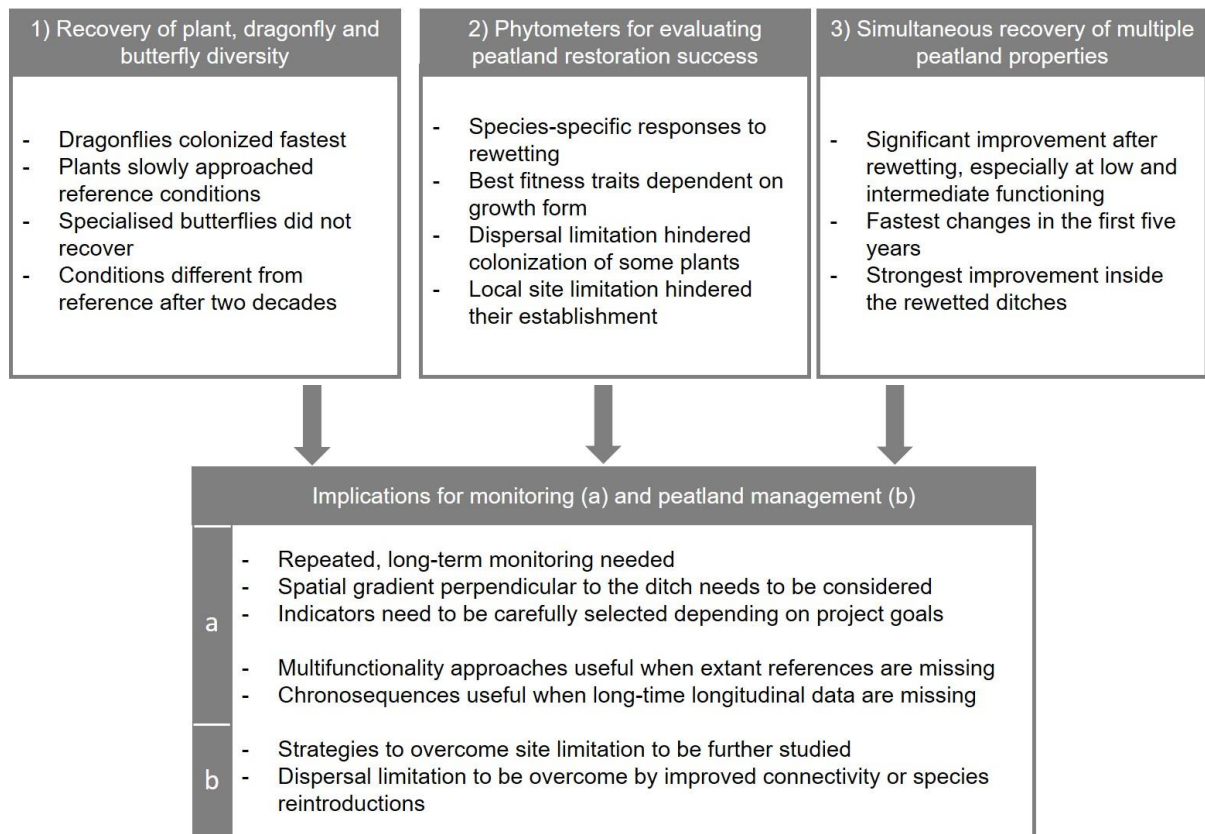


Fig. 14: Main findings of the thesis and their implications for peatland management.

Identifying references and targets for restoration

A key principle for evaluating success of ecological restoration is the identification of an appropriate reference model, that informs about the target of restoration and serves for comparison with restored systems (MCDONALD et al. 2016). For example, Article 1 and 3 of this thesis aimed at estimating the degree of peatland recovery after rewetting. Supported by previous meta-analyses (REY BENAYAS et al. 2009, MORENO-MATEOS et al. 2017, JONES et al. 2018), I concluded twice a considerable peatland improvement, but an incomplete recovery after two decades, that might be interpreted as a recovery debt (MORENO-MATEOS et al. 2017). The latter is defined as the temporal reduction of ecosystem properties occurring during recovery, and is estimated via the comparison to a reference at a certain point in time. Hence, the reference considerably influences the interpretation of results. In this thesis, I used two different reference models, i.e. an extant (Article 1) and a theoretical reference one (Article 3).

