Master's Thesis

Diversify or specialize: Disturbances influence trait evolution in *Pinus*

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Front page: Forest of *Pinus taeda*, northern Florida, 1/2013

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Introduction to the Master's thesis

The aim of my master's thesis was to assess trait and niche evolution in pines within a phylogenetic comparative framework. I was particularly interested in studying the role of trait evolution shaping diversification.

Since tracing the evolution of traits only makes sense if the observed trait values correlate with the phylogenetic structure of the analyzed species I first worked out the basics acquired for comparative analyses in pines. Chapter 1 therefore deals with the construction of a pine phylogeny and assessing the degree of phylogenetic signal of various traits. Recently, there have been great advances in sequencing plastome genomes in pines, which I could make use of for inferring a phylogeny including all recognized pine species. Additionally, a wealth of information on pine traits is now available due to a tremendous amount of studies that focused on numerous features of pines ecology, biogeography, evolution, systematics or taxonomy. I compiled a single trait databases from various sources and publications and I analyzed their correlation with the phylogeny.

I was intrigued by the manifold evolutionary adaptations of pine species' life history characteristics to different fire regimes and therefore continued to focus on fire response traits. Chapter 2 presents my analyses on the impact of fire regimes on trait evolution and diversification in pines and provides fascinating insights into niche specialization and how these affect diversification.

Given the comprehensive data set compiled in my thesis, including numerous trait states, detailed distribution maps combined with the underlying niche parameters, and a comparably well-resolved and complete phylogeny, various comparative hypotheses in ecology and evolution could further be tested. The data set developed in this master's thesis can therefore also serve as a basis for teaching as well as for demonstration studies.

1 Strong phylogenetic signal in pine traits

1.1 Abstract

Evolutionary processes shape the currently observed, extant species distribution of pines, and their underlying niche and trait characteristics. Phylogenetic information is instrumental for analyzing the macroecological patterns, and more specifically, for studying the role of trait and niche evolution in *Pines* to better understand the emergence of these macroecological patterns. Several studies have analyzed trait evolution of single sections within the pine phylogeny, yet no study has conducted an extensive approach including all recognized pine species. Here, I built a phylogeny consisting of all known pine species based on eight plastome genes and compiled a data set consisting of different morphological, physiological trait and niche variables to test the degree to which each trait correlates with phylogeny. My results indicate that a comparatively well-resolved phylogeny can be inferred from using single plastome genes and presents a good basis for further phylogenetic comparative methods. Additionally, my analysis also point to the non-independency of observed trait values and niche variables due to shared evolutionary history. I found high phylogenetic signal for the majority of analyzed traits. Thus, I discuss the importance to implement phylogenetic information and phylogenetic comparative methods to assess hypotheses in macroecological studies in pines.

1.2 Introduction

There is clear evidence that the earth's climate will continue to warm over the next century (IPCC, 2007) and these environmental changes will have drastic effects on the distribution and diversity of contemporary organisms (Brown, 1995). There is a need to understand the general principles and the underlying natural processes that shape these patterns in order to make predictions of these effects on the conservation of biodiversity and on future macroecological patterns (Hernandez *et al*., 2013). Therefore, macroecological studies examine relationships between species and their environment across spatial gradients in order to explain statistical patterns of abundance, distribution and diversity (Brown, 1995). Such macroecological studies converge data of different disciplines (ecology, systematics, evolutionary biology, paleobiology and biogeography) to scope for generalizations, not only for large spatial scales but also for large time scales (Brown, 1995). But one has to be aware that macroecological patterns are not independent of the evolution of lineages involved in generating these patterns (Hernandez *et al*., 2013). Therefore, the insertion of evolutionary history into macroecological studies is essential, not only for inferring large time scales but also for considering the dependency of trait states (resulting from the evolutionarily relatedness of species). Phylogenies track the characteristics of different evolutionary processes that shape the trait distribution on contemporary species (Pagel, 1999). Hence, combining phylogenies with trait information (which is "comparative biology") serves to understand the evolutionary past and to learn how present patterns have emerged

(Pagel, 1999). The methods of analyzing trait or niche relationships over phylogenies are referred to as "phylogenetic comparative methods", often simply termed "comparative methods". Furthermore, the inclusion of phylogenies in macroecological studies is increasingly feasible due to the newly emerging and advanced methods in genetic sequencing and the easy access of gen sequences, which are stored in GenBank (Benson *et al.*, 2007).

