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Succession comprises a sequence of threshold-induced community assembly processes towards multidiversity

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Abstract

Research on ecological successions and community assembly shaped our understanding of community establishment, co-existence, and diversity. Although both lines of research address the same processes such as dispersal, species sorting, and biotic interactions, they lack unifying concepts. However, recent theoretical advances proposed to integrate both research lines and thus provided hypotheses on how communities assemble over time and form complex ecological systems. This framework predicts a sequence of stochastic and niche-based processes along successional gradients. Shifts in these assembly processes are assumed to occur abruptly once abiotic and biotic factors dominate over dispersal as main driver of community assembly. Considering the multidiversity composed of five organismal groups including plants, animals, and microbes, we empirically show that stochastic dispersal-dominated community assembly is replaced by environmental filters and biotic interactions after around 60 years of succession in a glacier forefield. The niche-based character of later successional processes is further supported by a pronounced decline in multi-beta-diversity after the shift in assembly processes. Our results support recent theories and provide new insights into the emergence of multidiverse and complex ecosystems. Our study will stimulate updates of concepts of

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community assembly considering multiple taxa with unique and complementary ecological roles and help to bridge the gap between research on successions and community assembly.

Introduction

Succession and community assembly research are neighboring fields in ecology, each with a long history of constructive debates and a large body of literature. Both research lines are founded on overlapping concepts considering processes such as dispersal, environmental filtering, biotic interactions, and stochasticity as structuring elements of local communities and ecosystems. Nevertheless, succession and community assembly research focus on different spatial and temporal scales, which may have hindered a mutual exchange of ideas (Chang & HilleRisLambers, 2016). Succession research relates to the initial development of ecosystems and communities over time. Community assembly studies, on the other hand, try to elucidate the drivers of local diversity patterns regardless of temporal components. Attempts to synthesize the two fields led to the development of an integrated conceptual framework of succession and community assembly dynamics. Here, drivers of community structure are considered from an explicitly temporal perspective, assuming a temporal sequence of assembly processes shifting from dispersal to niche-based processes along the course of succession (Chang & HilleRisLambers, 2016). The proposed framework also emphasizes the importance of threshold dynamics, predicting that gradual changes in the abiotic and biotic environment are followed by rapid shifts in the predominant processes that determine community assembly (Suding & Hobbs, 2009; Kadowaki & al., 2018). These shifts are expected to be associated with various community level responses such as changes in diversity, species composition and functionality (Scheffer & al., 2001; Suding & Hobbs, 2009; Chang & HilleRisLambers, 2016). Recent research suggests that sudden ecosystem shifts are not restricted to changes in species composition of single organismal groups but that local diversity patterns emerge from on-site interactions between multiple taxa (Lu & Hedin, 2019; Berdugo & al., 2020). Multidiversity, an aggregate measure of biodiversity that integrates the standardized diversities of multiple taxa (Allan & al., 2014), has been shown to reflect ecosystem functionality (Delgado-Baquerizo & al., 2020), species composition (Felipe-Lucia & al., 2020) and

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multitrophic interactions (Manning & al., 2015) more accurately than diversity measures considering only one taxon. Additionally, the responses of different organismal groups to successional gradients may differ either due to stochastic or deterministic drivers (Kaufmann, 2001; Blaalid & al., 2012; Fenton & Bergeron, 2013; Dini-Andreote & al., 2015; Måren & al., 2018) and thus conclusions about the primary assembly processes may be biased in studies considering a single taxon only (Pulsford & al., 2016). Taken into account that multidiversity more precisely reflects ecosystem responses and functions, we tested predictions deduced from recent contemporary succession hypotheses using a dataset on multidiversity comprising inventories of plants, animals, bacteria and fungi along a successional gradient.

Most studies on multidiversity have been undertaken in well-developed ecosystems that have undergone severe anthropogenic alterations in the past and focused on the drivers of biodiversity decline (Allan & al., 2014; Manning & al., 2015; Felipe-Lucia & al., 2020). The mechanisms behind the successional emergence of multidiversity and ecosystem complexity under natural conditions, however, are yet poorly understood. Thus, considering multidiversity within a successional framework will help to gain new insights into the temporal dynamics of the processes that shape the initial emergence of biodiversity in natural ecosystems that comprise manifold organismal groups with unique and complementary ecological functions. The assumed changes of assembly processes along succession, a decrease in the importance of dispersal and a simultaneous increase of mutual interactions between organisms and the environment, is expected to lead to strong interdependencies between taxa in older successional stages (Odum, 1969; Chang & HilleRisLambers, 2016). For instance, interactions between plants and soil inhabiting microorganisms intensify with successional age (Chen & al., 2019) and regulate plant-animal interactions (Howard & al., 2020). Strong interdependencies between taxa result in aggregated co-occurrence patterns (Ohlmann & al., 2018), which lowers the potential for a high species turnover across local assemblages; and may thus be reflected in low beta-diversity.

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We adopted the concept of multidiversity to empirically test predictions of the integrated framework of succession and community assembly dynamics on an ecological gradient of primary succession following glacial retreat in the Austrian Alps (Junker & al., 2020). We assessed the multidiversity and multi-betadiversity of five organismal groups, including vascular plants, bryophytes, invertebrates, and soil inhabiting fungi and bacteria on 110 plots spanning 170 years of primary succession. We estimated multidiversity by the sum of ranked normalized Shannon-diversities and calculated multi-betadiversity as the mean Bray-Curtis dissimilarities between plots regarding the composition of individual taxa (see methods). According to the conceptual framework (Chang & HilleRisLambers, 2016), we predicted that community assembly will undergo a rapid shift that is induced by a sudden change of the biotic and abiotic environment. Accordingly, we identified a threshold in multidiversity development and estimated the relative importance of dispersal, environmental and biotic drivers on the assembly of the multidiverse community before and after the threshold. We further highlighted the more deterministic character of community assembly after the shift by comparing multi-betadiversity estimates of the early and late successional communities.

Methods

Study Design. The study was conducted in the long-term ecological research platform Ödenwinkel which was established in 2019 in the Hohe Tauern National Park, Austria (Dynamic Ecological Information Management System – site and dataset registry: https://deims.org/activity/fefd07db-2f16-46eb-8883-f10fbc9d13a3, last access: March 2021). A total of n = 135 permanent plots was established within the glacier forefield of the Ödenwinkelkees which was covered by ice at the latest glacial maximum in the Little Ice Age around 1850. For this study, we used a subset of n = 110 plots with complete datasets with all biotic and abiotic variables available. The plots represent a successional gradient spanning over 1.7km in length and were evenly distributed within the glacier forefield at an altitude ranging from 2070 to 2170 m a.s.l. Plots were defined as squares with an area of 1 m² and were all oriented in the same cardinal direction. Further details on

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the design of the research platform, exact plot positions and details on the surrounding environment can be found in Junker et al. (2020).