In Article 1 the least degraded peatland within the study area was used as a reference despite some methodological constraints. It was not completely undisturbed and turned out to be only useful for plants, while being largely unsuitable for comparison of dragonfly and butterfly diversity due to a lack of data (Article 1). Furthermore, there was only one available reference peatland making statistical comparisons with degraded or restored sites impossible or rather not meaningful. Consequently, the data had to be supported by the literature in order to derive reliable and convincing conclusions. This problem is common for heavily degraded ecosystems, where intact references are scarce, like for example peatlands in Central Europe (JOOSTEN & CLARKE 2002), grasslands in Southern Brazil (ANDRADE et al. 2015) or old-growth forests in the Northern boreal zone (JOSEFSSON et al. 2009).

When real-world reference data are missing, historical records could be used as an alternative (MCDONALD et al. 2016). Yet, these are even more scarce and the implementation of historic information into statistical analyses even more challenging. Also, we are facing rapid environmental changes like global warming or species invasions causing a shifting baseline (HIGGS et al. 2014) and questioning the suitability of historic information. Instead of defining a narrow and static target, references should incorporate the capacity of an ecosystem to resiliently evolve with changing environmental conditions (MCDONALD et al. 2016). Finally, novel ecosystems, that differ in composition and/or function from present and past ecosystems (HOBBS et al. 2009), lack any recent and historic references. In this case, alternative approaches have to be used for evaluating restoration success.

In Article 3, such an alternative approach for evaluating ecosystem recovery without a real-world reference is proposed. The target is defined based on a percentage of the highest observations (see threshold approach and multiple threshold approach in BYRNES et al. 2014) and can therefore be applied for any of the above cited cases. While it was developed in BEF-research (GAMFELDT et al. 2008, ZAVALETA et al. 2010), we were among the first to extend it to the field of restoration ecology (but see also CRUZ-ALONSO et al. 2019). It is most useful, when aiming at multiple goals or the so-called multifunctionality (HECTOR & BAGCHI 2007). Similarly, restoration usually measures ecosystem recovery based on several attributes (SOCIETY FOR ECOLOGICAL RESTORATION INTERNATIONAL 2004). Furthermore, it sometimes even has different targets, e.g. productivity, recreation or politically important ecosystem functions like the reduction of greenhouse gas emissions. Those can be contradicting, when several stakeholders are involved. In this case, the approach could be extended by weighting goals through stakeholder judgement (MANNING et al. 2018), and serve as a basis for decision-making.

Despite the above-cited theoretical benefits, the implementation of the approach is still at the beginning and needs to be further advanced. In terms of references, the definition of the theoretical optimum is object to discussion. While most authors suggest to use the 5% highest values (ZAVALETA et al. 2010, BYRNES et al. 2014), this (and any other) proportion is arbitrary (BYRNES et al. 2014). Furthermore, the approach assumes, that highest (or lowest) values are most desirable, while the ecological optimum could also correspond to intermediate values. An example from peatlands concerns the water table, that is often considered optimal around -10 cm. At higher water tables (i.e. flooding) CH₄ emissions are strongly increased, while at lower water tables peat is decomposing and CO₂ released (COUWENBERG et al. 2010). Finally, it can underestimate the recovery potential, since it only uses current values as an optimum, while ignoring the possibility of further improvement exceeding the existing state. This is especially problematic for small datasets, when comparing only few sites or short-time series. Nevertheless, in this thesis it appeared to be particularly useful for evaluating several sites in a time series.

Designing a long-term repeated monitoring for peatlands

Ecological restoration aims at the highest possible recovery relative to a reference (MCDONALD et al. 2016). However, the definition of full recovery depends not only on the reference, but also on the moment of evaluation. In most cases, targets are not reached immediately, but recovery is an ongoing process and ideally a continued trajectory towards the desired outcome. When evaluating success, it is therefore fundamental to estimate the

degree of progression, i.e. where the ecosystem can be located on the trajectory. Thus, time series of previously restored ecosystems can help identifying common dynamics and processes. In this thesis, I tracked 18 years of peatland recovery, that can serve as a model for future monitoring and evaluation of success.