Since species and their corresponding traits are not independent due to their shared common ancestry, related species tend to resemble each other more than they would resemble if drawn at random from a phylogenetic tree. This trait similarity among related species is called "phylogenetic signal" (Blomberg & Garland, 2002). An important and basic step in comparative methods is to measure the phylogenetic signal of the traits under survey, because we only gain insight into trait evolution if these traits show an association with the phylogeny (Nunn, 2011). If, however, there are no phylogenetic signals in traits, it might be appropriate to examine variation among these traits without controlling for phylogeny (Nunn, 2011). For this reason it is a key step to test for phylogenetic signal prior to studies of character evolution (Thomson *et al.*, 2013). Further, if traits reveal high phylogenetic signal, it is possible to predict trait values of a species that lacks trait measurements simply based on the knowledge of the species' position on the tree. Additionally, we can trace back the evolutionary history of a trait that has phylogenetic signal through ancestral state reconstruction (Nunn, 2011).

The genus *Pinus* is an excellent study organism to address macroecological and evolutionary questions, since their evolutionary history ranges over 150 My, because *Pinus* and related genera are rich in fossil records, and because pines have successfully adapted to almost every forest habitat on the Northern Hemisphere (Klymiuk & Stockey, 2012; Parks, 2012). Furthermore, the distribution ranges of all species are mapped and available, the genus is rich in highly varying traits regarding e.g. seed, cone, needle or bark characteristics, and all species have many gene sequences deposited in GenBank (Benson *et al.*, 2007). Pines have diversified into two major subgenera by the end of the Mesozoic: into *Pinus* subgenus *Strobus* (with one fibrovascular bundle per needle) and *Pinus* subgenus *Pinus* (with two fibrovascular bundles per needle) (Richardson, 2000). Basically, these two subgenera followed two different evolutionary strategies: (1) species of the subgenus *Strobus* mostly have adapted to a range of physiologically stressful sites that are e.g. low in nutrients or water availability, or are very cold; (2) species of the subgenus *Pinus* have often radiated into fire-prone environments (Keeley, 2012). The evolution of pines, the largest genus among all conifers, resulted in ca. 113 extant species (depending on taxonomic concept) that occupy very small to very large distribution ranges on dry to wet, warm to frozen, nutrition rich to extremely poor soils. In response to this wide range of different habitats, the genus has evolved many different trait states and adaptations. The underlying evolutionary pathway can be traced by analyzing the phylogeny of pines and their trait states. Unsurprisingly, there exists a range of studies conducted on the genus *Pinus* that give insight into their evolutionary history (Millar, 1998), morphology (Little & Critchfield, 1969), genetics (Gernandt *et al.*, 2005; Parks, 2012), life history (Grotkopp *et al*., 2002), or character evolution (He *et al*., 2012).These studies have compiled and used many different traits that are now available for further comparative analyses.

