

# Biodiversity–ecosystem function relationships change through primary succession

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Ecologists traditionally use environmental parameters to predict successional shifts in compositional characteristics of local species assemblages (environmental control). Another important focus in ecology is to understand functional roles of species assemblages in determining local environmental properties (diversity control). Then, the question emerges: which is the cause, and which is the consequence? To clarify the causal relationships between species assemblages and environmental properties, we focused on seral changes in species/functional diversity of vascular plants in tundra ecosystems of the High Arctic. We found that, although species richness was influenced by soil properties in the earlier stages of primary succession, the causalities were reversed in the later stages. We also found functional differentiation among coexisting species in the later stage, suggesting that the ‘complementarity effect’ of diversity on ecosystem functions likely increased with ecosystem development through time. By contrast, particular species had little disproportional influence on soil properties, suggesting that the ‘selection effect’ as an alternative mechanism was less important. This result was likely attributed to the importance of facilitation in the marginal High Arctic environment. Plant–microsite associations are shaped by feedback mechanisms and therefore, neither plant nor microsite is a single absolute predictor of the other. Although our observational study has limitations, we demonstrate a possibility that the relative magnitude of the influence of one on the other can change in the process of succession, emphasizing that the causalities underlying biodiversity–ecosystem function relationships change through succession.

Succession, the sequential appearance and/or replacement of species following disturbance, new land formation or deglaciation, has been a central theme throughout the history of ecology. There is now a rich body of information on the drivers of succession, which may help predict possible changes in the ecosystem state in response to environmental parameters (Prach and Walker 2011, Meiners et al. 2015). Another important focus in ecology includes possible effects of species assemblages on their environment (Naeem et al. 2009). This has led to a wealth of studies on biodiversity–ecosystem functioning, which now have a focus on a wide range of ecosystem functions (e.g. biomass production, carbon sequestration, litter decomposition, nutrient cycling, invasion resistance and so on; Cardinale et al. 2012, Tilman et al. 2014). Then, an important question emerges: which is the cause and which is the consequence? Clarifying the causality underlying relationships between species assemblages and environmental/ecological properties is not straightforward (Grace et al. 2016). This is because of synergetic influences and inherent feedbacks between species and the environment (Wookey et al. 2009, van der Putten et al. 2013). However, with the increasing threats to biodiversity,

a better understanding of causes and consequences of species loss and changes in diversity is now a high research priority (Díaz et al. 2013).

Interest is increasing in species and community effects on ecosystem functions because of the potential to inform ecological applications (Mace et al. 2012). For example, the order of species for introduction into degraded habitats can be selected according to the functional roles (effect traits) of species (Laughlin 2014). Another example is that, based on the changes and losses of species and traits, inferences can be obtained on possible consequences to ecosystem services they provide (Oliver et al. 2015). However, although these approaches have a common focus on functional roles of different species, the conceptual divide between them is significant. Whereas the former has a temporal perspective and recognizes that the significance of species changes through time (i.e. causes), the latter approach focuses on the roles of species assemblages (i.e. consequences) without having a clear perspective on how they are organized. Because species–environment (or environment–species) relationships are variable in direction, magnitude, and structure through time, their mutual causalities must be assessed carefully. In

this regard, vegetation succession provides a great opportunity because causalities in both directions drive the process (van der Putten et al. 2013). In early stages of succession, early colonizers are strongly filtered and restricted by the environment; however, the environment is subsequently and increasingly being modified by biota living above- and belowground during the processes of ecosystem development (Chapin et al. 1994, Mori et al. 2008).

To infer the cause and consequence relationships between biota and environment, we focused on diversity of vascular plants as a candidate explanatory (effect) and/or response variable in a vegetation system. Our primary objectives are 1) to evaluate the degree to which environmental conditions were a primary determinant of species diversity or vice versa at different developmental stages of succession, and then 2) to deduce when and how the direction of the causality changed with time. To assess the above issues, we focused on primary succession on a well-vegetated glacier foreland in the High Arctic, which is above 80°N latitude and is likely one of the northernmost ecosystems on Earth to have such relatively lush vascular vegetation (Mori et al. 2008).

Primary succession in the Arctic is the focus of this research for three reasons. First, physical conditions are harsh (Bliss 1999); therefore, the roles of environment on the emergence and survival of plants can be evaluated (Bliss and Petersen 1992, Matthews 1992, Jones and Henry 2003). Second, under less productive environments, the expectation is that communities are organized deterministically by the virtue of niche partitioning among species (Chase 2010, Mori et al. 2013b); there is thus a possible high species complementarity – an important process underlying the diversity effects (Tilman et al. 2001). Third, the complementarity effect is expected to become more prominent in harsh environments, e.g. because of the importance of facilitation (Callaway et al. 2002, Callaway 2013), although this possibility is tentative and therefore requires further assessment (Wang et al. 2013). To assess these possibilities, we specifically focused on functional characteristics of species in addition to their taxonomic identity; we analysed functional trait diversity because of the inferences obtained for both the mechanisms underlying community organization and the impacts of communities (Cadotte et al. 2013, Mori et al. 2013a). We hypothesized that species in a local community are functionally divergent (functional differentiation) when niche complementarity is realized (Ratcliffe et al. 2016). We are particularly interested in possible changes in functional diversity of local communities at each seral stage through succession; this will help us to infer when local species assemblages start to partition niche interspecifically and thus have a possible complementarity structure. Based on above, we aimed to unify succession and biodiversity research and then explored some of the implications from combining these research efforts.

## Material and methods

### Site description

The study site (80°52'N, 82°50'W) is in the proglacial area at the southern front of Arklio Glacier in the Krieger Mountains

near Oobloyah Bay, Ellesmere Island, Nunavut, Canada (Fig. 1a). According to climate data from the nearest weather station at Eureka (80°00'N, 85°56'W), the study region is characterized by a polar climate with low temperature and precipitation (Okitsu et al. 2004): mean temperatures of the warmest (July) and the coldest (February) months are 3.1°C and –38.4°C, respectively. Mean annual temperature and mean annual precipitation are –18.4°C and 74.2 mm, respectively (from 2011–2015).