There are important temporal trends in peatland recovery in the 18 years after rewetting (Article 1 and 3). Even if changes are significant from the first year on (Article 1 and see also MELI et al. 2014), trajectories are not linear over the whole time period. Instead, fastest changes occur in the first five years (Article 3). Those are explained by an early-successional transitional state, that differs in vegetation structure and diversity from later-successional phases (Article 1). At the same time, older peatlands show large variation. While some sites (Article 1) or parts of these sites (i.e. ditches; Article 3) seem to progress towards the target, others deviate from this trajectory. These findings highlight the need for long-term monitoring (>20 years). For peatlands, I suggest more frequent observations (i.e. 2–3 years) in the first 10 years, while 5–10 years' intervals should be sufficient later. This enables the flexible adaptation of goals and potentially necessary management intervention. Generally, a self-sustaining peat accumulation can be expected after about 30 years (GORHAM & ROCHEFORT 2003), so that at least 30 years of monitoring are necessary for adequately concluding on peatland restoration success and making sure, that no further intervention is necessary.

While long-term time series are scarce due to limited funding within short-term projects, peatland restoration has become common practice in nature conservation. In regions, where several comparable sites have been restored with similar methods, chronosequences can serve as a substitute in the absence of long-term longitudinal data and generate reliable results. Obviously, they have some disadvantages like the risk of false extrapolations (WALKER et al. 2010). Therefore, some assumptions must be met. For example, in restoration ecology, they can only be used, if restoration methods do not evolve too much with time; they are more appropriate for convergent successional trajectories and ecosystems with low frequency and severity of disturbance (WALKER et al. 2010) as well as ecosystems with low beta-diversity, high connectivity and rapid response of organisms (BANET & TREXLER 2013). In this thesis, most sites had been restored with similar methods, which allowed for a reliably study of a long chronosequence. However, it was not possible to compare different methods without a considerable (and not feasible) increase in sampling effort. Furthermore, the oldest restoration sites were spatially clumped, because restoration had been initiated by one local forestry authority. Nevertheless, they can help understand ecological processes under circumstances, where long-term data cannot be generated in any other way (WALKER et al.

2010). However, comparable sites have to be carefully selected in order to avoid misinterpretations.

Besides temporal aspects, the spatial configuration is crucial for designing a monitoring program, that is well-adapted to the phenomenon of interest. In this thesis, I decided to sample vegetation and abiotic environment directly inside the (blocked) ditches as well as their direct surrounding from 1 to 11 m distance. Positive effects of rewetting should first become visible within the blocked ditches, while the subsequent gradual benefits to the whole peatland are slower (HEDBERG et al. 2012). Article 3 confirmed this, since many ecosystem properties inside the ditch recovered faster than outside the ditch. However, a gradual spreading could not be proven. For example, the water table outside the ditch did not increase with time, highlighting the spatial limitation of rewetting. While HAAPALEHTO et al. (2017) observed the contrary, i.e. a better recovery farther away from the ditch, their findings also prove a spatial gradient, that consequently has to be reflected by a spatial monitoring design. I recommend assessing changes in different distances to drainage ditches, that depend on the size of the dam and the expected rise of the water table. In this thesis, 11 m were enough, while HEDBERG et al. (2012) saw differential responses up to 25 m away from the ditch.

Selecting adequate indicators of restoration success

Conclusions on success or failure of restoration projects largely depend on the indicators used (LINDENMAYER & LIKENS 2010). Article 3 showed for example, that the water table was not significantly increased on the long-term by the rewetting measures. If this had been the only assessed environmental indicator, the restoration measures would seem unsuccessful. However, a decreased degree of decomposition and an increased water holding capacity prove, that restoration could sufficiently activate peat accumulation. For citing another example, an analysis of butterflies alone would have led to different conclusions than an analysis of dragonflies or plants, since only specialist species of the two latter successfully colonized the restored peatlands (Article 1). This confirms, that judgements of biodiversity recovery are highly influenced by the assessed taxonomic organisms (MELI et al. 2014). Moreover, Article 2 revealed species-specific responses to rewetting, showing that *E. vaginatum* benefitted more from restoration than *D. rotundifolia* and *V. oxycoccus*. Therefore, the statement of MELI et al. (2014) from assessed taxonomic groups expands even to the species level.

