

The phylogenetics of succession can guide restoration: an example from abandoned mine sites in the subarctic

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Summary

1. Phylogenetic tools have increasingly been used in community ecology to describe the evolutionary relationships among co-occurring species. In studies of succession, such tools may allow us to identify the evolutionary lineages most suited for particular stages of succession and habitat rehabilitation. However, to date, these two applications have been largely separate. Here, we suggest that information on phylogenetic community structure might help to inform community restoration strategies following major disturbance.

2. Our study examined phylogenetic patterns of succession based on a chronosequence of three abandoned subarctic mine spoil heaps (waste piles) dating from the early 1970s, mid-1970s and early 1980s. The vegetation at each mine site was compared to the surrounding vegetation, and community structure on mines was explored assuming species pools at nested spatial scales.

3. We found that the adjacent vegetation was more phylogenetically clustered than the vegetation on the mines, with mines demonstrating weaker phylogenetic community structure. Using simulation models, we showed that phylogenetic dissimilarity between mine sites did not depart from null expectations. However, we found evidence for species sorting along abiotic gradients (slope and aspect) on the mine sites that had been abandoned for the longest.

4. *Synthesis and applications.* Understanding the trajectory of succession is critical for restoration efforts. Our results suggest that early colonizers represent a phylogenetically random subset of species from the local species pool. Over time, there appears to be selection for particular lineages that come to be filtered across space and environment. The species most appropriate for mine site restoration might, therefore, depend on the successional stage of the community and the local species composition. For example, in later succession, it could be more beneficial to facilitate establishment of more distant relatives. Our findings can improve management practices by providing relatedness information for known successful colonizers and by informing seeding decisions with knowledge of the surrounding and regional species pools. The application of phylogenetics to restoration ecology and succession is relatively new, but it has the potential to provide novel insight into the dynamics of changing community structures during succession.

Key-words: chronosequence, community assembly, net-relatedness index, null models, phylogenetic beta-diversity, phylogenetic diversity, species pool, species richness

Introduction

Abandoned mine sites pose a distinct challenge in the field of restoration ecology because they are often stripped of

organic matter, have nutrient poor soils and can be located in harsh climates. Succession of mine sites has been studied using traditional measures of diversity, such as taxonomic richness and evenness to explore patterns of species re-establishment (Prach 1987; Densmore 1994; Jochimsen 1996; Parrotta, Knowles & Wunderle 1997;

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Prach & Pyšek 2001; Densmore 2005). These measures can provide a coarse index of community change in species number or abundance, but they provide little information about community membership and species interactions (Blomberg, Garland & Ives 2003; Funk *et al.* 2008; Verdú, Gómez-Aparicio & Valiente-Banuet 2012). For example, richness metrics do not reveal how a community is restructured through time or whether specific clades are dominant at a particular point in succession, an important factor in restoration efforts. Recently, phylogenetic approaches have been used to interpret the forces structuring communities following disturbance (Cavender-Bares *et al.* 2004; Letcher 2010; Verdú, Gómez-Aparicio & Valiente-Banuet 2012; Whitfeld *et al.* 2012; Mo *et al.* 2013; Purschke *et al.* 2013). Phylogenetics can provide information on species ecological similarity and function in the environment (Faith 1992), therefore having potential to aid restoration and habitat management (Webb *et al.* 2002; Cadotte *et al.* 2009; Cavender-Bares *et al.* 2009).

Metrics of phylogenetic diversity (PD) were first developed to capture underlying diversity in phenotypic features (Faith 1992) and later to describe evolutionary relationships among species in a community (Webb *et al.* 2002). Phylogenetic community structure is typically quantified with respect to either clustering (community members are more closely related than expected by chance) or overdispersion (community members are more evenly distributed throughout the phylogeny than expected by chance). Assuming that traits are evolutionarily conserved and that phylogenetic distances measure functional trait differences, clustered communities are thought to arise from environmental filtering by abiotic factors, where co-occurring (and closely related) species have similar adaptations to particular environmental conditions. Overdispersion is associated with competition among ecologically similar species, resulting in the co-occurrence of more distantly related species (Webb *et al.* 2002; Cavender-Bares *et al.* 2009). However, different processes may give rise to similar patterns. For example, competition may drive patterns of either overdispersion or clustering, depending on the traits being selected for (Mayfield & Levine 2010).