Sampling. In 2019, we identified all vascular plant and bryophyte species present on the plots and estimated their cover with a resolution of 0.1 %. We sampled above-ground arthropod diversity by installing two pitfall traps on each plot. Traps were set active for a total of n=7 days. The abundance of all arthropods, excluding Collembola and Acari, larger than 3 mm was counted. The abundance of Collembola and Acari and of animals smaller than 3mm was estimated based on random samples of aliquots of the total sample. All arthropods and other animals are identified to the order level. Soil inhabiting bacteria and fungi were sampled from soil cores from an approximate depth of 3cm. Soil-microbiome samples were analyzed by next-generation sequencing and microbiome profiling of isolated DNA was performed by Eurofins Genomics (Ebersberg, Germany). Prior to the statistical analysis of microbial communities, we performed a cumulative sum scaling (CSS) normalization (R package “metagenomeSeq” v1.28.2) on the count data to account for differences in sequencing depth among samples. Detailed information on the sampling strategies of all organismal groups can be found in Junker et al. (2020). Temperature measurements were done by installing temperature loggers (MF1921G iButton, Fuchs Elektronik, Weinheim, Germany) 10 cm north of each plot centre, at a depth of 3 cm below ground. Mean seasonal temperature was calculated on the basis of the recordings ranging from 26th of June to 16th of September representing the period in which the plots were free of permanent snow cover before and after the winter 2019/2020. In 2020, soil samples were taken and soil nutrients (Ca, P, K, Mg and total N_2) as well as soil pH were measured on all plots (except for plot 129) by AGROLAB Agrar und Umwelt GmbH (Sarstedt, Germany). Soil nutrient analysis was performed according to the Ö-Norm Boden: L 1087: 2012-12 (K and P - mg/1000g), L 1093: 2010-12 (Mg - mg/1000g) and L 1083: 2006-04 (pH). Total N2 (%) was determined according to the DIN EN 16168: 2012-11. Detailed information on the sampling strategy can be found in Junker et. al (2020).

Calculation of multidiversity and breaking point analysis. Multidiversity is defined as the cumulative diversity of a number of taxonomic groups (Allan & al., 2014). The multidiversity of the *n* =

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110 plots composed of the diversities of vascular plants, bryophytes, invertebrates, fungi, and bacteria present in each plot and was defined as follows: First, we calculated the Shannon diversities (H) of each of the taxonomic groups in each plot. Second, we ranked the plots by increasing diversity for each of the five taxonomic groups individually, i.e. for each plot we received n = 5 ranks. The mean rank of each plot was defined as multidiversity *mD*. For better interpretability of the index, we then normalized the mean ranks as $x' = ((x - \min(x)) / (\max(x) - \min(x))$ to scale them between zero and one. Ranks were used to give the same weighting to each taxonomic group despite deviations in the absolute values of Shannon diversity and to reduce the impact of outliers in *mD* values. To account for differences in the sampling depth of the microbial raw dataset, we performed multiple rarefactioning prior to the calculation of Shannon diversity by averaging the results of n = 999 iterations (R package "rtk" v0.2.5.7) instead of using the CSS-normalized dataset.

According to the hypothesis of community assembly dynamics (Chang & HilleRisLambers, 2016) and by visual inspection of the relationship between multidiversity and time since deglaciation we expected two different stages of community establishment along the successional gradient. These stages are separatable by the transition from a developing (characterized by an increase in multidiversity) to a more stationary ecosystem (characterized by non-monotonic variation in multidiversity over time). Such non-linear associations are suggestive of regime-shifts of the ecosystem and can be interpreted as ecological thresholds (Groffman & al., 2006). We screened the age gradient for predicted threshold by using breaking point analysis. We iteratively fitted all possible piecewise linear models with *mD* values as the dependent and plot index number as the independent variables and defined the breaking point as the plot number that allowed the fitting of the two piecewise linear models with the lowest mean standard error (Crawley, 2012). The resulting plot index was used to distinguish between early and late successional stages.

Community taxa occurrence. To visualize the distribution of individual taxa and thus the community wide taxonomic turnover along the successional gradient, we estimated the abundance optimum of each taxon that occurred on at least three plots. Abundance optima were estimated by

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calculating the mean plot of occurrence weighted by the abundance of each taxon (i.e. cover for vascular plants and bryophytes, individual count for invertebrates and CSS-normalized read number for microorganisms). We calculated the relative abundance per plot for each taxon by using z-scores of abundances. For each taxon, the mean abundance was set as 0 with one standards deviation as +1 or -1. Resulting z-scores were then rescaled between -1 and 1. Range size was estimated by calculating the variance of occurrence plots (i.e. the span of plots on which a taxon was found along the gradient) weighted by the abundance of the taxon on the respective plots.

Path analysis. We used path-analysis i) to model the influence of the abiotic environment on the diversities of all taxonomic groups individually ii) to estimate the strength of community covariances between the diversities of those groups iii) to infer the effect sizes of the diversity of each group on total *mD* and iv) estimate the strength of indirect effects of the exogenous variables that are mediated through the organismal groups on *mD.* We built separate models with identical structure for the early (n = 49 plots) and late (n = 61 plots) successional stages. The stages were delineated by the threshold identified in the breakpoint analysis. Exogenous variables in the model were time since deglaciation and mean soil temperature of the growing season. Time since deglaciation reflects the plot age and can be seen as a proxy for the increasing chance of heterogenous dispersal events that occur over time. The mean temperature of the growing the growing season is an estimate for environmental heterogeneity and has been shown to directly and indirectly affect diversity on various trophic levels (Ohler & al., 2020). All variables were We first ran a full model that included soil pH and soil nutrient content as additional exogenous variables. None of the two variables showed a significant direct effect on any organismal group or a significant indirect effect on multidiversity during either the young or late successional stage. Accordingly, we stepwise removed the two variables from the model while cross-checking whether the effect strength of one variable became significant in the absence of the other variable. As no significant effects occurred or the model fit significantly decreased, we decided to remove both variables from the final model. Within the model, the strength of residual covariance between the diversities of all taxonomic groups was estimated while accounting for influences the of

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time since deglaciation and temperature. If corrected for an underlying common cause, such as environmental autocorrelation, strong covariances between members of a community can be interpreted as biotic interactions and especially positive community covariances are indicative of facilitative effects within the community (Houlahan & al., 2007; Ranta & al., 2008). All path-models were estimated using the R-package "lavaan" v0.6-7.