Monitoring outcomes are also strongly influenced by the assessment scale. Single species or properties are not able to reflect the full complexity range of an ecosystem (LINDENMAYER

& LIKENS 2011), especially when several restoration goals are to be fulfilled. This can be achieved with integrative methods like the multifunctionality approach suggested in Article 3. Another tool, that was proposed by MUELLER et al. (2014), involves a standardised multivariate approach including different taxonomic groups. On the other hand, integrative approaches or indices are often not useful for deriving detailed decisions on how to improve the current management as needed for 'adaptive restoration' (Article 3), that includes an adaptation of the initial management in case of unforeseen deviations from the goals (ZEDLER & KERCHER 2005, HERMANN & KOLLMANN 2015). Instead, the study of single species as phytometers for example (Article 2), gives detailed information on the reasons for their presence and therefore enables conclusions for an improved management, e.g. the need for further manipulation of site conditions or reintroductions. All in all, a suitable scale of peatland monitoring cannot be generalised, but needs to be chosen according to project goals.

While there are numerous possibilities of indicators, that could potentially be assessed in restoration monitoring, usually financial resources and time are limiting in most projects (RUIZ-JAEN & AIDE 2005). For this thesis, a large range of peatland restoration indicators was studied (Table 2), that can be used as a basis for future monitoring planning. Most indicators showed a significant response with time since restoration or a significant improvement of the degraded state, highlighting their general suitability for tracking peatland recovery. However, while their associated role in peatlands largely differs, many of them are interrelated (Fig. 15). For example, many growth traits (e.g. length of shoots and plant biomass, tussock diameter and biomass) are correlated (Article 2). Some peatland properties of Article 3 (e.g. *Sphagnum* cover and number of peatland specialists, calcium and magnesium, ammonium and water holding capacity) were also strongly correlated. Even more generally, the recovery of biodiversity and ecosystem services is correlated (MELI et al. 2014). These dependencies show on the one hand, that many properties can be simultaneously restored. On the other hand, they highlight, that it is not necessary to assess all indicators, when resources are limited. Instead, a careful selection can significantly reduce the sampling effort, while still providing sufficient data in order to report on project-relevant dynamics. The results of this thesis can help in this selection process (Fig. 15, Table 2). A detailed evaluation of peatland restoration indicators is also given by TIEMEYER et al. (2017).

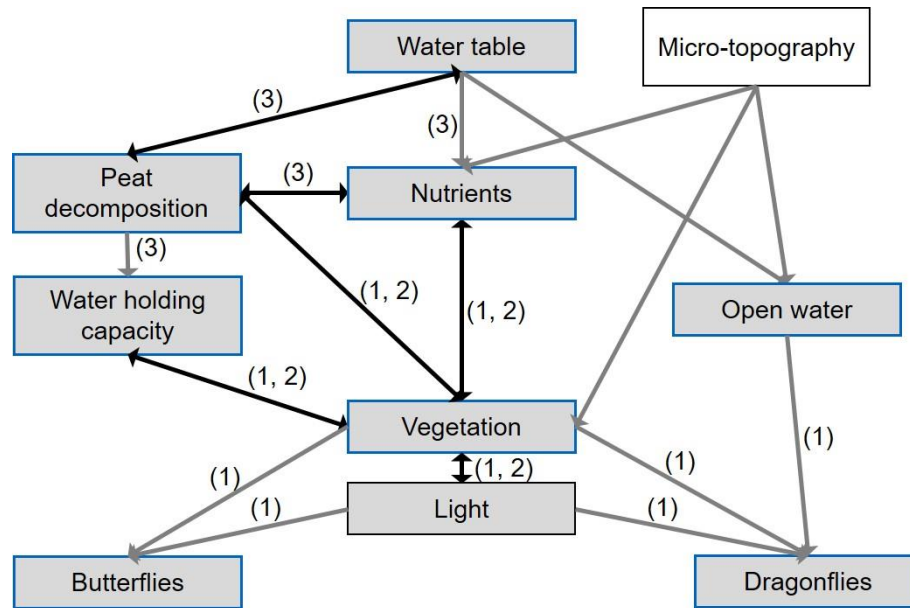


Fig. 15: Relationship between peatland restoration properties at the site scale, that were individually assessed for the thesis (grey boxes; microtopography was not measured). Their dependency was analysed in the three included articles. The main articles for analysis are indicated via the respective numbers in brackets. Grey arrows indicate a unilateral relationship, black arrows a reciprocal influence of the involved properties.