The geography has been shaped by periglacial processes, resulting from a long development time (Barsch 1981). The Arklio Glacier has glacial moraines that developed over different periods since the Last Glacial Period (King 1981). According to geomorphological observations and relative dating measurements of weathering rind thickness in angular rock fragments (Hasegawa 2003), combined with related preceding studies (Barsch 1981, King 1981), the developmental periods of these moraines have been estimated. Specifically, King (1981) obtained a total of 25 radiocarbon dates for this proglacial area that ranged from  $44\,000 \pm 2500$  to  $730 \pm 60$  years, and included the present. These results suggest ice-free conditions of this glacier foreland during the Last Glacial; thereby, the indication is that the vegetation developed over an exceptionally long time, approximately 25 000–35 000 years (Okitsu et al. 2004). However, the study area is in the region of the northwest Queen Elizabeth Islands, which is generally considered to have been covered by the Innuitian Ice Sheet during the Last Glacial (Atkinson and England 2004); therefore, the time the study area has been deglaciated remains tentative.

The focus of this study was four glacial moraines with different periods of establishment (Fig. 1) that represented different terrain ages. The youngest, Moraine E (early stage), is located just below Arklio Glacier and consists of fresh, sharp boulders, with establishment estimated as during the Little Ice Age (400–250 years ago). Moraine M (middle stage) was established during the Holocene (3300–2400 years ago); whereas Moraine ML (middle–late stage) was established during the last stage of the Last Glacial (15 000–8000 years ago). The oldest moraine, Moraine L (late stage), was assumed to have originated in the Last Glacial (35 000–25 000 years ago). Based on the age order of the moraines, we constructed a chronosequence of primary succession following deglaciation. The potential maximum ice-free period of the study area was estimated as at least 25 000 years (Okitsu et al. 2004), providing an opportunity to investigate fairly long-term ecosystem development. With such a long ice-free period, it is difficult to assume that the initial condition of each moraine was equivalent. However, the order of establishment of these moraines is based on reliable evidence and the older moraines show a more developed successional status. Contrary to expectations, despite the harsh High Arctic location, the area shows an atypically highly vegetated physiognomy that retains many vascular plant species (Fig. 1b), which is a reflection of the long-term primary succession without species replacement (Mori et al. 2008). Major vascular plants on glacial moraines in the study area include dwarf shrubs (e.g. *Dryas integrifolia*, *Cassiope tetragona*, and *Salix arctica*), forbs (e.g. *Saxifraga oppositifolia*, *S. tricuspidata*, *Epilobium latifolium*, and *Papaver radicatum*) and graminoids (e.g. *Carex misandra*,

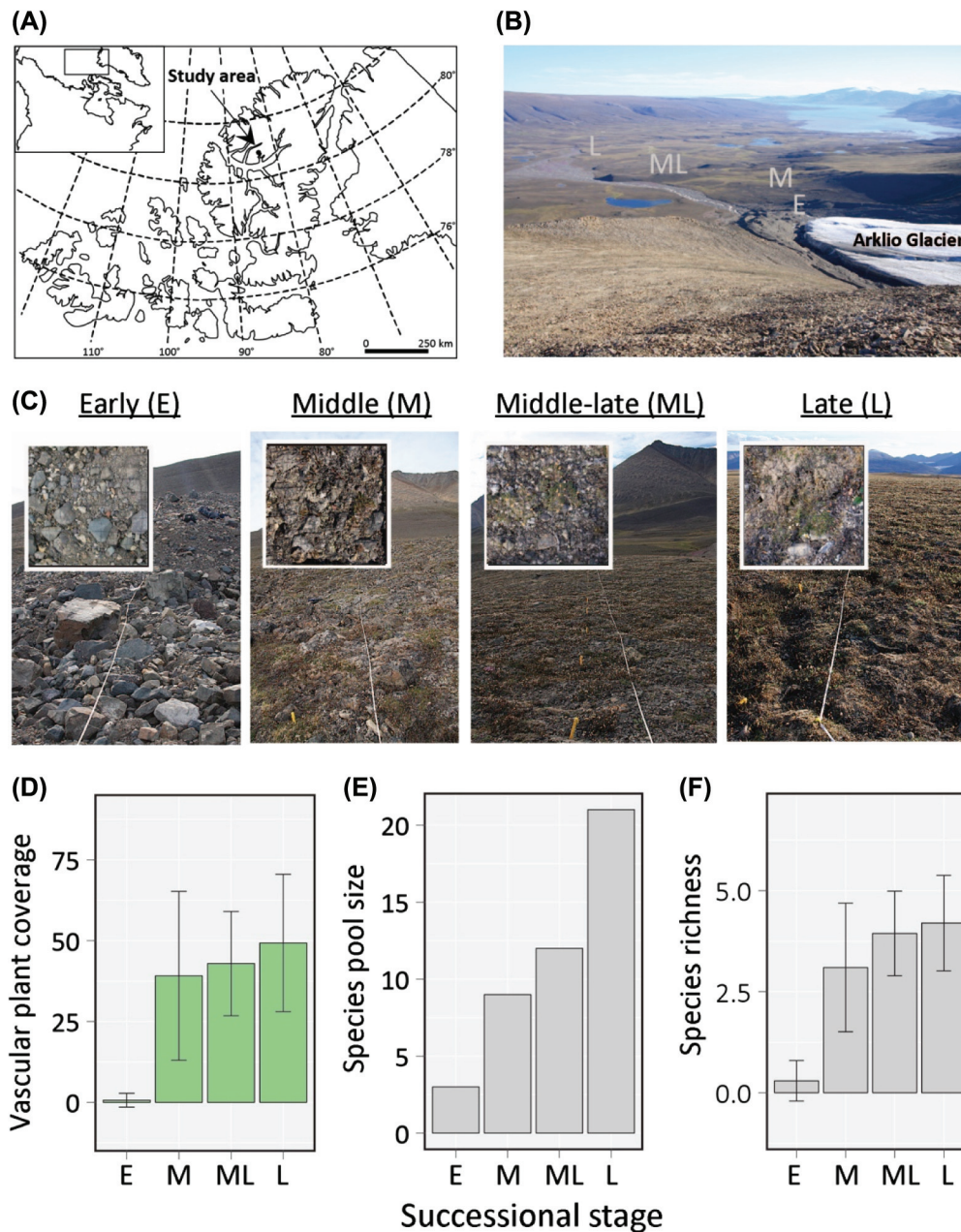


Figure 1. Properties of the study site in the high Arctic tundra of Canada. (A) geographical location. (B) physiognomy of the study site. (C) study transects on four moraines that each represent a different successional stage. (D) surface cover (%), (E) size of species pool, and (F) local species richness (mean  $\pm$  SE) of vascular plants for each successional stage (i.e. moraine).