Multibetadiversity. We defined Multibetadiversity (*mbD*) as the cumulative averaged pairwise-dissimilarity across a number of organismal groups. First, we split the total community composition data table (sites x species, n = 110 plots) for each organismal group into two tables containing the plots before (n = 49 plots) and after (n = 69 plots) the threshold. Second, we performed Bootstrapping (BS) on the subset tables for each of the n = 5 organismal groups. BS was done for each organismal group on both successional stages separately. Each BS-replicate consisted of the following steps: First, we generated n = 1000 new community tables for each organismal group by randomly sampling n = 49 plots (number of plots in the early successional stage) from the subset tables allowing replacement draws. Second, we calculated the mean Bray-Curtis dissimilarity for each of the resulting community tables. Subsequently, we calculated *mbD* as the mean of the n = 5 dissimilarity values per BS-replicate. BS was necessary to account for differences in sample sizes and to obtain a confidence interval for the resulting beta diversity estimates per successional stage.

Results

We screened the gradient for the predicted shift from a developing (characterized by an increase in multidiversity) to a more stationary ecosystem (characterized by non-monotonic variation in multidiversity over time) using breaking point analysis, which detects changes in the slope of associations. According to Groffman (2006) breaking points represent ecological thresholds, which is characterized by a rapid change of the slope in the association between time since deglaciation as explanatory variable and multidiversity as dependent variable in our study. We identified such a threshold after 63 years of ecosystem development. Resulting piecewise linear models showed a significant increase in multidiversity during the early successional stage and a non-significant

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relationship for the late successional stage (early: t_{57} = 7.01, p < 0.001, r^2=0.51; late: t_{53}=0.24, p=0.80, r^2=0.001; Fig.1a). The threshold became also evident in the change of community composition with different sets of taxa before and after the breaking point. Prior to the threshold, communities mainly consist of species that reach their abundance optima early in succession. These pioneering species were soon accompanied by taxa with no clear preference of early or late successional stages leading to an increase in multidiversity over time. After the threshold, specialists for early successions are replaced by specialists for late successional stages, consequently multidiversity remained stationary over time (Fig. 1b).

Further, the framework predicts that shifts from a developing to a more stationary ecosystem are associated with alterations in the community´s assembly processes (Chang & HilleRisLambers, 2016). Dispersal events are regarded as stochastic or neutral events that occur at a random frequency (Lowe & McPeek, 2014). In a successional setting, this translates to an increased chance of successful colonization events on a plot over the course of time. Accordingly, we expected a strongly dispersal driven assembly before the threshold and a pronounced influence of the environment, as well as increased biotic interactions that can be expressed as community covariances (Houlahan & al., 2007) after the threshold.

To quantify the relative importance of dispersal and environmental drivers, we specified a path model in which time since deglaciation (as a proxy for dispersal as main driver) and mean seasonal soil temperature (as environmental factor that is important for diversity of several trophic levels (Ohler & al., 2020)) act as exogenous variables and directly affect diversities of single organismal groups. The total effects of the dispersal and environmental drivers on multidiversity were estimated as indirect effects mediated through the organismal groups. We also tested the effects of other environmental variables, such as soil nutrient content and soil-pH value but could not detect any significant effects and thus removed these variables from the final model (see methods and Supplementary tables). Biotic interactions were modeled as the residual covariance among the diversity values of all organismal groups. The path analysis provided good model fit (Model fit: $p_{chi\text{-}square} > 0.05$; CFI >0.95; TLI ≥ 0.9; SRMR

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< 0.09; $RMSEA_{early}$ < 0.05; $RMSEA_{late}$ = 0.079 with lower bound of confidence interval = 0) and revealed different influences of the exogenous variables between the early and late successional environments (Figure 2). During early succession, time since deglaciation had a strong positive effect on the diversity of all organismal groups, whereas the effect of temperature was only significant for bacteria. Time since deglaciation also had a significant positive indirect effect on total multidiversity during early succession, whereas temperature did not affect multidiversity (Figure 2a). Furthermore, diversities of the five organismal groups varied independently of each other suggesting little or no mutual influences. In late succession, mean soil temperature had significant positive direct effects on the diversity of vascular plants and bryophytes and a significantly positive indirect effect on multidiversity. Plot age had no longer an effect on multidiversity and we detected positive residual covariances between vascular plant, invertebrate and bacterial diversities with fungal diversity, suggesting mutual influences between taxa (Figure 2b). Our data do not allow to directly test for mutual influences between organismal groups on the taxon level, but we find a strong pattern of positive community covariances after accounting for environmental variation, that is indicative of facilitative processes and biotic dependencies within the community (Houlahan & al., 2007; Ranta & al., 2008). During the initial period of ecosystem formation, communities are built up by organisms that enter a plot by non-directed dispersal. Thus, stochastic mechanisms (i.e. drift, dispersal) dominate the assembly process, which is represented in the path analysis by the linear increase of multidiversity with time. After the threshold, multidiversity became stationary and the stochastic community assembly processes was replaced by more deterministic assembly processes: the strong effect of time since deglaciation disappeared in favor of local, niche-based processes, such as environmental filtering and biotic interactions that are reflected in the pronounced effect of temperature on multidiversity and increased biotic covariances (Chase & Myers, 2011).

One prediction of the shift from dispersal dominated stochastic events in early successional stages to niche-based processes in late successional stages is that beta-diversity among communities will decrease after the threshold. To test this prediction, we calculated a measure of total community

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dissimilarity, multi-betadiversity for both successional stages. We bootstrapped Bray-Curtis similarity matrices for *n* = 1000 times for each of the five taxa individually and calculated multi-beta-diversity as the mean similarity of the five organismal groups per bootstrapping draw for the early and late successional stage. Bootstrapping was necessary to account for different sample sizes in the two successional stages and to obtain confidence intervals for multi-beta-diversity indices. Despite different trajectories of betadiversity for different organismal groups, multi-betadiversity was significantly lower in the late successional stage, indicating more homogenous communities across the plots (Fig. 3).

Discussion

Our results are the first empirical test of the conceptual framework integrating succession and community assembly dynamics proposed by Chang & HilleRisLambers (2016). We showed that threshold dynamics play an important role in the assembly of multidiverse communities under natural conditions and that these thresholds are associated with substantial changes in the community assembly processes. So far, the importance of threshold dynamics have been recognized for anthropogenically altered ecosystems either as catastrophic shifts with respect to climate change (Scheffer & al., 2001; Berdugo & al., 2020) or for restoration efforts of anthropogenically altered landscapes (Suding & Hobbs, 2009; Kadowaki & al., 2018). Acknowledging the effects of threshold dynamics during the development of natural multidiverse ecosystems, and their universality in ecological systems provides valuable insights into the patterns and processes of initial terrestrial-ecosystem development. Although different organismal groups follow individual assembly trajectories during primary succession, multidiversity is mainly promoted by stochastic drivers during the initial phase of ecosystem development, most assumably by heterogenous dispersal events. Over the course of succession, stochasticity is replaced by environmental filtering and biotic interactions as the structuring mechanism of multidiversity. Understanding the relative importance and temporal dynamic of deterministic and stochastic processes is a key challenge in community ecology, especially in natural systems and has been in the center of broad debates among ecologists. Thus, our study is a

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strong contribution to the long-required synthesis of community ecological theories into succession research, acknowledging the fundamental importance of abrupt state shifts in natural ecosystems. These results are not only a proof of concept but also stress that succession is a multi-faceted rather than a linear process that comprises a sequence of assembly processes towards multidiversity and ecosystem complexity.