Ecosystem functions of restored peatlands are best described by abiotic conditions. The water table, the degree of peat decomposition, water holding capacity and nutrients are directly related to decomposition processes, that indicate, if peat is actively accumulating (Article 3). Some of these measures can also indirectly indicate the potential of restored peatlands to mitigate climate change. Greenhouse gas emissions have not been directly measured in this thesis. Possible methods include the eddy covariance technique (TIEMEYER et al. 2017) or modelling approaches like the “peatland emissions predictor” (PEP)-modell (DRÖSLER et al. 2013) or the GEST approach (COUWENBERG et al. 2011). Species assemblages also indicate the functionality of the ecosystem. PH and conductivity have been assessed, but did not differentiate within or between the assessed sites, since the selected peatlands were very similar in terms of mire type (CONRADI & FRIEDMANN 2013). Plants are suitable indicators of abiotic conditions (ELLENBERG et al. 2001). When used as phytometers they can indicate site limitation (Article 2). However, plants can show some delay in response to habitat changes. The abundance of plant functional groups indicates the successional stage of peatland recovery (Article 1). More mobile taxonomic groups like dragonflies colonize faster and indicate restoration success at early-successional stages. Butterflies largely depend on vegetation as larval food plants, and are therefore more suitable indicators at later successional stages. They also indicate a good connectivity with suitable habitats and source populations in the peatland surrounding.

GENERAL DISCUSSION

Table 2: Indicators for peatland recovery, that have been studied in this thesis and most important results, their indicator potential, their recovery with time over a period of 18 years (as studied in Article 3) or compared to the degraded state (as studied in Article 2) and their development trajectory. The last two columns indicate, in which article the respective indicator was studied and give examples of further literature.

Indicator	Associated role in peatlands	Significant recovery		Temporal trend	Article	Further literature (examples)
		with time	from degraded			
Ecosystem functions						
Peat decomposition	influences hydraulic conductivity, indicates active peat accumulation	+		linear	3	BADEN & EGGELSMAN 1963; GROVER & BALDOCK 2013; FRANK et al. 2014; MUSTAMO et al. 2016; REZANEZHAD et al. 2016
Water table	influences habitats for plants, influences decomposition and nutrient dynamics, indirect measure of greenhouse gas fluxes	-	-	slightly unimodal	2	JUNGKUNST & FIEDLER 2007; BREEUWER et al. 2009; VERHAGEN et al. 2009; COUWENBERG et al. 2010; BEETZ et al. 2013
Water holding capacity	indicates porosity and decomposition of peat, influences habitats for plants	+		linear	1, 2, 3	BOELTER 1964; HALLEMA et al. 2015; REZANEZHAD et al. 2016
Nitrate	indicate mineralisation, aerobic	-		no change		
Phosphate	conditions, influence habitats for plants	+		slightly unimodal		
Ammonium		+		slightly unimodal		
Sulfate	indicates oxidation, peat compaction, eutrophication	+		slightly asymptotic	1, 2, 3	FREEMAN et al. 1993; HOLDEN et al. 2004; KIECKBUSCH & SCHRAUTZER 2007; SCHUMANN & JOOSTEN 2008; FRANK et al. 2014
Potassium	influence habitat conditions for plants	+		slightly asymptotic		
Calcium	indicate drainage	+		slightly asymptotic		
Magnesium		+		slightly asymptotic		
Plants						
Graminoid cover	indicates early recovery phases, minerotrophic conditions		-	unimodal	1	KLÖTZLI & GROOTJANS 2001; MATTHEWS et al. 2009; POTVIN et al. 2015
Ericaceae cover	indicates later recovery phases, ombrotrophic conditions		-	linear	1	GONZÁLEZ et al. 2013, POTVIN et al. 2015
Moss coverage	indicates humid conditions	+	-	linear	3	TURETSKY et al. 2012; LABERGE et al. 2013; MILLER et al. 2015