*C. nardina*, *Luzula confusa* and *Poa arctica*), depending on the developmental stages of moraines (Okitsu et al. 2004, Mori et al. 2008).

### Field survey

In July 2008, we established a 100-m line transect along a ridgeline of each of the study moraines (Fig. 1c). On Moraine E, transect length was set to 50-m because of the relatively small moraine morphology. On each transect, we established  $0.5 \times 0.5$  m quadrats at 2-m intervals (at 1-m intervals for Moraine E) (in total, 204 quadrats; 51 quadrats  $\times$  4 transects). Within each quadrat, we recorded all species of vascular plants and measured the height of the tallest plants.

Using a frame with fixed  $5 \times 5$  cm grids (in total 100 grids within the size of study quadrats), we also measured the percent cover (%) of each species, vegetation type (i.e. vascular plants, bryophytes, or lichens/cryptogams), rocks ( $\geq 2$  mm, including boulders) and fine sediment particles ( $< 2$  mm) within each quadrat. We measured the longest diameter of the largest rock (cm) found in each quadrat; for this measurement, we did not remove any litter and measured only the unburied part of the largest rock. Thus, with an increase in vegetation cover, rock cover decreased. Within each quadrat, we measured soil water content (%) at three random positions using a soil moisture sensor and averaged these values to represent local soil moisture availability; this measurement of soil water content was conducted over two days on the



four moraines. Before the moisture measurements, no precipitation was observed for at least two weeks. We measured the depth of plant litter and mineral soil at three locations adjacent to the quadrat boundary to obtain mean values. Mineral soil was sampled from the 0.5 to 2 cm depth after removing plant litter, and these samples were returned to the laboratory for carbon (C) and nitrogen (N) measurements using a CN analyser. We used the values for accumulation of total soil C and N as focal ecosystem properties (functions). In other studies of biodiversity–ecosystem functioning, these soil properties have been used as a proxy for belowground functions (Fornara and Tilman 2008, Gotelli et al. 2011, Maestre et al. 2012). Following Hooper et al. (2005), we primarily use ‘ecosystem properties’ to refer to the size of these compartments. Moreover, soil N is a critical limiting factor for ecological processes during primary succession following deglaciation because soil N depends entirely on biological fixation (McKane et al. 2002).

### Functional traits and diversity

For the vascular plants on the study transects, we collected data for the following functional traits: plant growth form (i.e. shrub, forb, or graminoid), plant height (cm), seed mass (mg), seed bank longevity (y), specific leaf area ( $\text{mm}^2 \text{mg}^{-1}$ ), leaf life span (months), leaf lignin content (%), leaf N content (%), leaf C content (%), leaf phosphorus (P) content (%), aboveground-to-belowground biomass ratio (no units), root N content (%), root P content (%), pollination type (i.e. insect, wind, and/or other), dispersal mode (i.e. gravity, wind, water, or animal), and mycorrhizal association (i.e. ectomycorrhizal, ericoid, arbuscular, no-association, or unknown). These trait data for the species of the study were assembled from Osono et al. (2006), Iversen et al. (2015), and TRY database (Kattge et al. 2011) based on Fitter and Peat (1994), Cornelissen et al. (2004), Kerkhoff et al. (2006), Kleyer et al. (2008), Royal Botanical Gardens KEW (2008), Craine et al. (2009) and Reich et al. (2009). For leaf chemical properties, when data were available from multiple sources, we used data of Osono et al. (2006) that were collected from the study moraines. Data for these multiple traits were used to calculate functional turnover. We also estimated the trait community-weighted mean (CWM) (Garnier et al. 2004), which represents the overall community-level trait values by accounting for the abundance of each species in each location (i.e. percent cover of each species within each quadrat). We used average trait values for each species, as have done elsewhere (Bernard-Verdier et al. 2012, Purschke et al. 2013, Li et al. 2015).

We calculated functional turnover following the framework of Hardy and Senterre (2007), which has been used elsewhere (Baraloto et al. 2012, Purschke et al. 2013, Mori et al. 2015b). In this study, functional turnover among local communities (i.e. quadrats) was calculated using the  $\tau_{\text{ST}}$  statistic, defined as  $1 - D_w/D_a$ , where  $D_w$  is the mean within-community functional distance and  $D_a$  is the functional distance between different species sampled from different local communities in a focal system. Positive and negative values of  $\tau_{\text{ST}}$  indicate that species within local communities are functionally more and less similar to species from different communities, respectively (functional convergence

and divergence, respectively). Because the indices  $D_w$  and  $D_a$  are constructed from pairs of individuals of distinct species,  $\tau_{\text{ST}} > 0$  is not attributed to taxonomic similarity among locations but is explained by trait similarity (Baraloto et al. 2012).

### Data analyses

Statistical analyses were conducted with the R ver. 3.0.2 statistical software package (<www.r-project.org>), using ‘vegan’, ‘FD’, ‘picante’, ‘spacodiR’, ‘nlme’, ‘lavan’, ‘lavaan.survey’, and ‘survey’ packages.

#### Linear models

To examine a possible correlation between species richness of vascular plants and focal belowground functions (soil C and N content) for each successional stage (i.e. moraine), we used generalized least-squares (GLS) models to consider spatial autocorrelation among quadrats. Following Chisholm et al. (2013), we used a maximum likelihood method with a spherical autocorrelation structure and compared different models based on Akaike information criterion (AIC).

For these GLS models to explain spatial variations in soil C and N on each moraine, we included soil moisture availability, maximum rock size, vegetation height, litter and soil depths, and percentage microsite cover of each vegetation and rock/sediment category, in addition to species richness as a primary explanatory variable. Following previous studies (Gamfeldt et al. 2013, Mori et al. 2016), all variables were centred and standardized (z-score). The parsimonious models were selected using stepwise selection (based on the lowest AIC values). Therefore, because all variables were standardized, slope values represented the size of the effect; an effect size of zero indicates no effect of the explanatory variable on the response variable (Chisholm et al. 2013). Furthermore, as explained in the introduction (see the objective 1) and 2)), we also aimed to test the alternative hypothesis for the effects of soil properties on species richness; we thus replaced the primary explanatory variable with a response variable in the above models. More specifically, we used soil properties as independent variables to explain the spatial variation in species richness of vascular plants for each successional stage. Again, we used identical third variables and continued the above procedures for GLS model selection. For the above analyses, we did not include both soil C and N simultaneously in models because they were highly correlated ( $r > 0.95$ , all  $p < 0.0001$ ).