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Figures

Figure 1: Multidiversity and multi-taxa-community composition along the successional gradient. A) Multidiversity increases during the early successional stage and remains stationary as succession continues. The vertical dashed line indicates the estimated threshold in multidiversity development, which is the threshold in community assembly as predicted by the framework of Chang & HilleRisLambers (2016). Grey regression lines indicate the correlation between multidiversity and time since deglaciation in the successional stages before and after the threshold (early: t_{57} = 7.01, p < 0.001, r^2=0.51; late: t_{53}=0.24, p=0.80, r^2=0.001); grey dashed horizontal line marks the breaking point. B) Single taxa occurrence along the successional gradient for each taxon that occurs on at least three plots along the gradient. Tiles indicate the relative abundance of each taxon at a given plot relative to the mean abundance of the taxon along the gradient. Relative taxon abundance is color-coded and reflects z-scores with the mean abundance as 0 and one standard deviation as +1 or -1, rescaled between -1 and 1. Multidiversity is indicated as red density plot on top of the community composition plot. Grey density plot on the left side indicates the range size of the taxa, i.e whether their occurrence is restricted to a narrow range of the successional gradient or whether taxa occur along the whole gradient. Black bars on the right represent the organismal group of the taxa in each row, symbols of organismal groups are ordered by decreasing frequency; white dashed horizontal line marks the threshold.

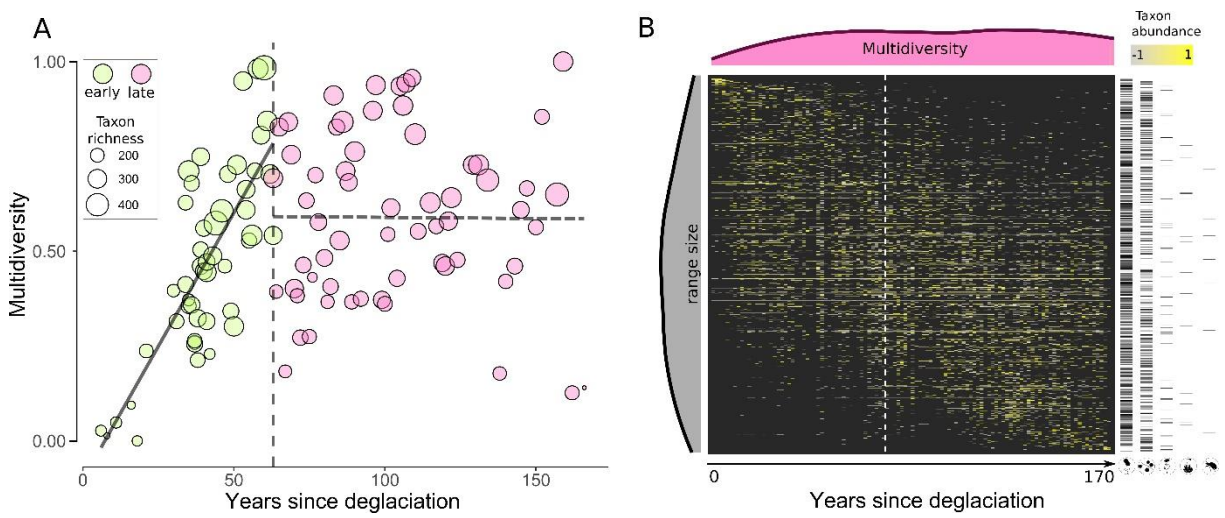

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Figure 2: Path analysis regarding the effects of stochastic and deterministic drivers on the multidiverse community for the early and late successional stages. Time since deglaciation and mean seasonal temperature act as exogenous variables with directed effects on the diversities of vascular plants, bryophyte diversity, invertebrates, and soil inhabiting fungi and bacteria. Indirect effects of exogenous variables on multidiversity were calculated by mediation analysis through the direct effects of the organismal groups on multidiversity. Biotic interactions are modeled as covariances between organismal groups. Numbers represent standardized path coefficients and are given for significant paths only.