GENERAL DISCUSSION

Indicator	Associated role in peatlands	Significant recovery		Temporal trend	Article	Further literature (examples)
		with time	from degraded			
<i>Sphagnum</i> coverage	indicates wet conditions, (future) active peat accumulation	+		linear	1, 3	VAN BREEMEN 1995; SOTTOCORNOLA et al. 2007; BREEUWER et al. 2009; GROOTJANS et al. 2012; POTVIN et al. 2015
Richness	indicates (past) disturbance		-	slightly unimodal	1	MINAYEVA et al. 2017; PRACH & WALKER 2018
Specialist number		-	+	unimodal	1, 3	
Specialist coverage	indicates poorly decomposed peat, medium-term peatland recovery	+		linear, slightly unimodal	3	GUNNARSSON et al. 2000; PARISH et al. 2008, HAAPALEHTO et al. 2017
Assemblage			+	-	1	
Phytometer fitness	indicate adequate habitat conditions for the respective species, indicate dispersal limitation when compared to local occurrence				2	VERHEYEN & HERMY 2004; BAKKER et al. 2006; BAETEN et al. 2010; DIETRICH et al. 2013; DIETRICH et al. 2015; BOURGEOIS et al. 2016
Dragonflies						
Richness			+	slightly unimodal		
Habitat specialists			+/-	slightly unimodal		
Assemblage	indicate early-successional stages of peatland recovery with suitable ponds		+	-	1	ROUSH & AMON 2003; KADOYA et al. 2008; ELO et al. 2015
Ponds			+	-		MAZEROLLE et al. 2006; HANNIGAN et al. 2011; BROWN et al. 2016
Butterflies						
Richness			-	slightly unimodal		
Habitat specialists			-	no change		
Assemblage	indicate later-successional stages of peatland recovery with good connectivity to nectar and forage plants in the surrounding		+	-	1	RÁKOSY & SCHMITT 2011; SWENGEL & SWENGEL 2015; NOREIKA et al. 2016
Forage plants			+/-	Linear or no change		

Implications for peatland management

All three main articles of this thesis point out, that rewetting could improve the ecological status of peatlands, but that even after two decades, conditions similar to intact peatlands were not reached (Fig. 16). Article 1 showed that most biodiversity variables were enhanced by rewetting, but almost none of them reached the level of the reference peatland. Article 3 showed that a 50% recovery or intermediate levels of functioning could be achieved within 18 years. This is also very similar to results of MORENO-MATEOS et al. (2017) for wetlands, as they showed that around 50% could be restored in terms of abundance, while it was less for diversity. HAAPALEHTO et al. (2017) drew similar conclusions for forestry-drained peatlands, as their recovery was promising, but spatially heterogeneous. Nevertheless, more than half of the important peatland properties could be significantly improved with time since restoration (Article 3).