While community phylogenetics has traditionally focused on competition and filtering, the field of ecological restoration has focused more on the role of positive biotic interactions that initiate succession (Padilla & Pugnaire 2006; Verdú, Gómez-Aparicio & Valiente-Banuet 2012). Community phylogenetic approaches might help to inform our understanding of succession by revealing patterns of species \times species and species \times environment interactions. Within a community phylogenetics framework, we may expect patterns that reflect a shift in dominant forces through successional time, that is, from environmental filtering to facilitation and then competition once species have established. This pattern is supported by several recent studies (e.g. Verdú *et al.* 2009;

Whitfeld *et al.* 2012; Mo *et al.* 2013; Purschke *et al.* 2013), although alternative patterns of phylogenetic succession have been shown (e.g. general overdispersion across successional stages; Letcher 2010).

However, with few exceptions (e.g. Letcher 2010), phylogenetic studies of succession have typically considered only a single species pool, whereas recent reviews have highlighted the importance of defining the appropriate species pool (or spatial scale) in phylogenetic analyses of community structure (Swenson *et al.* 2006; Cavender-Bares *et al.* 2009). Within the context of succession, it is well known from island biogeography theory that the probability of species arrival to a site is related to the size and distance of the source population (MacArthur & Wilson 1963). For example, species composition in basalt quarries increasingly resembled that of nearby grassland communities over time, which illustrates how community reassembly is strongly influenced by nearby species pools (Novák & Konvička 2006). Combining information on both the phylogeny and the spatial scale of the species pool allows us to quantify changes in community structure and describe patterns of succession, while accounting for differences in the identity and diversity of species available for establishment.

Using a chronosequence of mine sites composed of piled waste material in the Canadian subarctic, we explored the effect of time since abandonment (age) and the progress of succession by examining the plant communities on each mine site with respect to species pools across differing spatial scales. We predicted that (i) the species growing on the mine sites would be more phylogenetically clustered, have lower species richness (SR) and lower PD compared to their surroundings due to the harsh and nutrient poor conditions of the more recently abandoned mines. We expected to detect this pattern across spatial scales, including the plot level, due to the heterogeneity of the mine environment. As time since abandonment increases, we predicted (ii) an increase in SR and PD and a decrease in species clustering, with biotic process becoming more dominant at finer spatial scales (see Cavender-Bares *et al.* 2009). Last, we expected (iii) a greater influence of local environment on species distribution on the older mines, as species are sorted into their preferred niches over time (Grubb 1977; Zobel *et al.* 2000; Questad & Foster 2008). Our aim was to uncover naturally occurring shifts in community structure as succession progresses, which could be used to inform restoration practice aimed at maintaining the integrity of subarctic plant communities.

Materials and methods

STUDY SITE

Data were collected from a chronosequence of three abandoned mining waste piles located near Schefferville, Quebec, Canada. The mines – Gagnon (54°83'56.98"N, –66°90'64.38"W), Retty

(54.867124°N, -66.999806°W) and Timmins (54.900451°N, -67.096216°W) – were chosen for comparison because they were formed from similar material and share general attributes in overall size, elevation and relief. The three sites were mined for iron ore by the Iron Ore Company from 1964 to 1982 and were closed in the early 1970s, mid-1970s and early 1980s, respectively. An unpublished study by S. Boudreau (2012) on the soil chemistry of the mines in this region reported that soil quality and nutrient availability are unlikely to account for differences in plant cover on the mines. Additionally, the report indicates that the population of viable seeds in the mine soil was limited and majorly consisted of mosses, which were not considered in this study. Thus, succession on each site reflects the process of recolonization.

DATA COLLECTION

Quadrats (1 m²) were established at 10-m intervals along three transects on the mine piles, one longitudinal and two cross sections ($N_{\text{Gagnon}} = 121$ plots, $N_{\text{Retty}} = 140$ plots and $N_{\text{Timmins}} = 153$ plots). A similar procedure was used to sample the immediately adjacent undisturbed vegetation at each site with quadrats established every 10 m along three transects at Gagnon and Retty, and two transects at Timmins, resulting in 50 vegetation quadrats for Gagnon and Retty, and 42 for Timmins. Plots in the surrounding vegetation were placed in largely non-forested areas for better comparison with the mines (mine piles are unlikely to become forested). Species richness and percentage cover (relative abundance) of all vascular plants were recorded in each plot, and tissue samples for each species were collected and submitted to the Barcode of Life Database (BOLD) for sequencing (Appendix S1, Supporting Information for specimen details and associated GenBank accession numbers). Vouchers were deposited in the Marie-Victorin Herbarium (Montreal, Quebec, Canada). Rarefaction curves were calculated and show sufficient sampling at all sites (Fig. S1). In all plots, we recorded slope and aspect using a clinometer.