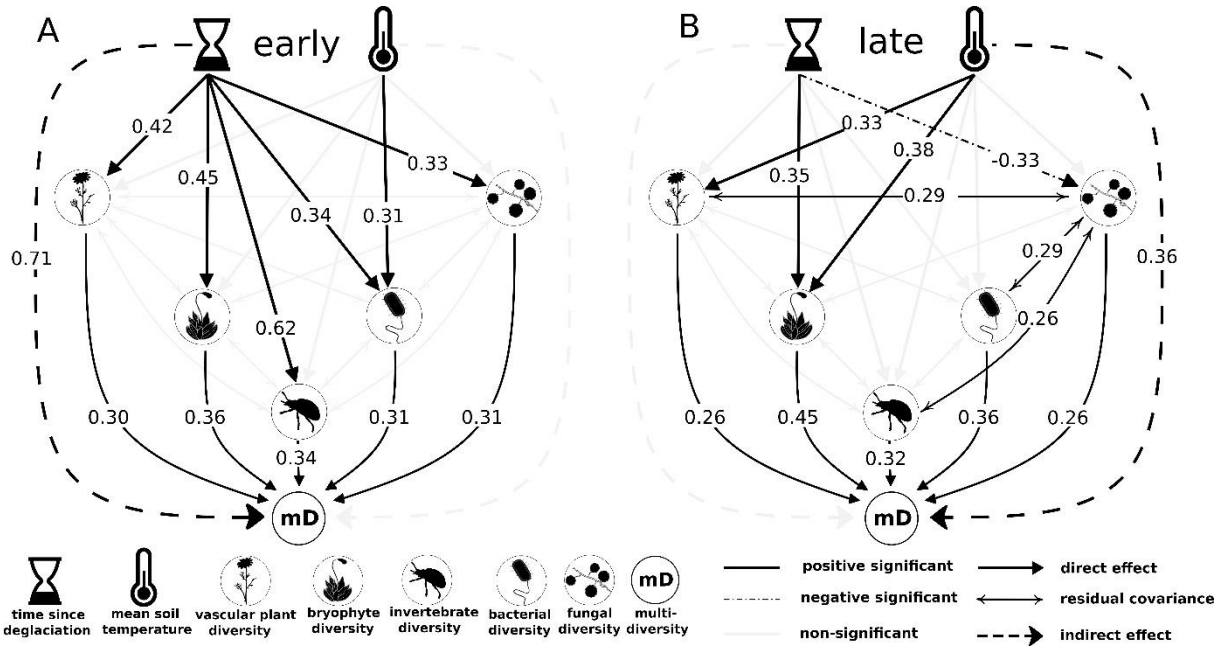

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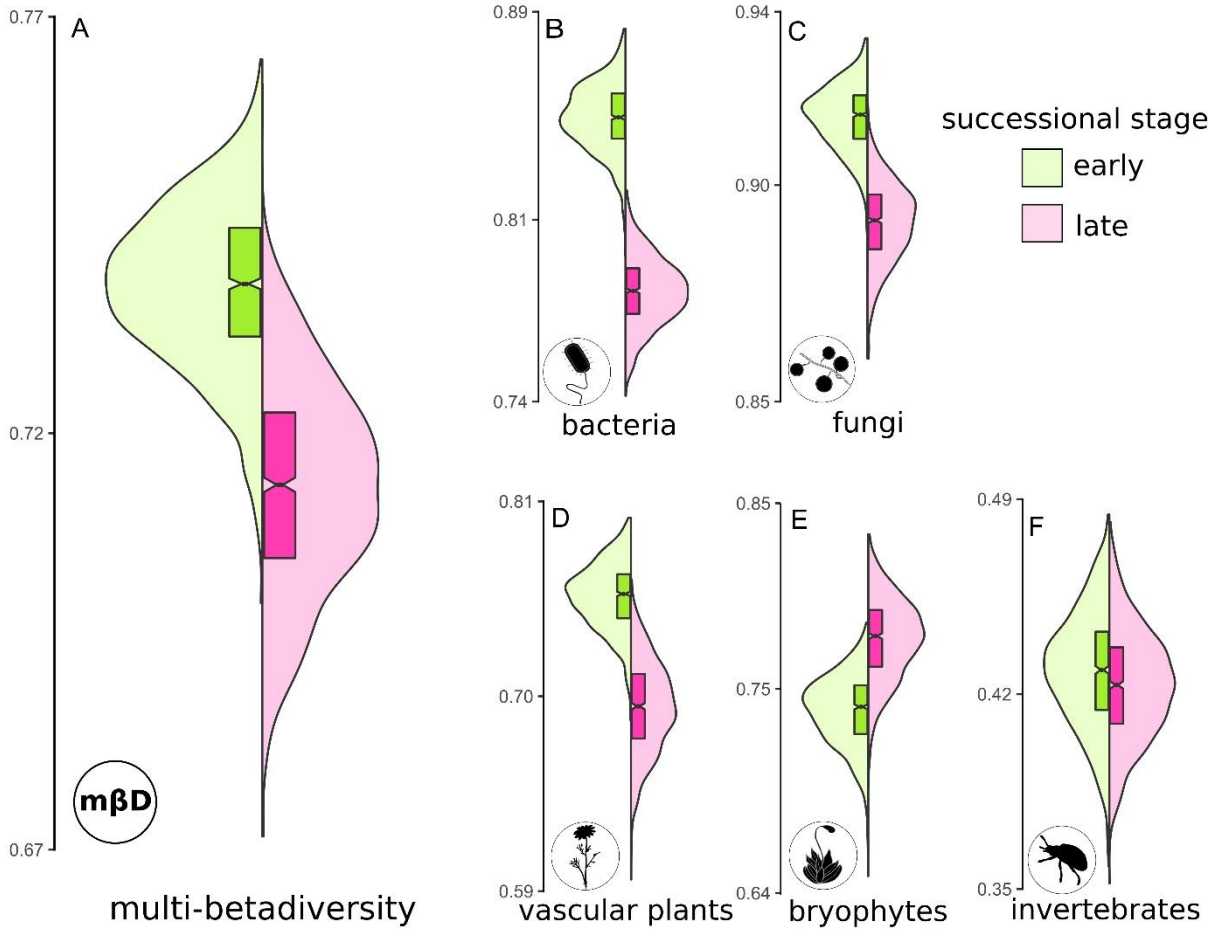
Figure 3: Betadiversity values for each organismal group and community-wide multi-betadiversity values for the early and late successional stages. Mean Bray-Curtis dissimilarities were used to calculate betadiversity and multi-betadiversity values. Green violin plots resemble the dissimilarity values of the early successional stage (n=49 plots), rose violin plots indicate the late successional stage (n=61 plots). Density plots indicate the distribution of the mean dissimilarities for n=1000 bootstrap draws. Boxplots indicate the upper and lower quartile of the estimates and the size of the notch represents the confidence interval of the median. A) mean of all organismal groups, i.e. multi-betadiversity B) bacteria C) fungi D) vascular plants E) bryopyhtes F) invertebrates



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Contributions

R.R.J. conceived and initiated the study. M.H., X.H., V.R.H. and R.R.J conducted field work. M.H. performed the processing and analysis of the data with main inputs from R.R.J. and X.H.. M.H. and R.R.J. drafted the initial version of the manuscript. All authors contributed critically to the interpretation of the results, revising, and approving the final version of the manuscript.

Competing interests

The authors declare no competing interests.

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Supplementary

Supplementary table 1: Summary of the path analysis of the effects of time since deglaciation and temperature on organismal groups and multidiversity (final model).

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	Early			**Late**			**Full**		
	z	p	Estimate	z	p	Estimate	z	p	Estimate
					Regression Slopes				
Vasc. plants									
Temperature	0.57	.568	0.16	2.51	.012	0.23	4.19	.000	0.38
Time s. degl.	2.89	.004	1.37	-0.39	.698	-0.05	3.48	.000	0.29
Bryophytes									
Temperature	0.28	.776	0.06	2.93	.003	0.43	2.32	.020	0.24
Time s. degl.	3.09	.002	1.17	2.69	.007	0.54	1.70	.090	0.16
Bacteria									
Temperature	2.32	.020	0.60	0.79	.431	0.11	2.43	.015	0.26
Time s. degl.	2.57	.010	1.11	-0.02	.985	-0.00	0.92	.355	0.09
Invertebrates									
Temperature	-0.84	.404	-0.19	1.41	.159	0.20	2.09	.036	0.22
Time s. degl.	4.60	.000	1.78	0.77	.441	0.15	2.61	.009	0.25
Fungi									
Temperature	-0.29	.770	-0.08	-0.09	.931	-0.01	1.38	.167	0.15
Time s. degl.	2.14	.033	0.92	-2.46	.014	-0.50	-1.45	.147	-0.14
Multidiversity									
Bacteria	7.08	.000	0.30	7.01	.000	0.35	9.78	.000	0.32
Bryophytes	7.76	.000	0.43	9.06	.000	0.38	12.31	.000	0.41
Vasc. plants	7.17	.000	0.28	4.96	.000	0.37	8.96	.000	0.32
Invertebrates	8.32	.000	0.37	6.41	.000	0.30	9.93	.000	0.33
Fungi	7.35	.000	0.35	4.76	.000	0.22	8.41	.000	0.28
					Residual Variances				
Vasc. plants	4.95	.000	0.91	5.52	.000	0.37	7.42	.000	0.68
Bryophytes	4.95	.000	0.58	5.52	.000	0.98	7.42	.000	0.90
Bacteria	4.95	.000	0.76	5.52	.000	0.86	7.42	.000	0.93
Invertebrates	4.95	.000	0.61	5.52	.000	0.94	7.42	.000	0.88
Fungi	4.95	.000	0.75	5.52	.000	1.00	7.42	.000	0.96
Multidiversity	4.95	.000	0.08	5.52	.000	0.12	7.42	.000	0.11
Temperature	4.95	.000	0.31	5.52	.000	0.93	7.42	.000	0.77
Time s. degl.	4.95	.000	0.11	5.52	.000	0.49	7.42	.000	0.90
					Residual Covariances				
Bacteria w/Fungi	-0.90	.371	-0.10	2.19	.029	0.27	1.78	.076	0.16