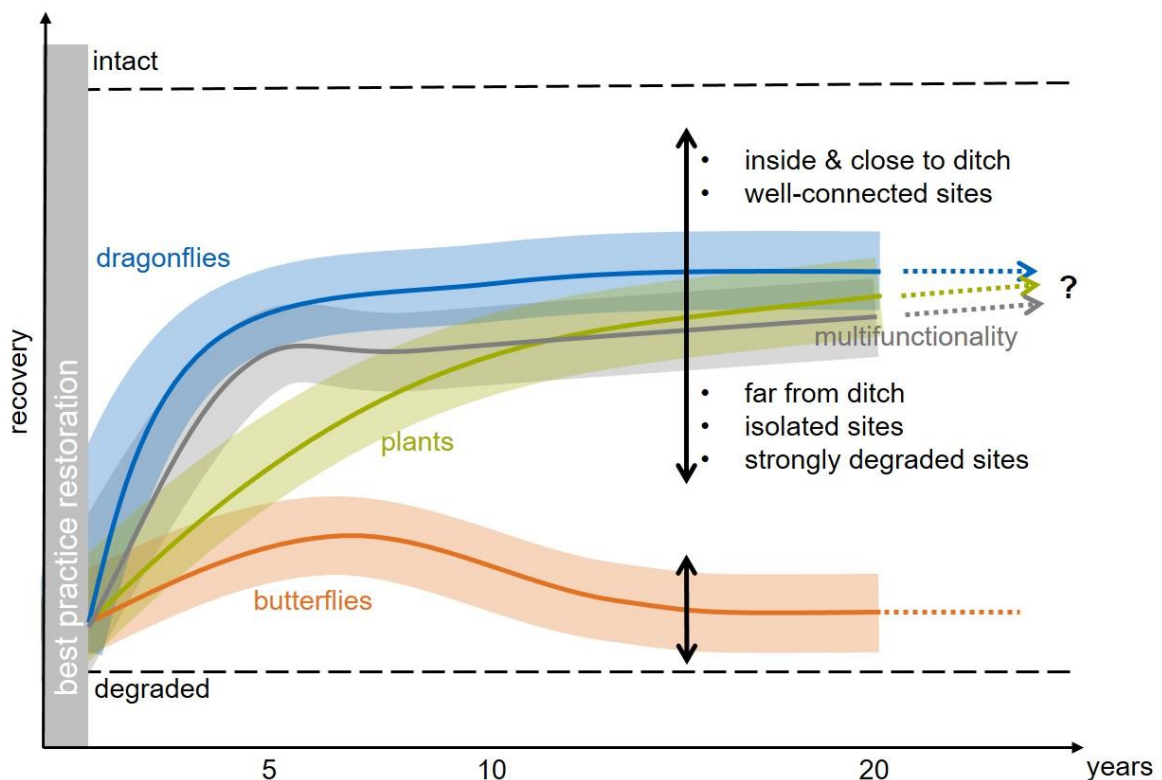


Fig. 16: Recovery trajectories of rewetted montane peatland. The figure is based on a generalisation of the main findings of this thesis. The shaded area represents potentially different results depending on the position within the peatland (inside/ outside the rewetted drainage ditch), its connectivity to intact or successfully restored sites with source populations and its initial degree of degradation.

These findings can be interpreted in two ways: First, they prove that rewetting is effective for counteracting peatland degradation related to drainage and afforestation. Second, pre-degraded intact conditions or simultaneous desirable levels of multiple properties could not

be reached within the observed time span (Article 1 and 3). Since peatlands are slowly recovering (Article 3) there certainly is more time needed until full recovery (Fig. 16). However, while there are still considerable fluctuations in diversity attributes in early phases (e.g. plant species assemblage, dragonfly richness; Article 1), there are generally only few further changes after 5–10 years (averaging approach; Article 3). It seems most likely, that not all properties could be simultaneously restored to the most desirable level. For example, specialist species number and nitrate concentrations did not improve with time (Article 3), and characteristic butterfly diversity and some expected plant species were missing in the restored sites (Article 1).

For wetlands, the degree of recovery mainly depends on restoration actions, ecosystem type and degree of degradation (MELI et al. 2014). While additional restoration measures (see below) might further improve the restored sites, the ecosystem type and degradation cannot be influenced by management. Those factors should be the basis for estimating the recovery potential and need to be considered during the planning process of restoration projects or adaptive management approaches. It is crucial to set achievable goals based on peatland history of origin and level of degradation (SCHUMANN & JOOSTEN 2008, SCHRAUTZER et al. 2013; Fig. 16) for effectively and efficiently evaluating restoration success. Nevertheless, additional management possibilities should be further explored. Even if the study design of the thesis does not allow for the comparison of different restoration methods (since the most similar peatlands were selected for the chronosequence), the three main articles of this thesis give some ideas on further improvement of rewetted peatlands, that are worth being pointed out.

The two major problems are local site limitation, especially further away from the filled ditches (Article 2 and 3), and dispersal limitation of some species or taxonomic groups. (Article 2, STROBL & KOLLMANN 2018). In heavily degraded peatlands highly altered peat and hydrology are often hindering a full recovery (SCHOPP-GUTH & GUTH 2003, SCHUMANN & JOOSTEN 2008). Article 3 showed, that peatland properties mostly improved locally in the direct surrounding of rewetted drainage ditches, and the water table was not significantly increased with time. Instead, it seemed to slightly decrease after a first increase. An insufficient water supply is also emphasized by the high cover of Ericaceae, a low cover of *Sphagnum* (Article 1) and the partial site limitation of *D. rotundifolia* and *V. oxycoccos* (Article 2). Where the water table is lower than -30 cm, *Sphagnum* cover stayed below 30% of coverage (STROBL et al. 2018a), since low water tables favour plants of hummocks and peatland margins like *Calluna vulgaris* or *Vaccinium* spp. (POTVIN et al. 2015). Furthermore, even if the degree of peat decomposition significantly decreased with time, it was still below

levels of intact peatlands after two decades (Article 3). Decomposed peat loses its water storage capability, prevents peat moss (*Sphagnum* spp.) colonization (SMOLDERS et al. 2003) and consequently compromises peat formation and a stable high water table (VAN BREEMEN 1995). However, site limitation is unlikely to be the only cause for incomplete recovery. Article 2 also proves dispersal limitation for all three study species and Article 1 for characteristic peatland butterflies, since the restored sites are poorly connected to source populations.