PHYLOGENY RECONSTRUCTION

We estimated a molecular phylogeny based on two sequenced plant DNA barcodes obtained from voucher specimens: *rbcL* and *matK* (Hollingsworth *et al.* 2009). In some cases, amplification of the DNA barcodes failed and gaps were filled using sequences from GenBank (Appendix S1). Sequences were aligned using MAFFT ver. 7 (Katoh & Standley 2013) and BioEdit (Hall 1999). The phylogeny was constructed in MrBayes 3.2 (Ronquist & Huelsenbeck 2003) using a GTR+G+I evolutionary model for *rbcL* and HKY+G for *matK*, as determined using the function *modelTest* in the *phangorn* R library (Schliep 2011). We ran 5 million generations and rooted the consensus tree on *Cystopteris montana* (L.) Bernhardt ex Desvaux. We dated the phylogeny using *chronopl*, from the *ape* package (Paradis, Claude & Strimmer 2004) and three calibration points: the monilophytes were dated to a maximum age of 354 mya (Bateman 1991), eudicots at 124 mya (Hughes & McDougall 1990) and saxifragales at 91 mya (Hermesen *et al.* 2003). We verified that the consensus tree generated was robust by conducting sensitivity analyses across alternatively resolved trees (Appendix S2 for more details). The resulting consensus tree included 43 taxa from the region and was used for all subsequent analyses.

DEFINING THE SPECIES POOLS

We used hierarchically nested species pools to explore community composition at three different spatial scales: regional, local and mine site.

Regional pool

The regional pool consists of all species across all plots in the study (mine sites and surrounding vegetation).

Local pool

The local pool consists of the species on a mine and in its surrounding vegetation; we thus defined three local pools, one each for Gagnon, Retty and Timmins.

Mine pool

The mine pool represents the species existing on the respective mine (excluding the surrounding vegetation).

Our regional pool is a collection of the local pools from all three sites. An alternative would be to use a regional species list from the area; however, it is difficult to define the extent of such a pool as the topography and environment of the region are highly variable. Therefore, we decided to limit our regional pool to the relevant subset of species closer to, and more likely to establish on, the mine sites.

ANALYSES OF PLANT COMMUNITIES

Analyses were performed using the *ape* (Paradis, Claude & Strimmer 2004), *picante* (Kembel *et al.* 2010) and *vegan* (Oksanen *et al.* 2013) packages in R ver. 3.0.2 (R Core Team 2014). Species richness and PD were calculated separately for each mine site; plots were combined to generate one measure of SR and PD for each mine. To determine whether PD differed from expectations given the local pool, we used a null model to compare the observed PD on each mine to 1000 null communities of equivalent SR by randomly shuffling species in the community matrix while maintaining plot richness. We generated *P* values by calculating the proportion of null PD values that were greater than the mean observed PD of the plots for each mine ($\alpha = 0.05$).

The net-relatedness index (NRI), a measure of phylogenetic relatedness among community members, was calculated at the plot and mine site level using both abundance-weighted and non-weighted metrics. Abundance-weighted metrics allow abundant species to have a greater influence on the calculation of species co-occurrence. We calculated NRI on plots with SR greater than one using the *ses.mpd* function from the *picante* package (Kembel *et al.* 2010) with 1000 null iterations; NRI is equal to $-1 \times \text{ses.mpd}$ (standardized mean pairwise distance). A positive NRI value indicates phylogenetic clustering, while a negative value indicates phylogenetic overdispersion. To explore species pool effects, we conducted the following comparisons: first, we contrasted NRI between the three mines (combining the plots for each separate mine) assuming the regional species pool; secondly, we evaluated NRI at the plot level within mine sites assuming (i) the same regional pool, (ii) the local pool and (iii) the mine pool.

Welch's two-sample *t*-tests for unequal sample sizes were performed to determine whether communities on mine sites significantly differed from the adjacent vegetation. We assessed differences between the three mines using an ANOVA followed by a Tukey test for post hoc analyses.

We used phylogenetic beta-diversity metrics to quantify the phylogenetic similarity between mine sites using the *phylosor* function (Bryant *et al.* 2008) in the *picante* R package (Kembel *et al.* 2010), which calculates the proportion of shared evolutionary history, or branch lengths, between two communities. Observed beta-diversity values were compared to null values generated by randomly shuffling taxa on the regional phylogeny, while maintaining richness and abundances on each pile (1000 iterations). We also calculated phylogenetic beta-diversity among mine plots assuming the local species pool. *P* values were calculated using the same method as for PD, described above.