#### Structural equation modelling

To further disentangle the relationships between species diversity and soil properties, we constructed several confirmatory models using structural equation modelling (SEM; Supplementary material Appendix 1 Fig. A1). This approach is useful to integrate key predictions from competing theories into a network of multivariate expectations that cannot be well assessed based on bivariate analyses (Grace et al. 2016).

The models included species richness of vascular plants as diversity effects with other endogenous variables to explain soil C or N as response variables, which included soil moisture availability, maximum rock size, vegetation

height, litter and soil depths, and percentage microsite cover for each vegetation and rock/sediment category (Supplementary material Appendix 1 Fig. A1A). Considering another hypothesis that plant diversity cannot be a primary predictor of ecosystem properties (Bengtsson 1998, Schwartz et al. 2000, Fraser et al. 2015, Burley et al. 2016), we constructed alternative models (Supplementary material Appendix 1 Fig. A1B) following Lange et al. (2015). For these SEM analyses, we considered the nested structure of the data set (quadrats were established within each transect). Before the analysis, all variables were centred and standardized (Laliberte et al. 2014, Lange et al. 2015). Following previous studies (Lange et al. 2015, Grace et al. 2016, Fujii et al. 2017), we had a stringent criterion for model selection. To avoid over-fitting, any path with a standardized coefficient  $< 0.10$ , if nonsignificant, was removed from the model. We repeatedly adjusted models to find an adequate model with the lowest values of root mean square error of approximation (RMSEA), with values  $< 0.05$  suggesting an adequate fit. The fit of models was assessed with a  $\chi^2$ -test associated with a  $p$ -value  $> 0.05$ . Based on the above criteria, we constructed all possible models reflecting the conceptual flow shown in Supplementary material Appendix 1 Fig. A1 and repeatedly excluded unimportant variables until the most parsimonious models were found.

Furthermore, we constructed additional SEMs using CWM values of leaf C and N instead of species richness. Because CWM values could not be calculated for communities on Moraine E due to the limited number and frequency of occurrence of vascular plants, these additional calculations were limited to the data set without communities on this youngest moraine. We repeated the above procedure for model construction and selection, but the models used with either species richness or CWM values (leaf C or N) as an explanatory variable to explain soil C or N. Notably, we did not include CWMs of leaf C to explain soil N and vice versa. The alternative models used soil C or N as an explanatory variable and species richness or CWM values (leaf C or N) as a response variable. We constructed the most parsimonious models according to the identical criteria described above and compared the models based on AIC values.

### Functional diversity modelling

We used a null model to determine whether species within local communities were more (or less) functionally similar than the random expectation from the species pool. Communities were randomized using an algorithm that shuffles species identity within a species-by-location matrix (independent swap algorithm; Gotelli 2000). The model preserves the number of species in each location, species turnover between locations, and frequency of occurrence of each species across all locations. We conducted 9999 randomizations to calculate the standardised effect size (SES; difference between observed value and mean of randomized values divided by standard deviation of randomized values) of the  $\tau_{ST}$  statistic (standardised functional turnover). The SES indicates the magnitude of the deviation from the expectation of a random (stochastic) assembly process, and positive and negative values indicate more and less functional turnover, respectively, than that expected by chance. Higher and lower functional turnover represent functional clustering

and overdispersion (differentiation), respectively. Statistical significance of the functional turnover at each successional stage was evaluated based on the SES values of  $|1.96|$ . Notably, this type of null modelling is sensitive to differences in abundance among locations, but no adequate method to correct this sampling effect is currently available for abundance data based on percentage cover (Mori et al. 2015a); therefore, we used presence/absence data of each species within each quadrat to calculate functional turnover among quadrats. We repeated the estimation of functional turnover for each of the study moraines; the species pool was defined as the list of species observed on each moraine because different species emerged on different successional stages, which also allowed us to evaluate the degree of functional differentiation at each successional stage. The functional turnover for communities on Moraine E was not evaluated for the identical reasons described in the analyses of SEMs using CWMs.

### Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.7tv64> (Mori et al. 2017).

## Results

### Plant community structure changes through successional development

Along the gradient of successional stages, vascular plant coverage increased with increasing moraine age (Fig. 1d). Similarly, the size of species pool (Fig. 1e) and local species richness (Fig. 1f) of vascular plants increased with increasing moraine age.

CWM values of vascular plant communities for each successional stage are shown in Fig. 2. CWMs of plant height and leaf life-span were taller and longer, respectively, on Moraine M than those on Moraines ML and L. CWMs of leaf N and P content were lower in Moraines M and ML than those in Moraine L. No significant differences were found for other leaf traits, root traits, seed masses or above-ground/belowground biomass ratios among successional stages (moraines). Using these multivariate plant functional traits, functional turnover of vascular plant communities was calculated for each successional stage (Fig. 3). Vascular plant communities were significantly overdispersed (functional differentiation) only at the late successional stage (Moraine L; Fig. 3); whereas the communities on earlier successional stages (Moraines M and ML) were neither clustered nor dispersed (Fig. 3).

### Diversity–soil property relationships

From the GLS models used to explain the spatial variation in species richness of vascular plants, soil C or N content had a significant positive effect on vegetation on Moraines M and ML but had no effect on vegetation of Moraine L (Fig. 4). From the GLS models used to explain the spatial variation in soil C and N, species richness of vascular plants had a significant positive effect regardless of vegetation successional