For counteracting problems of site limitation, three management possibilities should be further explored in the field. First, I observed that with time trees re-established at rewetted peatlands, leading to higher transpiration and thus lowering the water table. Their removal would decrease transpiration and increase light availability for peatland-specific species (HEDBERG et al. 2012). Dragonflies benefitted from sunny pools (Article 1) as well as *D. rotundifolia* and *E. vaginatum* (Article 2). However, when removed in early phases of peatland recovery, tree removal might enhance peat mineralisation due to high solar irradiation (BERNRIEDER 2003). Second, the dams might be too small. If they are too narrow, the water is not sufficiently spreading into the whole peatland. If they are too low, water might not be hold back in times of high runoff, which not only leads to the loss of water, but also causes erosion. Third, the partial removal of the (upper) decomposed peat layer can initiate the establishment of peat mosses and other characteristic plants.

Dispersal limitation – like observed for *D. rotundifolia* and *E. vaginatum* (Article 2) as well as for butterflies (Article 1) – should preferentially be counteracted by an improved connectivity. Since the study area is largely forested, butterflies could benefit from open corridors connecting peatland sites to flower rich grassland (LIPSKY 1999). New rewetting projects should ideally be carried out near intact or successfully restored peatlands, that can serve as source populations. If peatlands within the dispersal distance of characteristic species are restored, they are more easily colonized and (meta-)populations strengthened by the increased availability of habitat patches. If sufficient connectivity cannot be created within a region and characteristic species are not yet present in the restored sites, they might alternatively be reintroduced. Potential reintroduction methods include sowing, planting or transfer of vegetation or peat from source peatlands (SLIVA & PFADENHAUER 1999, ROCHEFORT et al. 2003, GROSVERNIER & STAUBLI 2009).

While this thesis does not inform about the suitability of different measures, the above cited additional restoration measures (e.g. dam reinforcement, further tree removal, plant reintroduction) might further improve the rewetted peatlands. They should be systematically tested in an adaptive restoration process, that adjusts measures on a trial-and-error basis

(ZEDLER & KERCHER 2005) and/ or an experimental setup, that simultaneously compares different measures (HERMANN & KOLLMANN 2015).

CONCLUDING REMARKS

At the beginning of this thesis, I wanted to know, how rewetted peatlands recover with time and how the conclusions change depending on the applied evaluation approach. The answer is not straightforward. The results generally show, that peatlands do recover, but not all properties recover fully within two decades and not all develop linearly. The three articles, that are the basis of this thesis, identify which monitoring targets need further attention, and the general discussion gives recommendations for further improvement. Nevertheless, the here collected data does not tell, if recovery is still to be continued after two decades or if the maximum status that can be reached with the applied methods, has already been achieved. Therefore, future studies should investigate even longer time series. Furthermore, the chronosequence approach has its limits, since it does not allow for the comparison of different restoration methods. Experimental and engineering approaches in long-term longitudinal data series are needed to better understand their functioning and further advance the current rewetting techniques.

As stated in the introduction the applied monitoring approaches mainly differ in their scale of comprehensiveness and explanatory potential. I cannot recommend one method more than another, since their usefulness depends on the restoration and monitoring targets; be it the protection of one population of a rare species, the restoration of a characteristic species assemblage, the recovery of a specific function like carbon storage, or the conservation of ecosystem processes. Sometimes one site is expected to fulfil all of these goals. However, conservation and restoration targets can be heavily contradicting making it difficult to find an adequate management. Monitoring is then laborious and results often disappointing, since a high functionality in divergent properties is not possible. It is therefore crucial to realistically think about the possibilities beforehand. Since some developments cannot be foreseen, it is also advisable to adapt the vision throughout the recovery process. However, before giving up and accepting an incomplete recovery, we should still try to understand the underlying reasons and advance the management strategies to their best.

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