Finally, to explore the effect of local environment on community composition, we used non-metric multidimensional scaling (NMDS) to describe the spatial relationship between species on the pile and associated environmental data (slope and aspect). Aspect was linearized using the Topographic Solar Radiation Aspect Index (TRASP), which converts aspect into values ranging from zero to one (Roberts & Cooper 1989). Values of zero correspond to a northward orientation (NNE) and values of one are assigned to south-facing slopes (SSE). NMDS was performed using the *metaMDS* function from the *vegan* package, fitting both slope and TRASP as vectors with the function *envfit* from the *vegan* package (Oksanen *et al.* 2013). Significance values are from the squared correlation coefficient between observed and modelled values given 999 permutations.

Results

DIVERSITY ACROSS MINE SITES

The local vegetation pool differed in richness and species composition between locations, with 27 species at Gagnon, 37 species at Retty and 32 species at Timmins, respectively, representing 64%, 88% and 76% of the sampled regional pool (42 species). The communities on mine piles also differed in richness, with 16, 25 and 26 species for Gagnon, Retty and Timmins, respectively, representing 59%, 68% and 81% of the local pool richness (Fig. 1). *Betula glandulosa* Michx. was the most abundant species in each local pool; however, the most abundant (here defined as the highest percentage cover per plot) species on the mine piles varied between sites, with *Alnus viridis* Chaix DC. dominating at Gagnon and Timmins while *Salix planifolia* Pursh was most abundant at Retty (Fig. 1).

Phylogenetic diversity followed a similar pattern to that of SR, where Retty had the highest PD, followed by Tim-

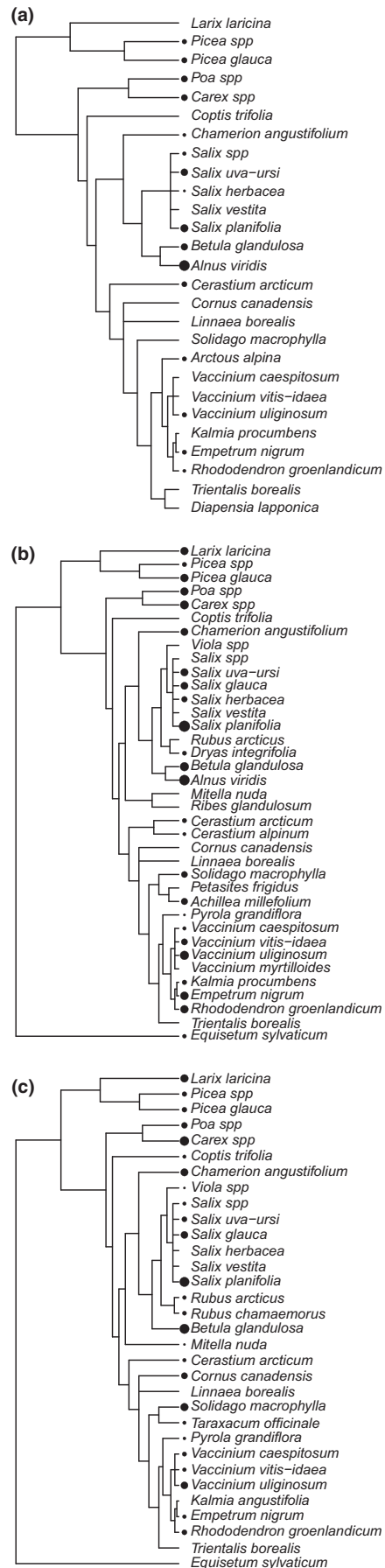


Figure 1. Local phylogenies for each mine site: Gagnon (a), Retty (b) and Timmins (c). Abundances (represented by circles) are shown for species occurring on each mine. Abundances are not shown for those species which occur solely in the surrounding vegetation of a given mine. The abundances were divided by the number of plots on each mine and log-transformed to standardize percentage cover per plot, per pile.

mins and Gagnon ($PD_{\text{Retty}} = 1794.67$, $PD_{\text{Timmins}} = 1748.42$ and $PD_{\text{Gagnon}} = 1201.98$). However, PD did not differ from the null expectation for any mine ($P_{\text{Gagnon}} = 0.67$, $P_{\text{Retty}} = 0.273$ and $P_{\text{Timmins}} = 0.509$). Further, when all plots were considered together, mines were neither significantly clustered nor overdispersed (Table 1). In addition, the phylogenetic turnover between mines (mine-level phylogenetic beta-diversity) did not differ from the null expectation based upon sampling the same number of species at random from the regional pool (Table S1).