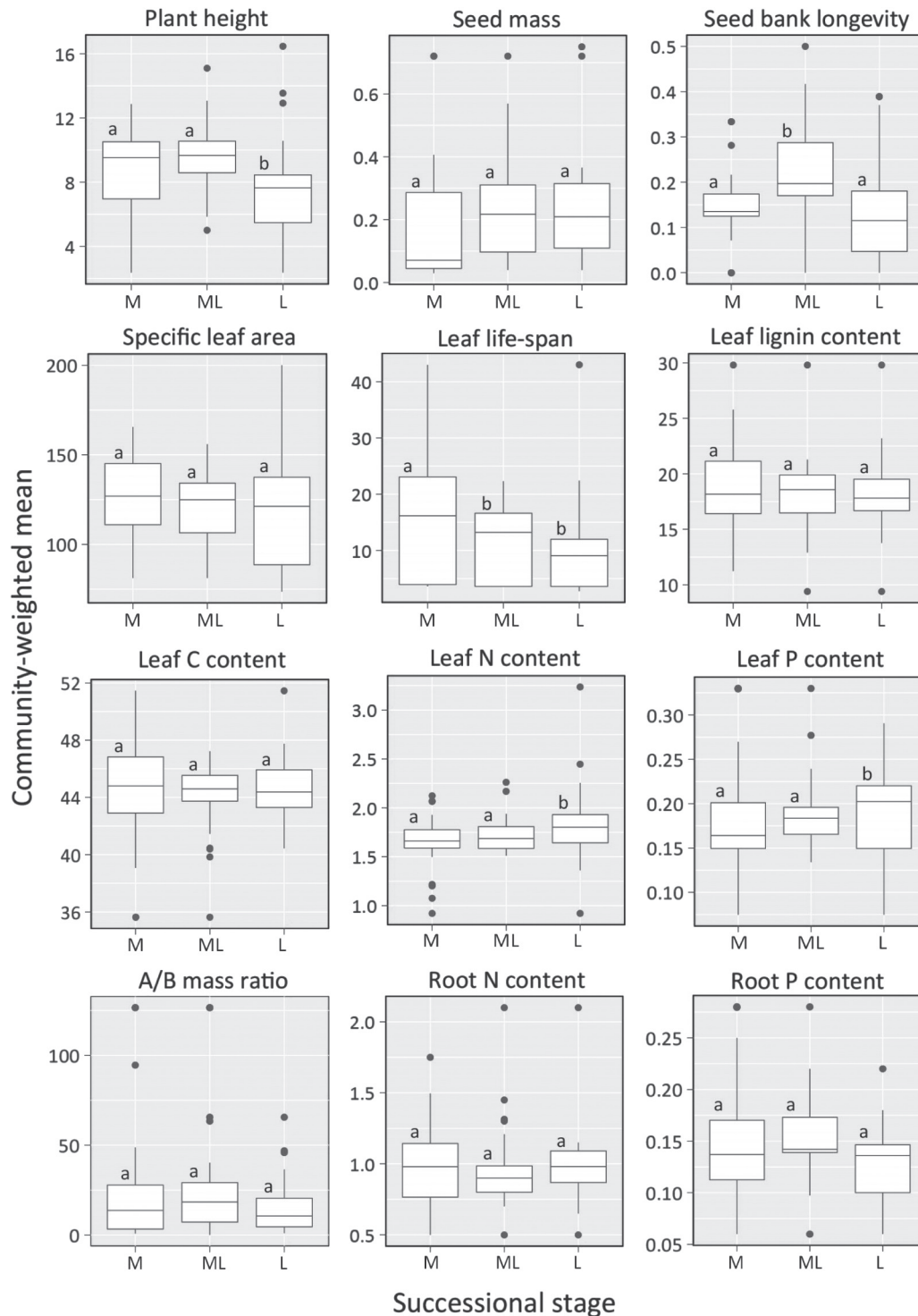


Figure 2. Boxplots showing community weighted mean (CWM) values of plant functional traits for each successional stage. M, ML and L represent middle, middle-late, and late stages of vegetation succession, respectively. Differences in CWM values were tested with Tukey's HSD test; different letters represent significant ( $p < 0.05$ ) differences in values among stages (moraines).

stage; whereas the effect was marginal ( $p < 0.1$ ) for vegetation on Moraine M, the effects were significant ( $p < 0.05$ ) for vegetation on Moraines ML and L (Fig. 4).

SEM results showed that the amount of soil C and N increased with the successional stage, and these increases were mediated by the increases in species richness of vascular plants and litter depth on the terrain (Fig. 5). For the

overall contribution of these two selected variables in determining soil properties, the contribution of species richness was greater than that of litter depth (Fig. 5). For both types of model, surface rock cover was an important variable to explain vegetation height, species richness, litter depth, and the focal final soil properties, particularly for soil C, which was negatively affected by the coverage of rocks/boulders

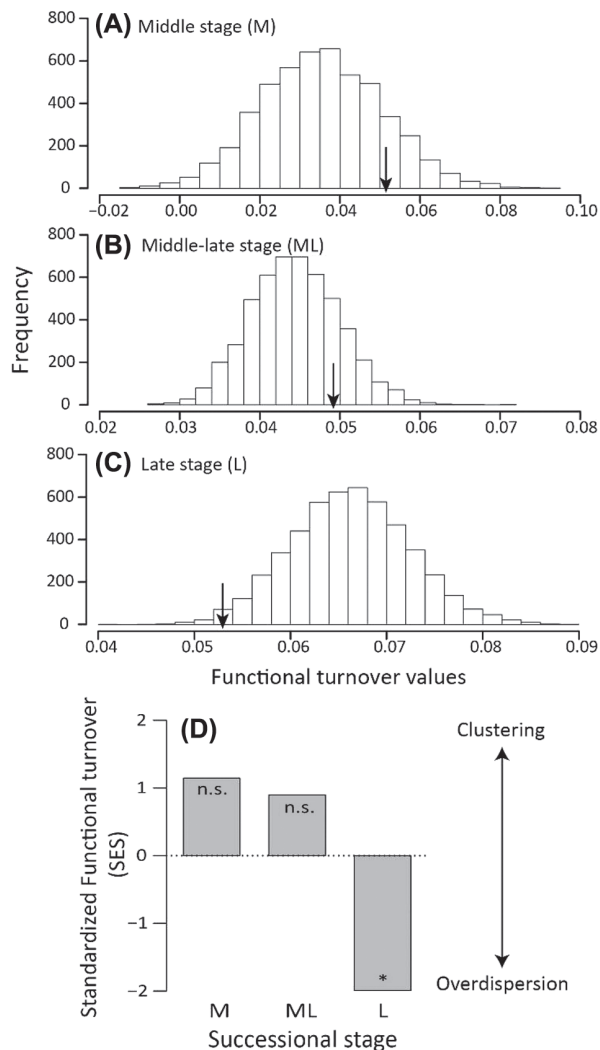


Figure 3. Functional turnover of local communities of vascular plants in each successional stage. M, ML and L represent middle, middle-late, and late stages of vegetation succession, respectively. (A–C) Distribution of null values of functional turnover obtained from 9999 randomizations. Arrows indicate the observed values of functional turnover. (D) Standardized effect size (SES) of functional turnover. Significance levels: \*  $p < 0.05$ ; n.s.  $p > 0.1$ .

(Fig. 5a). For soil N, this effect of surface rock cover was not remarkable, and species richness was the most important variable to have a direct effect on this soil ecosystem property (Fig. 5b). For alternatively hypothesized models that changed the flow direction between species richness of vascular plants and soil properties (Supplementary material Appendix 1 Fig. A1B), no model with RMSEA values less than 0.05 was found and all of these models were significant at  $p < 0.05$  for the  $\chi^2$ -statistic, indicating that the models were a poor fit to the observed variance–covariance matrix.