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Bryophytes w/Fungi	1.10	.273	0.11	0.63	.531	0.08	1.07	.284	0.10
Vasc. plants w/Fungi	0.44	.659	0.05	2.14	.032	0.17	2.42	.016	0.19
Invertebrates w/Fungi	-1.82	.068	-0.18	1.95	.052	0.25	1.39	.164	0.12
Bryophytes w/Bacteria	1.45	.146	0.14	0.04	.968	0.00	1.32	.188	0.12
Vasc. plants w/Bacteria	-0.87	.384	-0.10	0.81	.417	0.06	0.57	.566	0.04
Bacteria w/Invertebrates	-1.17	.243	-0.11	0.86	.391	0.10	0.82	.412	0.07
Vasc. plants w/Bryophytes	-0.06	.953	-0.01	1.20	.228	0.09	0.76	.448	0.06
Bryophytes w/Invertebrates	-0.39	.694	-0.03	0.04	.968	0.00	0.53	.597	0.05
Vasc. plants w/Invertebrates	-1.07	.284	-0.12	0.77	.441	0.06	0.65	.515	0.05
Temperature w/Time s. degl.	3.15	.002	0.09	-3.15	.002	-0.30	1.62	.105	0.13
					Constructed				
Time indirect	7.08	.000	2.20	0.75	.454	0.12	2.71	.007	0.23
Temp. indirect	0.87	.385	0.16	2.86	.004	0.34	4.51	.000	0.41
					Fit Indices				
RMSEA	0.00			0.08			0.08		
RMSEA.CI.LOWER	0.00			0.00			0.00		
RMSEA.CI.UPPER	0.22			0.28			0.22		
CFI	1.00			0.99			1.00		
TLI	1.08			0.92			0.94		
χ^2	0.87(2)	.646		2.84(2)	.242		3.37(2)	.186	
DF	2.00			2.00			2.00		
RMR	0.00			0.01			0.01		

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Supplementary table 2: Summary of the path analysis of the effects of time since deglaciation, temperature, pH-value and soil nutrients on organismal groups and multidiversity (model not used).

	Early			**Late**			**Full**		
	z	p	Estimate	z	p	Estimate	z	p	Estimate
				Regression Slopes					
Vasc. plants									
Temperature	0.79	.430	0.19	1.69	.092	0.13	4.20	.000	0.39
Time s. degl.	2.64	.008	1.37	0.32	.752	0.04	2.43	.015	0.24
Soil nutrients	2.41	.016	0.42	-1.53	.126	-0.13	0.90	.369	0.08
pH-value	1.25	.211	0.20	-1.19	.232	-0.12	-0.55	.580	-0.05
Bryophytes									
Temperature	0.26	.794	0.05	3.36	.001	0.44	2.31	.021	0.24
Time s. degl.	2.54	.011	1.13	2.15	.032	0.49	0.81	.419	0.09
Soil nutrients	0.03	.978	0.00	0.70	.482	0.09	1.01	.310	0.11
pH-value	-0.21	.833	-0.03	-0.48	.632	-0.08	-0.75	.452	-0.07
Bacteria									
Temperature	2.66	.008	0.63	0.70	.484	0.08	1.96	.051	0.21
Time s. degl.	2.45	.014	1.24	-0.22	.823	-0.05	-0.08	.936	-0.01
Soil nutrients	-0.55	.583	-0.09	0.76	.447	0.09	1.06	.288	0.11
pH-value	0.33	.741	0.05	-1.17	.242	-0.18	-1.84	.066	-0.18
Invertebrates									
Temperature	-0.64	.522	-0.13	1.27	.204	0.16	1.08	.279	0.11
Time s. degl.	4.77	.000	2.10	0.68	.497	0.15	2.18	.029	0.24
Soil nutrients	-1.73	.084	-0.26	0.16	.873	0.02	-0.57	.572	-0.06
pH-value	0.82	.412	0.11	-0.86	.388	-0.14	-1.72	.085	-0.17
Fungi									
Temperature	-0.31	.758	-0.07	0.87	.387	0.11	1.34	.182	0.14
Time s. degl.	1.80	.071	0.91	-3.33	.001	-0.73	-2.69	.007	-0.30
Soil nutrients	0.43	.665	0.07	2.82	.005	0.36	2.16	.030	0.23
pH-value	0.18	.857	0.03	-0.44	.660	-0.07	-1.80	.072	-0.18
Multidiversity									
Bacteria	7.04	.000	0.30	7.01	.000	0.35	9.72	.000	0.32
Bryophytes	7.78	.000	0.43	9.61	.000	0.38	12.32	.000	0.41
Vasc. plants	7.15	.000	0.28	4.87	.000	0.37	9.07	.000	0.32
Invertebrates	8.33	.000	0.37	6.42	.000	0.30	9.89	.000	0.33