PLOT-LEVEL STRUCTURE ACROSS MINE SITES

First, we examined plot-level phylogenetic community structure using the mine-restricted pool. The mean standardized effect size for NRI was significantly greater than zero for all mines except for weighted measures on Timmins (Table 2), but did not differ significantly between mines (ANOVA; $F_{\text{non-weighted}} = 1.611$, $P_{\text{non-weighted}} = 0.158$; $F_{\text{weighted}} = 1.802$, $P_{\text{weighted}} = 0.168$).

Secondly, using the local pool, we again found evidence that the mean standardized effect size for plot NRI was

Table 1. Standardized effect size (Z) and P values reported for weighted and non-weighted measures of NRI for each mine using the regional species pool. Mine plot abundances were summed across each mine and divided by the number of plots per mine

	$Z_{\text{non-weighted}}$	$P_{\text{non-weighted}}$	Z_{weighted}	P_{weighted}
Gagnon	-0.43	0.66	0.76	0.17
Retty	-1.60	0.95	0.42	0.41
Timmins	-0.43	0.63	-0.007	0.61

Table 2. Mean standard effect size (Z) for net-relatedness index (NRI) per plot for each site (G = Gagnon, R = Retty, T = Timmins and V = surrounding vegetation) using species pools delimited by the species present within the mine (Mine pool), those species present in the mine and adjacent vegetation (Local pool) and the pooled species across all three mine sites and respective adjacent vegetation (Regional pool). Statistics are provided for both weighted and non-weighted measures of NRI. Asterisks indicate whether standardized effect sizes of NRI were significantly different than zero, as determined by a one-sample t -test (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$)

	$Z_{\text{non-weighted}}$	$P_{\text{non-weighted}}$	Z_{weighted}	P_{weighted}
Mine pool				
G	0.456**	0.405	0.458**	0.395
R	0.464***	0.392	0.426***	0.400
T	0.198*	0.491	0.135	0.499
Local pool				
G	0.124*	0.134	0.107*	0.139
R	0.280**	0.455	0.184*	0.495
T	0.290***	0.480	0.686*	0.517
Regional pool				
G	0.285	0.474	0.284*	0.477
R	0.149	0.511	0.155	0.497
T	0.130	0.543	0.124	0.528
V	0.463***	0.348	0.168	0.454

significantly greater than zero for all mines (Table 2). However, plots on both Gagnon and Retty were significantly less clustered than plots in the adjacent vegetation (Welch t -test; $P_{\text{non-weighted}} < 0.01$ for Gagnon and Retty; Fig. 2) using non-weighted measures, although not when weighted by abundances. In contrast, plots on Timmins (the youngest site) did not significantly differ in phylogenetic dispersion from the adjacent vegetation irrespective of weighting (Fig. 2; Table S2 for associated statistics).

Thirdly, we evaluated plot NRI using the regional species pool and found standardized effect sizes were not significantly different than zero, except in the case of weighted NRI on Gagnon (Table 2). The three mines did not differ in NRI, although Retty was significantly less clustered than the surrounding vegetation plots without abundance weighting (Table S3).

Finally, we evaluated phylogenetic beta-diversity among plots on each mine site using the proportion of shared branch lengths between plots. We found that phylogenetic beta-diversity was not significantly different from a null expectation derived from resampling the local species pool for any of the mine sites ($P_{\text{Gagnon}} = 0.453$, $P_{\text{Retty}} = 0.610$, $P_{\text{Timmins}} = 0.395$).

ENVIRONMENTAL PREDICTORS OF COMMUNITY DISSIMILARITY

Neither slope nor aspect was a significant predictor of species distribution on Timmins, the youngest mine pile ($R^2_{\text{slope}} < 0.01$, $P_{\text{slope}} = 0.824$; $R^2_{\text{aspect}} < 0.01$, $P_{\text{aspect}} = 0.962$; Fig. 3). In contrast, both slope and aspect were strongly significant for Retty, the mine pile of intermediate age ($R^2_{\text{slope}} = 0.147$, $P_{\text{slope}} = 0.001$; $R^2_{\text{aspect}} = 0.129$, $P_{\text{aspect}} = 0.002$; Fig. 3), and marginally significant but with lower explanatory power for Gagnon, the oldest mine ($R^2_{\text{slope}} = 0.091$, $P_{\text{slope}} = 0.074$; $R^2_{\text{aspect}} = 0.100$, $P_{\text{aspect}} = 0.062$; Fig. 3). The ordinations showed that *Chamerion angustifolium* (L.) Holub was found more often on shallow slopes, or on the top of mines, while the presence of *Salix* and *Empetrum nigrum* L. increased as slope increased. Species on steeper slopes were also found to be on south-facing slopes, which are generally exposed to greater insolation throughout the year. Conversely, species on shallow slopes or flat surfaces were more often found in a northward orientation. On Retty, the presence of *Poa* L. increased as slope decreased, while *Equisetum sylvaticum* L. was more common on steeper slopes. *A. viridis*, *Solidago macrophylla*, *C. angustifolium*, *Vaccinium caespitosum* Michx. and *Dryas integrifolia* Vahl were found on moderate slopes (Table S4 for species numbers corresponding to Fig. 3).