Because some traits, such as leaf N content, changed with vegetation succession (Fig. 2), we constructed SEMs that replaced species richness with CWMs of leaf C or N and found the most parsimonious models (using the data subset without data from Moraine E; Table 1). Overall model fit of the SEMs using CWMs of leaf C or N was comparable with

those using species richness (all RMSEA values  $< 0.001$ ,  $p > 0.3$  [ $\chi^2$ ]; Table 1). However, these models showed that CWMs of leaf C or N were not significantly associated with soil C or N; whereas in the models based on species richness, the significant positive effect on soil C or N remained (Table 1). To summarize, species richness of vascular plants remained the primary variable to explain the spatial variation in soil C and N.

## Discussion

We found that species richness of vascular plants was the important explanatory variable that determined soil ecosystem properties of a glacier foreland in the High Arctic (Fig. 5). This importance of species richness was particularly evident in the later stage of primary succession (Fig. 4) and was likely a result of stronger niche complementarity (functional differentiation) among coexisting species (Fig. 3). Although some previous studies suggest changes occur in the direction and magnitude of diversity–function relationships along environmental gradients (Steudel et al. 2012), such shifts in diversity–function relationships through stages in vegetation development have not received explicit consideration. Moreover, although the effects of plant species richness are the focus of these biodiversity studies (Tilman et al. 1996, Loreau et al. 2001), successional development of plant communities has not been necessarily well incorporated into the assessment of the diversity–function relationships (but see Weis et al. 2007, Lasky et al. 2014), in particular for natural communities. With this study, new insights into diversity–function relationships during succession are provided. Specifically, we focused on a possible shift in the cause-and-consequence relationships between species richness and local ecosystem properties (i.e. function) of natural communities along a primary successional gradient.

In systems governed by directional succession (as opposed to non-directional succession characterized by periodic occurrence and disappearance of a very few limited species; Svoboda and Henry 1987), which includes our study system (Fig. 1), abiotic factors predominate in the selection of organisms that emerge and persist in the earlier stages of primary succession, and then biotic factors become more important in the organization of ecological communities (Connell and Slatyer 1977). Thus, the relative importance of abiotic and biotic drivers changes through succession, with abiotic filtering of species by harsh environmental conditions in the early stages followed by gradual modification of the environment by these and other species that appear later. One of the primary mechanisms to link biodiversity–ecosystem function is the complementarity effect based on niche differentiation (Loreau and Hector 2001, Loreau et al. 2001), likely leading to the positive diversity effects in late-successional communities (Fig. 4) shaped by functional differentiation (Fig. 3). In the High Arctic tundra, although it occurs (Hodkinson et al. 2003), interspecific competition is quite weak; species are rarely excluded by others, thus leading to directional succession without species replacement (Svoboda and Henry 1987, Jones and Henry 2003). With this type of vegetation development



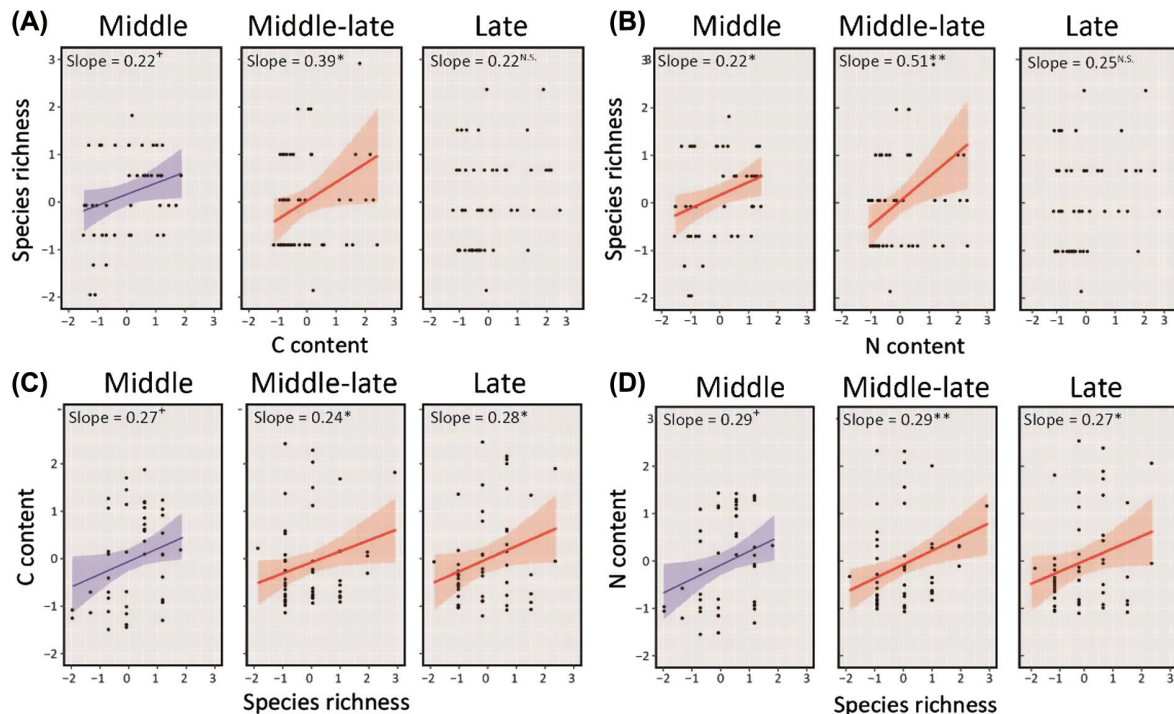


Figure 4. Possible cause-and-consequence relationships between species richness of vascular plants and soil properties (C and N). Solid lines and shaded areas indicate a significant fit with 95% and 90% confidence intervals (red and blue, respectively) of generalized least-squares (GLS) models with the lowest AIC values, respectively. Slope values are shown with significance levels: \*\* $p < 0.01$ ; \* $p < 0.05$ ; + $p < 0.1$ ; n.s.  $p > 0.1$ .