Critchfield and Little (1969) first studied the morphology of pines and came up with a phylogeny based on truly morphological characters. Later, Grotkopp *et al. (2004)* constructed composite estimates of a *Pinus* phylogeny based on supertree methods and presented a more comprehensive tree but still only an approximation of a pine phylogeny. After the revolution of genetics and the availability of DNA sequences, Gernandt *et al.* (2005) published the first genus-wide molecular taxonomy of *Pinus*. Their study was based on two chloroplast genes (*matK* and *rbcL*), including over 2800 aligned base pairs from 101 species. They were able to clarify most of the broad relationships within *Pinus*. They presented a well-supported and generally accepted taxonomic framework consisting of two subgenera (*Pinus* and *Strobus*), four sections (sections *Pinus* and *Trifoliae* in subgenus *Pinus,* sections *Parraya* and *Quinquefoliae* in subgenus *Strobus*, and 11 subsections (in section *Trifoliae:* subsection *Australes, Ponderosae* and *Contortae*; in section *Pinus*: subsection *Pinus and Pinaster*; in section *Quinquefoliae*: subsection *Strobus, Krempfianae and Gerardianae*; in section *Parraya*: subsection *Cembroides, Balfourianae* and *Nelsoniae*) (Gernandt *et al*., 2005). However, they failed in resolving the most species-rich clades at lower taxonomic levels and ended with numerous unresolved relationships. Through the use of next-generation sequencing, Parks (2012) was able to include nearly complete plastome sequences for almost all recognized pine-species. With these improvements he could not only present a phylogeny with support for the previous known framework (Wang *et al*., 1999; Gernandt *et al*., 2005; Eckert & Hall, 2006), but also with the most highly supported (and better resolved) topology to date for the worlds pine species (Parks, 2012). Nevertheless, both studies failed to include all known pine species (Gernandt's phylogeny included 101 spp, Park's phylogeny covered 107 spp), and the placement of a number of species into subclades had low posterior probability support (e.g. *P. latteri* or *P. merkusii*).

By now, only comparably few studies that use phylogenetic comparative methods have been conducted on pines despite their numerous advantages and excellent data availability. In this study, I present a phylogeny with improved fossil calibration and complete sampling for almost all recognized species, compared to previous studies (Gernandt *et al*., 2005; Parks, 2012). Specifically, I ask the following questions: (1) can a well-resolved and -supported phylogeny be built from a lower number of gene sequences as opposed to using the complete plastome genome; and (2) to what degree do pine traits and niche characteristics show phylogenetic signal due to their evolutionary history.

To answer these questions, I built a phylogeny based on the most resolving gene sequences as identified by Parks (2012), and I analyzed a wide range of traits for phylogenetic signal. Such an inference builds a pre-requisite for further studies of trait evolution in pines. From these results, I was able to deduce hypotheses regarding the evolution of traits in *Pinus*. There exists no such comprehensive analysis over the whole genus *Pinus* until now.

1.3 Material and Methods

1.3.1 Phylogenetic inference

I constructed a phylogeny consisting of 113 *Pinus* species and 10 outgroup species (*Picea sitchensis, Cathaya argyrophylla, Abies firma, Keteleeria davidiana, Larix occidentalis, Pseudotsuga menziesii, Nothotsuga longibracteata, Tsuga sieboldii, Cedrus deodara, Pseudolarix amabilis*). To infer the phylogeny I compiled eight available plastid gene regions (*matK, rbcL, trnV, ycf2, accD, rpl20, rpoB* and *rpoC1*) by downloading their DNA sequences from GenBank (Benson *et al*., 2007). I primarily used the sequences uploaded by Parks (2012) if they have been available and complemented them by adding sequences of other studies (supplementary material S1). With these sequences I ran an automated alignment using MAFFT (Katoh *et al*., 2002), manually checked it and removed ambiguously aligned nucleotides using Gblocks with default settings (Talavera & Castresana, 2007). I combined the single sequences into a matrix of 123 species (including the 10 outgroup species) and 5402 nucleotides. To derive the phylogeny through Bayesian inference in BEAST (Drummond & Rambaut, 2007), I first constructed the required input-file by using BEAUti (Drummond & Rambaut, 2007) and integrated a starting tree generated by MrBayes (Ronquist *et al*., 2012). I used jmodeltest2 (Guindon & Gascuel, 2003; Darriba *et al*., 2012) to statistically select the best-fit models of nucleotide substitution for each partition based on Akaike's information criterion (AIC). The phylogeny with branch lengths proportional to time was derived by fossil calibrations following Leslie *et* al. (2012): Fossil *Picea burtonii* (Klymiuk & Stockey, 2012) was set to a minimum age of 133 My representing the divergence of *Picea-Cathaya*. Fossil *Larix altoborealis* (Lepage & Basinger, 1991) was set to a minimum age of 41 My representing the *Larix-Pseudotsuga* divergence. Fossil *Tsuga swedaea* (Lepage, 2003) *was* set to a minimum age of 41 My representing the *Tsuga-Nothotsuga* divergence. Following Leslie *et* al. (2012) I used priors with a lognormal probability distribution where the minimum age was set by the age of the fossil constraint and 95% confidence intervals of the probability distribution extend 20 million years (my) earlier than this minimum age. I used these settings for all of these calibration nodes excluding the *Tsuga* divergence because their seed cones first occur in the Eocene, but there are reports of their distinctive pollen grains form the Late Cretaceous (Leslie *et al*., 2012). Therefore I extended here the confidence intervals of the prior age distribution to 100 my years to include Late Cretaceous *Tsuga*-like pollen grains (Leslie *et al*., 2012). Contrary to Leslie *et al*. (2012) I chose to include *Pinus hokkaidoensis* (Stockey & Ueda, 1986) to date the divergence of *Pinus* subsection *Strobus* and *Pinus* subsection *Pinus* despite the uncertainty regarding their phylogenetic placement discussed in Leslie *et. al* (2012). I set a minimum age of 83 My and a 95% confidence interval of the probability distribution of 2 My (Willyard *et al*., 2007; Leslie *et al*., 2012). I applied an uncorrelated molecular clock with a lognormal prior. I ran three analyses independently in BEAST for 700×10^6 generations each. I evaluated the MCMC diagnostics in Tracer (Drummond & Rambaut, 2007) and checked for convergence of the three runs and that all ESS parameter values exceeded 150. I removed the first 52'501 trees as the burn-in period and inferred a maximum credibility tree using TreeAnnotator (Drummond & Rambaut, 2007). For all further analyses with comparative methods, I randomly selected 100 independent trees with logCombiner (Drummond & Rambaut, 2007) and generated an R-object (R Development Core Team, 2013) with these 100 fully resolved dated trees, with and without the outgroup species.