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Fungi	7.34	.000	0.35	4.78	.000	0.22	8.42	.000	0.28
				Residual Variances					
Vasc. plants	4.95	.000	0.80	5.52	.000	0.36	7.42	.000	0.68
Bryophytes	4.95	.000	0.58	5.52	.000	0.97	7.42	.000	0.89
Bacteria	4.95	.000	0.75	5.52	.000	0.83	7.42	.000	0.89
Invertebrates	4.95	.000	0.57	5.52	.000	0.93	7.42	.000	0.87
Fungi	4.95	.000	0.75	5.52	.000	0.88	7.42	.000	0.90
Multidiversity	4.95	.000	0.08	5.52	.000	0.12	7.42	.000	0.11
Temperature	4.95	.000	0.31	5.52	.000	0.93	7.42	.000	0.77
Time s. degl.	5.12	.000	0.09	5.63	.000	0.47	7.53	.000	0.90
Soil nutrients	4.95	.000	0.56	5.52	.000	1.26	7.42	.000	0.99
pH-value	4.95	.000	0.88	5.52	.000	0.61	7.42	.000	0.85
				Residual Covariances					
Bacteria w/Fungi	-0.88	.381	-0.09	1.95	.052	0.22	1.37	.172	0.12
Bryophytes w/Fungi	1.10	.270	0.11	0.35	.724	0.04	0.78	.436	0.07
Vasc. plants w/Fungi	0.30	.765	0.03	2.56	.011	0.19	2.25	.025	0.17
Invertebrates w/Fungi	-1.81	.071	-0.17	1.89	.059	0.23	1.31	.190	0.11
Bryophytes w/Bacteria	1.47	.142	0.14	-0.13	.894	-0.02	1.12	.262	0.10
Vasc. plants w/Bacteria	-0.81	.420	-0.09	0.85	.394	0.06	0.40	.690	0.03
Bacteria w/Invertebrates	-1.36	.175	-0.13	0.72	.473	0.08	0.67	.502	0.06
Vasc. plants w/Bryophytes	-0.04	.970	-0.00	1.28	.200	0.10	0.64	.522	0.05
Bryophytes w/Invertebrates	-0.38	.703	-0.03	-0.05	.961	-0.01	0.48	.632	0.04
Vasc. plants w/Invertebrates	-0.75	.454	-0.07	0.75	.453	0.06	0.62	.535	0.05
Time s. degl. w/Soil nutrients	1.71	.088	0.05	3.79	.000	0.41	4.70	.000	0.46
Time s. degl. w/pH-value	-3.23	.001	-0.14	2.26	.024	0.14	-1.59	.112	-0.11
Temperature w/Time s. degl.	2.21	.027	0.05	-0.55	.582	-0.04	2.41	.016	0.17
				Constructed					
Time indirect	6.47	.000	2.34	0.39	.698	0.07	1.09	.277	0.10
Temp. indirect	1.18	.240	0.19	3.08	.002	0.32	4.05	.000	0.36
pH indirect	1.05	.296	0.11	-1.50	.134	-0.20	-2.49	.013	-0.21
Soil nutr. ind.	0.21	.836	0.02	1.03	.302	0.11	1.68	.093	0.15
				Fit Indices					
RMSEA	0.21			0.31			0.25		
RMSEA.CI.LOWER	0.11			0.23			0.20		

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RMSEA.CI.UPPER	0.31		0.39		0.32	
CFI	0.93		0.81		0.87	
TLI	0.57		-0.24		0.17	
$\chi 2$	21.92(7)	.003	47.19(7)	.000	56.65(7)	.000
DF	7.00		7.00		7.00	
RMR	0.07		0.12		0.08	

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Supplementary table 3: Summary of the path analysis of the effects of time since deglaciation, temperature and pH-value on organismal groups and multidiversity (model not used).

	Early			**Late**			**Full**		
	z	p	Estimate	z	p	Estimate	z	p	Estimate
				Regression Slopes					
Vasc. plants									
Temperature	**0.83**	**.409**	**0.24**	**2.11**	**.035**	**0.21**	**3.34**	**.001**	**0.35**
Time s. degl.	3.14	.002	1.67	-0.34	.732	-0.04	3.19	.001	0.28
pH-value	1.18	.237	0.22	-0.54	.592	-0.06	-0.65	.516	-0.07
Bryophytes									
Temperature	0.23	.814	0.05	2.44	.015	0.39	1.62	.105	0.19
Time s. degl.	2.62	.009	1.13	2.75	.006	0.56	1.42	.156	0.14
pH-value	-0.19	.848	-0.03	-0.71	.479	-0.13	-0.84	.401	-0.10
Bacteria									
Temperature	2.33	.020	0.62	0.21	.832	0.03	1.29	.197	0.15
Time s. degl.	2.39	.017	1.18	0.10	.923	0.02	0.44	.660	0.04
pH-value	0.28	.781	0.05	-1.37	.170	-0.23	-1.76	.079	-0.21
Invertebrates									
Temperature	-0.67	.502	-0.16	0.98	.329	0.15	1.19	.233	0.14
Time s. degl.	4.37	.000	1.92	0.85	.397	0.17	2.18	.029	0.21
pH-value	0.66	.509	0.10	-0.87	.387	-0.15	-1.33	.184	-0.15
Fungi									
Temperature	-0.24	.807	-0.06	-0.62	.537	-0.10	0.28	.776	0.03
Time s. degl.	1.96	.050	0.96	-2.38	.017	-0.48	-1.93	.053	-0.20
pH-value	0.18	.855	0.03	-1.40	.162	-0.25	-1.93	.054	-0.23
Multidiversity									
Bacteria	7.08	.000	0.30	7.01	.000	0.35	9.78	.000	0.32
Bryophytes	7.76	.000	0.43	9.06	.000	0.38	12.31	.000	0.41
Vasc. plants	7.17	.000	0.28	4.96	.000	0.37	8.96	.000	0.32
Invertebrates	8.32	.000	0.37	6.41	.000	0.30	9.93	.000	0.33
Fungi	7.35	.000	0.35	4.76	.000	0.22	8.41	.000	0.28
				Residual Variances					
Vasc. plants	4.95	.000	0.89	5.52	.000	0.37	7.42	.000	0.68
Bryophytes	4.95	.000	0.58	5.52	.000	0.98	7.42	.000	0.90

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Bacteria	4.95	.000	0.76	5.52	.000	0.83	7.42	.000	0.90
Invertebrates	4.95	.000	0.60	5.52	.000	0.93	7.42	.000	0.87
Fungi	4.95	.000	0.75	5.52	.000	0.96	7.42	.000	0.93
Multidiversity	4.95	.000	0.08	5.52	.000	0.12	7.42	.000	0.11
Temperature	4.95	.000	0.31	5.52	.000	0.93	7.42	.000	0.77
Time s. degl.	4.95	.000	0.11	5.52	.000	0.49	7.42	.000	0.90
pH-value	4.95	.000	0.88	5.52	.000	0.61	7.42	.000	0.85
				Residual Covariances					
Bacteria w/Fungi	-0.90	.366	-0.10	2.03	.042	0.24	1.52	.129	0.13
Bryophytes w/Fungi	1.10	.270	0.11	0.51	.608	0.06	0.94	.347	0.08
Vasc. plants w/Fungi	0.42	.677	0.05	2.09	.037	0.17	2.35	.019	0.18
Invertebrates w/Fungi	-1.85	.065	-0.18	1.84	.065	0.23	1.19	.235	0.10
Bryophytes w/Bacteria	1.46	.143	0.14	-0.08	.934	-0.01	1.20	.230	0.10
Vasc. plants w/Bacteria	-0.93	.353	-0.11	0.73	.464	0.05	0.47	.635	0.04
Bacteria w/Invertebrates	-1.20	.231	-0.12	0.73	.467	0.08	0.62	.537	0.05
Vasc. plants w/Bryophytes	-0.03	.979	-0.00	1.17	.244	0.09	0.71	.477	0.05
Bryophytes w/Invertebrates	-0.38	.706	-0.03	-0.04	.969	-0.00	0.43	.668	0.04
Vasc. plants w/Invertebrates	-1.20	.231	-0.13	0.72	.473	0.05	0.58	.565	0.04
Temperature w/Time s. degl.	3.15	.002	0.09	-3.15	.002	-0.30	1.62	.105	0.13
Temperature w/pH-value	-2.90	.004	-0.24	-3.20	.001	-0.34	-4.75	.000	-0.41
Time s. degl. w/pH-value	-3.59	.000	-0.19	2.01	.045	0.15	-3.05	.002	-0.27
				Constructed					
Time indirect	6.74	.000	2.36	0.91	.361	0.15	2.05	.041	0.18
Temp. indirect	1.07	.286	0.19	2.05	.040	0.26	2.88	.004	0.29
pH indirect	0.97	.335	0.11	-1.78	.075	-0.25	-2.42	.016	-0.24
				Fit Indices					
RMSEA	0.12			0.04			0.08		
RMSEA.CI.LOWER	0.00			0.00			0.00		
RMSEA.CI.UPPER	0.29			0.22			0.20		
CFI	0.99			1.00			0.99		
TLI	0.88			0.98			0.92		