in the glacier foreland, we found that plant communities were not randomly assembled and that local communities at the late successional stage were functionally significantly more divergent than the expectation of random assembly. Functional (and phylogenetic) overdispersion is frequently considered as an outcome of competitive exclusion; however, some recent studies claim that this assumption may not always be correct (Mayfield and Levine 2010, Li et al. 2015). Indeed, the colonization of species that are functionally distant from resident species into local communities generates functional differentiation because the resource/niche overlap of these colonizers with residents is minimal (Li et al. 2015). Therefore, the niche complementarity at the late stage of primary succession without species replacement could be likely attributable to such a colonization process, not because of species extirpation or exclusion. Facilitation is another source of complementarity effects (Loreau and Hector 2001) and is a primary biotic driver of community organization in stressful environments (Michalet et al. 2006, Brooker et al. 2008, Cavieres et al. 2014). Facilitation is particularly important in the marginal environment of the Arctic tundra (Svoboda and Henry 1987, Jones and Henry 2003), which provides further support for the importance of the complementarity effect (but see Olofsson et al. 1999). Under severe environmental stress, with an increase in facilitation, multiple species can coexist because facilitation leads to functional complementarity between species (Michalet et al. 2006). For the glacial moraines, these two explanations for the increase in importance of complementarity effects (niche differentiation and facilitation) are not mutually exclusive and likely operate simultaneously.

In determining the effects of biodiversity on ecosystem properties and processes, an important alternative possibility must be considered: the sampling or selection effect is driven by functionally important/dominant species that are likely included more often in species-rich communities (Loreau and Hector 2001, Loreau et al. 2001). This effect was apparently unimportant in our study system because this atypically species-rich tundra is in a High Arctic environment that is harsh to most plant species. Although biologically-driven vegetation succession occurs, the sum of physical drivers is equal to or larger than that of biological drivers even in the late stage of succession (Mori et al. 2008). Some observational and experimental evidence indicate that the relative importance of the complementarity over the selection effect is high in harsh environmental conditions (Jucker et al. 2016, Ratcliffe et al. 2016), whereas the selection effect predominates in productive environments (Wang et al. 2013). Further, when ecosystem properties are disproportionately affected by some species because of their abundance and dominance, the influences of such species should be reflected in the overall model to explain the spatial variations in the focal ecosystem properties. In this study, we found no significant effects of CWM values of leaf C and N on soil C and N (Table 1), which suggested that dominant species (based on biomass ratio hypothesis; Grime 1998) had little influence on local ecosystem properties. Some community-level traits changed through successional development (Fig. 2). In particular, we found that minerals in leaves, such as N and P contents, were higher in the late stage (Fig. 2), which might be because the increase in soil nutrient availability on older developed terrains that can further



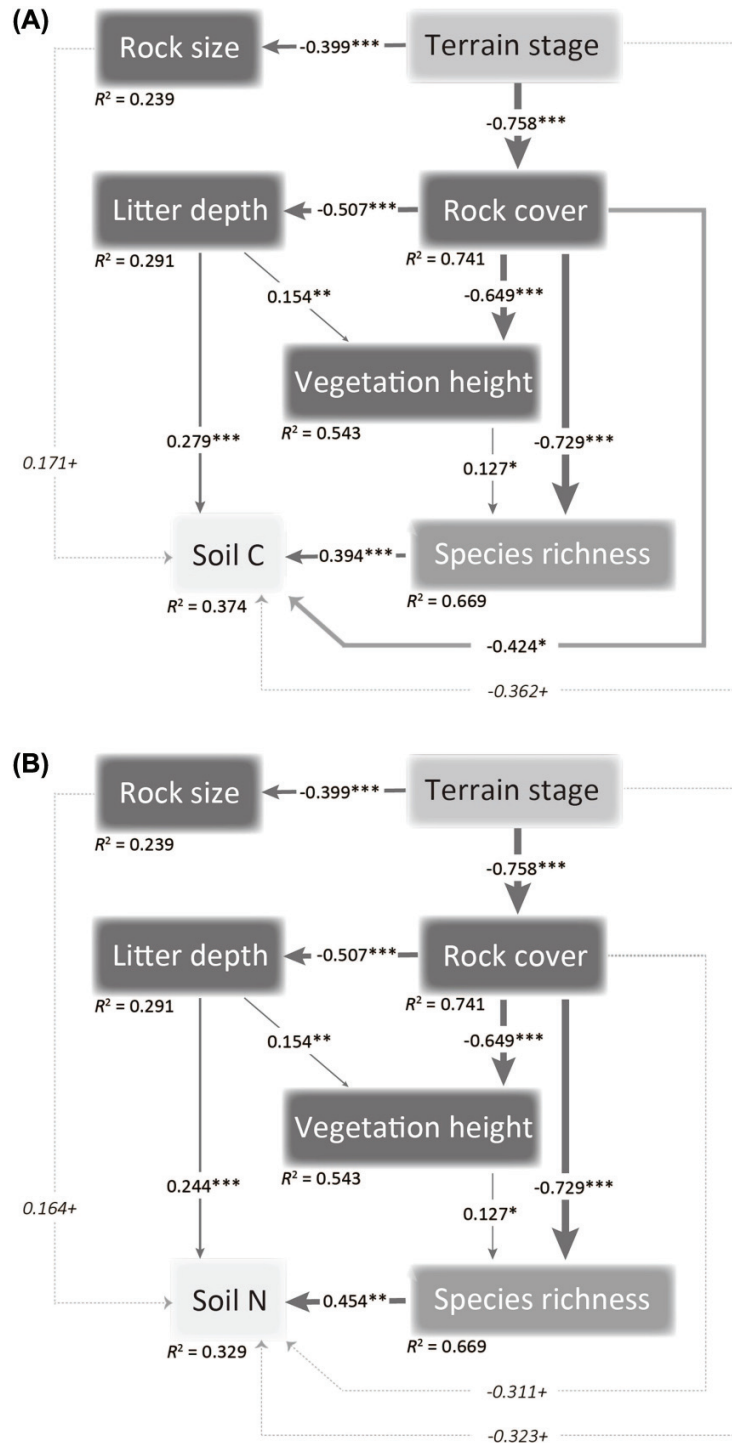


Figure 5. Path diagrams based on the parsimonious models of structural equation modelling (SEM), which explain the cause-and-consequence relationships between species richness of vascular plants and soil properties (C and N) along the vegetation succession. Root mean square error of approximation (RMSEA) values,  $\chi^2$ -statistics and the associated significance levels (p-value) were 0.000, 7.515, and 0.554 for soil C and 0.000, 7.558, and 0.579 for soil N, respectively.  $R^2$ -values, standardized coefficients and significance levels ( $^{***}p < 0.001$ ;  $^{**}p < 0.01$ ;  $^*p < 0.05$ ;  $^+p < 0.1$ ) are shown for each variable. The size of arrows is proportional to the size of the standardized coefficient.

facilitate plant community development (Chapin et al. 1994). In spite of these community-level changes along the primary successional gradient, CWMs of leaf traits were not a primary determinant of soil properties in this tundra landscape. Therefore, we suggest that the selection effect is not

a mechanistic explanation for diversity effects in this High Arctic tundra.