Discussion

We showed that even after 40 years of abandonment, mine sites in the Canadian subarctic remain species poor and ecologically distinct relative to the natural vegetation.

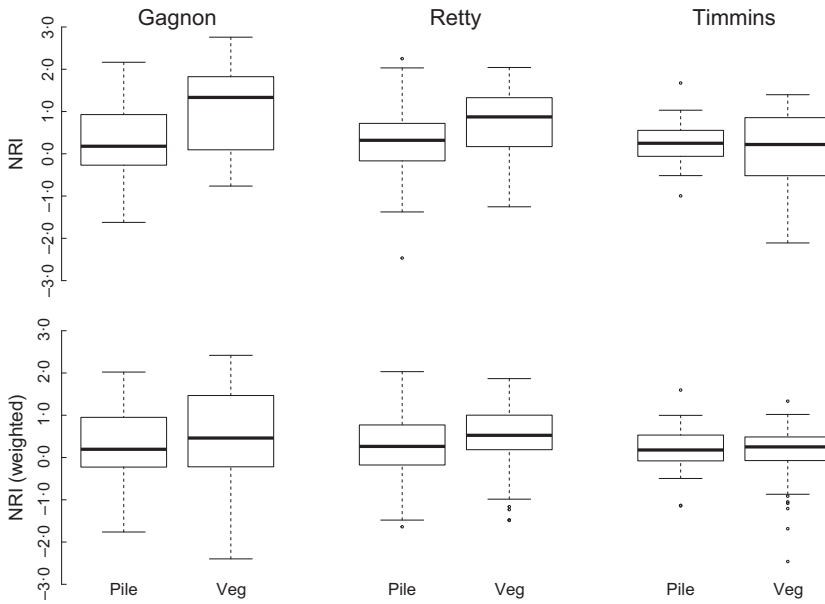


Figure 2. A comparison of standardized effect sizes of net-relatedness index (NRI), both non-weighted and weighted for abundances, between species communities in mine pile plots (Pile) and those in adjacent vegetation plots (Veg). Positive values indicate clustering and negative values indicate overdispersion.

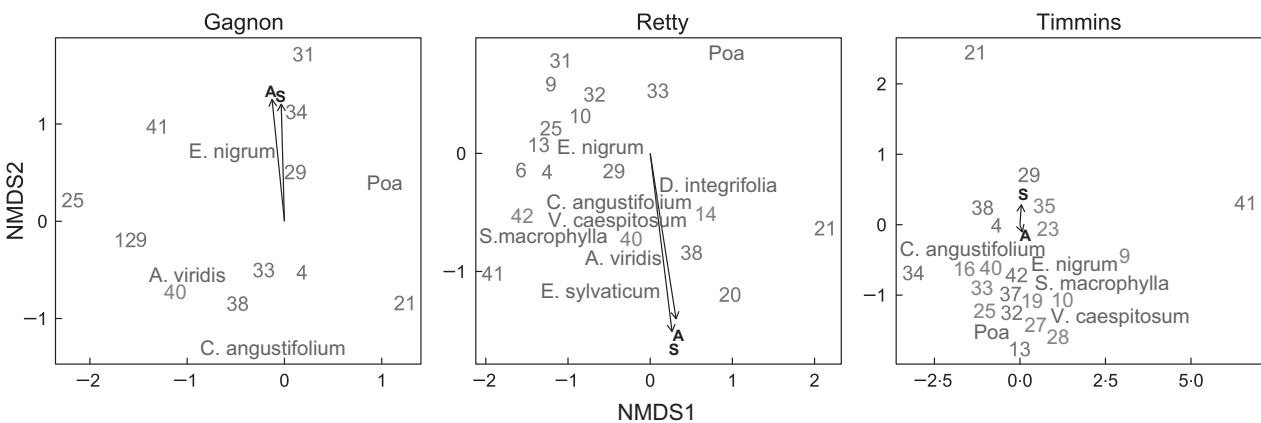


Figure 3. Non-metric multidimensional scaling (NMDS) showing trends in the spatial distribution of species along slope (S) and aspect (A) within mine piles. Arrow lengths denote prediction strength. Numbers correspond to individual species indicated in Table S4. Non-metric multidimensional scaling stress values, a measure of how well data are represented in two-dimensional space, were <0.15 for all mines (NMDS; $G_{stress} = 0.113$, $R_{stress} = 0.148$, $T_{stress} = 0.091$).