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$\chi 2$	5.07(3)	.167	3.31(3)	.347	5.13(3)	.163
DF	3.00		3.00		3.00	
RMR	0.01		0.01		0.01	

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Supplementary table 4: Summary of the path analysis of the effects of time since deglaciation, temperature and soil nutrients on organismal groups and multidiversity (model not used).

	Early			**Late**			**Full**		
	z	p	Estimate	z	p	Estimate	z	p	Estimate
				Regression Slopes					
Vasc. plants									
Temperature	0.45	.651	0.12	1.99	.047	0.19	4.28	.000	0.41
Time s. degl.	2.35	.019	1.09	0.05	.957	0.01	2.50	.012	0.24
Soil nutrients	2.37	.018	0.43	-0.97	.331	-0.09	0.96	.335	0.09
Bryophytes									
Temperature	0.28	.778	0.06	3.04	.002	0.48	2.58	.010	0.29
Time s. degl.	2.99	.003	1.17	2.11	.035	0.47	0.89	.373	0.10
Soil nutrients	0.02	.985	0.00	0.83	.405	0.12	1.11	.266	0.12
Bacteria									
Temperature	2.36	.018	0.61	1.16	.246	0.17	2.76	.006	0.31
Time s. degl.	2.62	.009	1.17	-0.50	.620	-0.10	0.11	.913	0.01
Soil nutrients	-0.52	.602	-0.09	1.14	.255	0.15	1.34	.180	0.15
Invertebrates									
Temperature	-0.75	.452	-0.17	1.49	.137	0.23	1.88	.060	0.21
Time s. degl.	4.99	.000	1.94	0.50	.614	0.11	2.35	.019	0.26
Soil nutrients	-1.64	.100	-0.25	0.47	.639	0.07	-0.23	.817	-0.02
Fungi									
Temperature	-0.32	.750	-0.08	0.94	.346	0.14	2.16	.031	0.24
Time s. degl.	1.96	.050	0.87	-3.55	.000	-0.75	-2.50	.012	-0.28
Soil nutrients	0.43	.667	0.08	2.79	.005	0.39	2.39	.017	0.26
Multidiversity									
Bacteria	7.08	.000	0.30	7.01	.000	0.35	9.78	.000	0.32
Bryophytes	7.76	.000	0.43	9.06	.000	0.38	12.31	.000	0.41
Vasc. plants	7.17	.000	0.28	4.96	.000	0.37	8.96	.000	0.32
Invertebrates	8.32	.000	0.37	6.41	.000	0.30	9.93	.000	0.33
Fungi	7.35	.000	0.35	4.76	.000	0.22	8.41	.000	0.28
				Residual Variances					
Vasc. plants	4.95	.000	0.82	5.52	.000	0.37	7.42	.000	0.68
Bryophytes	4.95	.000	0.58	5.52	.000	0.97	7.42	.000	0.89
Bacteria	4.95	.000	0.75	5.52	.000	0.84	7.42	.000	0.91
Invertebrates	4.95	.000	0.58	5.52	.000	0.94	7.42	.000	0.88

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Fungi	4.95	.000	0.75	5.52	.000	0.88	7.42	.000	0.91
Multidiversity	4.95	.000	0.08	5.52	.000	0.12	7.42	.000	0.11
Temperature	4.95	.000	0.31	5.52	.000	0.93	7.42	.000	0.77
Time s. degl.	4.95	.000	0.11	5.52	.000	0.49	7.42	.000	0.90
Soil nutrients	4.95	.000	0.56	5.52	.000	1.26	7.42	.000	0.99
				Residual Covariances					
Bacteria w/Fungi	-0.87	.385	-0.09	1.97	.049	0.22	1.54	.123	0.14
Bryophytes w/Fungi	1.10	.272	0.11	0.37	.710	0.04	0.86	.392	0.07
Vasc. plants w/Fungi	0.32	.748	0.04	2.58	.010	0.20	2.28	.023	0.18
Invertebrates w/Fungi	-1.78	.075	-0.17	1.91	.056	0.23	1.48	.140	0.13
Bryophytes w/Bacteria	1.46	.144	0.14	-0.08	.936	-0.01	1.20	.232	0.10
Vasc. plants w/Bacteria	-0.75	.455	-0.08	0.97	.334	0.07	0.46	.647	0.03
Bacteria w/Invertebrates	-1.32	.188	-0.13	0.80	.423	0.09	0.86	.391	0.07
Vasc. plants w/Bryophytes	-0.07	.946	-0.01	1.32	.187	0.10	0.66	.506	0.05
Bryophytes w/Invertebrates	-0.40	.690	-0.03	-0.01	.992	-0.00	0.56	.578	0.05
Vasc. plants w/Invertebrates	-0.62	.538	-0.06	0.84	.404	0.06	0.67	.500	0.05
Temperature w/Time s. degl.	3.15	.002	0.09	-3.15	.002	-0.30	1.62	.105	0.13
Temperature w/Soil nutrients	1.47	.142	0.09	-3.60	.000	-0.56	-2.39	.017	-0.20
Time s. degl. w/Soil nutrients	2.15	.031	0.08	3.77	.000	0.43	4.36	.000	0.43
				Constructed					
Time indirect	6.80	.000	2.18	0.06	.949	0.01	1.33	.184	0.13
Temp. indirect	0.85	.394	0.15	3.27	.001	0.41	4.99	.000	0.48
Soil nutr. ind.	0.24	.810	0.03	1.50	.134	0.17	2.03	.042	0.19
				Fit Indices					
RMSEA	0.06			0.16			0.08		
RMSEA.CI.LOWER	0.00			0.00			0.00		
RMSEA.CI.UPPER	0.26			0.30			0.19		
CFI	1.00			0.97			0.99		
TLI	0.96			0.67			0.93		
$\chi 2$	3.62(3)	.305		7.43(3)	.059		5.01(3)	.171	

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DF	3.00	3.00	3.00
RMR	0.01	0.01	0.01

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