In the process of primary succession following deglaciation in the High Arctic, species replacement rarely occurs (Svoboda and Henry 1987), even in this tundra with lush

Table 1. Results of SEMs based on a subset of data including CWMs of leaf traits for communities on middle, middle-late and late successional moraines. For these models, we also used CWM values of leaf carbon (Leaf C) and nitrogen (Leaf N) content as an alternative variable for the effect of plant diversity (Supplementary material Appendix 1 Fig. A1). The variables of soil C and N were highly positively correlated on all moraines; therefore, different models were constructed to avoid collinearity when each of these variables were included as an explanatory variable. Overall fitness of the most parsimonious models is shown with the result for the focal node (i.e. plant diversity effect on soil property versus soil property effect on plant diversity). All final models retained the plant diversity effect, but the independent effect was only significant for species richness. Values of Akaike information criterion (AIC) and root mean square error of approximation (RMSEA) are shown.

Model	SEM fitness				Focal node	
	AIC	RMSEA	$\chi^2$ -value	p-value	Effect (y~x)	p-value (y~x)
Soil C~CWM (leaf C)	1680.9	0.000	0.811	0.368	-0.025	0.220
Soil C~species richness	1158.8	0.000	0.848	0.838	0.335	< 0.01
Soil N~CWM (leaf N)	1697.0	0.000	1.297	0.730	-0.267	0.458
Soil N~species richness	845.4	0.000	0.811	0.368	0.403	< 0.01

vegetation (Mori et al. 2008). Thus, additional plant species emerge through time in addition to early colonizers. In general, this phenomenon is a consequence of the gradual increase in carrying capacity with successional development of the ecosystem (Connell and Slatyer 1977); that is, the availability of resources and habitats in the local environment primarily determines the number of species that persist. This assumption is likely also valid in our study system because the physical restrictions on microsite availability for plants caused by rocks and boulders deposited after deglaciations were the greatest determinant of species richness (Fig. 5). Other physical properties in the periglacial environment, such as gelifluction and geliturbation, may also have a substantial effect on vegetation structure (Cannone et al. 2004). However, species assemblages may not always be the response variable that is controlled by physio-environmental parameters, even in the Arctic (Wookey et al. 2009). With theoretical support from biodiversity studies, we propose that the flow from environment to species could be reversed at some seral stages during the long-term process of primary succession (Fig. 4).

Traditionally, the variability in environmental conditions, such as soil organic C, total N, and moisture, on glacier forelands has been primarily explained by terrain age (Matthews 1992). However, according to recent studies, plant–microsite associations are shaped by feedback mechanisms, and therefore, neither plant nor microsite condition is a single absolute predictor of the other. Moreover, the relative magnitude of the influence of one on the other may change in the process of ecosystem development (van der Putten et al. 2013). Although such mechanisms (e.g. plant–soil feedback) are now incorporated into recent biodiversity–ecosystem functioning studies (Kulmatiski et al. 2012), empirical evidence remains rudimentary. Note that our study based on correlational relationships would have limitations for precisely evaluating such dynamic feature of ecological systems, and thus cannot fully identify the causalities between communities and ecosystem properties. Although careful interpretation is needed for our results, we emphasize that, with information borrowed from a rich body of succession studies, we conclude that diversity–function relationships likely were dependent on the developmental status of the ecosystem. Overall, our observational evidence for the stronger roles of species richness in determining ecosystem properties in the later stages of

ecosystem development is consistent with current ecological theories developed through the synthesis of succession and biodiversity research.

## Implications

In this study, we explored a possible reversal of the causality between species diversity and ecosystem properties in natural communities. Because of the possible increases in diversity effects (particularly, interspecific complementarity) with time found in biodiversity experiments (Reich et al. 2012), communities formed through long-term natural processes deserve further attention to implement the knowledge gained from the research on biodiversity into practice. Therefore, successional studies that use a long-term chronosequence, such as our study, have much to offer (Walker et al. 2010), although caution is required because with this approach inferences on ecosystem dynamics through time are somewhat limited (Johnson and Miyanishi 2008).

Note that caveats surely exist in this study. Because communities could show different pathways of successional development (alternative stable state or alternative transient state) (Fukami and Nakajima 2011), it is possible that local communities and the associate ecosystem properties on the older terrains may not be necessarily a representative of those that will be observed on the presently younger terrains in future. Another uncertainty is that we did not consider possible intraspecific variations in functional traits under different environmental conditions (Craine and Reich 2001). Although plants could vary largely their properties depending on the conditions under which they are growing, our results for CWMs hardly reflect such possible variability of individual traits among different seral stages. Furthermore, we did not measure any process rates such as annual productivity and instead relied only on static data of soil properties. Although accumulations of C and N below-ground are important pools in biogeochemical cycles in terrestrial ecosystems (Fornara and Tilman 2008, Manning et al. 2015), translation of our findings to deduce the mechanisms underlying the observed patterns may therefore not be straightforward. Observational studies like ours inherently have limitations that cannot fully distinguish different mechanisms; however, if carefully assessed and interpreted, perspectives gained from field evidence are valuable and fundamental (Cadotte and Tucker 2017).

Notwithstanding above and other possible limitations, this study is novel. Note that our primary aim was not to provide quantitative evidence for the relative importance between environmental and diversity controls but to test a hypothesis of temporal changes on the direction of causality. Indeed, there have been an outstanding debate over the cause-and-consequence relationship between diversity and ecosystem properties (e.g. productivity; Fraser et al. 2015, Grace et al. 2016). In this regard, our findings suggest that temporal perspectives (i.e. developmental stages) must be fully incorporated into such debates and assessments. Considering the rapid expansion of biodiversity research in natural communities and the accumulation of data from biodiversity experiments for more than two decades, frontiers exist to combine the knowledge gained from both sources. In doing so, we propose that succession research – one of the oldest topics in ecology – provides a great opportunity.

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Supplementary material (available online as Appendix oik-04345 at <[www.oiksjournal.org/appendix/oik-04345](http://www.oiksjournal.org/appendix/oik-04345)>). Appendix 1.