Our evaluation of a chronosequence of abandoned mine sites revealed no obvious trend for increasing SR or PD with time since abandonment, suggesting that species are not accumulating as succession proceeds. Phylogenetic diversity peaked at Retty, the site of intermediate age, although this can be attributed to the greater diversity of species in the local pool. Our results revealed strong differences between mine piles and the surrounding vegetation and, unsurprisingly, showed that piles have much reduced SR and PD. However, we found little evidence to suggest that species on mine sites were environmentally filtered, as plant community structure on mines did not differ from null expectations. Further, the phylogenetic turnover between sites indicates that they were not sampling the same phylogenetic subset of plant lineages, as might be expected if conditions on the mines selected for particular species or clades. Instead, we found that the

phylogenetic similarity between mines was no greater than we would expect given random species communities of equivalent richness.

PHYLOGENETIC PATTERNS AT THE PLOT LEVEL

Given that each mine community is, by definition, a subset of both the local and regional species pools and that previous studies on succession have shown evidence of early recruitment of closely related species, likely due to environmental filtering of traits suited for early colonization (Letcher 2010; Mo *et al.* 2013; Purschke *et al.* 2013), it might be expected that the mine communities would be phylogenetically clustered, at least initially. Indeed, early colonizing species, such as *B. glandulosa*, *C. angustifolium* and *Larix laricina* (Du Roi) K. Koch, represent species with traits conveying good dispersal capabilities and

tolerance to unstable environments (e.g. low shade tolerance, propagation through branch layering and vegetative reproduction, and the ability to form mycorrhizal associations; Hermanutz, Innes & Weis 1989; Broderick 1990; Uchytíl 1991; Cripps & Eddington 2005). However, at the plot level, we found that the phylogenetic structure of vegetation on each mine was no more clustered than expected by chance, irrespective of the species pool considered. Further, plots on Gagnon and Retty were significantly less clustered than plots in the surrounding vegetation and thus do not provide evidence for species filtering. In addition, we did not detect significant phylogenetic turnover between plots within mine sites, indicating that the plant communities on each site were also relatively unstructured, although this might in part reflect the low SR of plots, limiting our statistical power to detect compositional differences.

Despite the lack of strong phylogenetic structuring, our data provides evidence that species on the older mines (Gagnon and Retty) are sorting by slope and aspect. At these sites, it is possible that there has been sufficient time for the establishment of species better adapted to local conditions, which have competitively displaced less well adapted, but closely related species, explaining the decrease in phylogenetic clustering noted above. In contrast to Retty and Gagnon, species established on Timmins (the most recently abandoned mine) do not show any evidence of spatial partitioning. We suggest that the weaker phylogenetic and spatial structure of vegetation in plots on this younger site might indicate either that the traits associated with the early establishment of recolonizing species are not phylogenetically structured, or simply that the species establishing on the mines are a random subset of the surrounding vegetation. As species begin to filter into their optimal niches over time, they may become dominant locally and out-compete more poorly adapted lineages.

It is perhaps surprising that we did not detect significant clustering or overdispersion within individual plots. This pattern runs counter to our initial predictions, although it is possible that the low SR of these plots limits its statistical power. One explanation is strong environmental filtering at the regional scale. Schefferville's latitude places it in the discontinuous permafrost zone, thereby imposing heterogeneity in soil thaw on the region and potentially selecting for species with adaptations to local conditions – clustering of species within the adjacent vegetation plots provides support for this hypothesis. Alternatively, slow growth rates in the subarctic may mean that ecological processes have not yet had time to leave a strong imprint on community structure in our data. By necessity, our study was limited due to the challenges in locating and working on suitable mine sites in the region. However, previous work based on patterns of natural succession in Labrador (Simon & Schwab 2005) suggests that the time-scale we considered should have been adequate to detect early to mid-succession changes.

SPECIES POOLS

We found evidence that species composition on mines was limited by the local species pool. For example, although *A. viridis* is considered a pioneer species in succession, it became highly abundant on Gagnon and Retty, perhaps due to its seed viability in deficient soils and vegetative growth (Oliver, Adams & Zasoski 1985; Haeussler & Coates 1986). As a nitrogen fixer, *A. viridis* is recognized as a valuable species for restoration projects (Plass 1977; Heilman & Ekuan 1982; Schlesinger & Williams 1984), accelerating rates of succession by facilitating the growth of other dominant plants (Densmore 2005). This species was not present on Timmins, which may be attributed to its absence from the surrounding vegetation. That *A. viridis* can be dominant at two of our sites, but is almost entirely absent at the third emphasizes the importance of accounting for the local species pool in studies of natural succession. Thus, we emphasize that it is important for both researchers and environmental managers to interpret their results in the context of the surrounding species pool.

Patterns in diversity across successional stages are well studied, but rarely consider the influence of local species pools. This omission is surprising considering the importance of dispersal and continued seeding for the establishment of species in these disturbed environments. Species pools defined at different scales may vary in richness, ecology and evolutionary history and thus provide different null expectations. For example, we observed that Retty, the mine of intermediate age, had both the highest SR and PD among the three mines. However, by including the surrounding species pool in the analyses, we were able to show that the higher richness on Retty was expected given the richness of the local pool. Species pool influences have long been recognized as important in restoration ecology (Zobel, Maarel & Dupré 1998), and recent advances have provided a more robust framework for disentangling ecological processes from species pool influences (e.g. Lessard *et al.* 2012). Our study illustrates the need to better integrate these advances within the restoration field.

MANAGEMENT IMPLICATIONS

Although our study of subarctic mine succession did not identify particular key clades relevant to the successional stage of each mine, we show that phylogenetic approaches have the potential to improve restoration practices and our general understanding of succession.

In the direct management of sites for restoration using planting or seeding, a phylogenetic approach can inform the choice and order of species introduction. If the established species have a clear phylogenetic pattern, managers might focus their efforts on clades that establish more frequently and that are positively associated with other species. An understanding that phylogenetic relatedness

between close relatives of known successful colonizing species, such as *A. viridis*, may indicate shared traits or stress resistance and could be a helpful concept for managers in choosing seed mixes. Additionally, clade-level comparisons become particularly useful for applying knowledge from one restoration project to another. The closest naturally occurring relative of successful early colonizers in one region could be used in comparable restoration projects across Canada or elsewhere where that species is absent but close relatives are present. For example, close relatives of *A. viridis* might be good candidates for restoration in areas where knowledge of the local plant community is limited.

In the absence of any clear phylogenetic pattern in species establishment, surveying the local and regional species pools can help to guide efforts towards restoring natural community structure. Local sampling also ensures the adaptation of ecotypes to the particular site environment. However, more regional sampling may also help ensure that a site's progression is not hindered due to the absence of species in the local pool. In our analysis, we showed that the establishment of species depended on local availability, and thus species selection and order would vary depending on the site examined. Additionally, site comparisons across regions may allow for more targeted community-wide restoration efforts. In our study, mine communities became increasingly overdispersed over time. We therefore suggest that the choice of seed mixes should mimic community patterns appropriate to the relevant successional stage. In our system, phylogenetically diverse seed mixes may be most appropriate given the community structure found on the mines. However, if mining activity was more recent, seed mixes which mimic facilitation might be preferred (Verdú *et al.* 2009).

Phylogenetics is more often thought of as the preserve of researchers; however, we suggest that managers will benefit from the inclusion of phylogenetic concepts in restoration practices. User-friendly software, such as phylomatic (Webb & Donoghue 2005) and phyloGenerator (Pearse & Purvis 2013), provides tools for the construction of large phylogenies using available data on taxonomy. These resulting phylogenies are openly available and could be better integrated along with phylogenetics concepts in restoration science through increased collaboration between researchers and managers.

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Data accessibility

Phylogenetic data: TreeBASE Study accession no. S17810

Species community data: DRYAD entry doi:10.5061/dryad.qt30h (Shooner, Chisholm & Davies 2015)

Species descriptions and sequence information: uploaded as online Supporting Information.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Genetic sequence information and accession numbers.

Appendix S2. Sensitivity analyses for phylogenetic uncertainty.

Figure S1. Rarefaction analysis of sampling effort.

Table S1. Phylogenetic beta-diversity between mines.

Table S2. *t*-Test comparing mine and surrounding vegetation NRI values.

Table S3. TukeyHSD test between the mines and surrounding vegetation.

Table S4. Species names and corresponding numbers from Fig. 3.