1.3.2 Trait data

I assembled a trait dataset that is comprised of morphological-, physiological- and genomic characters (supplementary material S2), as well as range characteristics (supplementary material S3). States for these traits were collected primarily from the following literature: Critchfield and Little (1966), Wakamiya *et al.* (1993), Richardson (2000), Grotkopp *et al.* (2002), Businsky (2004), Earle (2007), Farjon (Farjon, 2008, 2010), Eckenwalder (2009), Proches *et al.* (2012), and Meier (2013). Additional literature was used to complement trait information of single species (see supplementary material S2). I added the climate data in the form of statistical descriptions (min, max, mean, median from the species' distribution ranges) of the 19 bioclim variables from the WorldClim database (Hijmans *et al.*, 2005) and in the form of four axes of a principal component analysis (PC1 - PC4) originating from the statistical summaries of these 19 bioclimatic variables (see supporting material S2). Table 1 summarizes the integer and continuous traits while table 2 lists the factorial traits of the database I have compiled from the literature.

The compilation of the various traits of *Pines* from published literature resulted in a database consisting of 53 traits (supplementary material S2). I categorized the traits into three different groups based on the completeness to cover all pine species (supplementary material S4). The first group (greenish, see S4) presents traits that are available for all species, the second group (orangey, S4) is available for most species except a few, and the third (blueish, S4) is available only for some species.

1.3.3 Phylogenetic signal

In order to address the question whether significant phylogenetic signal exists in my dataset, I calculated for each trait Pagel's lambda (Pagel, 1999) as a measure of phylogenetic signal. I chose this measure because it has been shown (Münkemüller *et al.*, 2012) to provide a better effect size measure than e.g. Blomberg's K (Blomberg *et al.*, 2003) or Moran's I (Gittleman & Kot, 1990). Additionally, I tested whether the calculated lambda value was significantly different from lambda equals zero (no phylogenetic signal). For the discrete traits I used the package geiger (Harmon *et al.*, 2008) and the "ARD" model (an all-rates-different model, where each rate is a unique parameter) and for the

Table 1: *Statistical summary of all numerical traits used in the analysis of phylogenetic signal. Type indicates whether the information is stored as continuous or integer data type. NAs indicates for how many species the trait information is missing. Unit indicates the measurement unit, where missing values (-) stand for unitless indices. The explanation of the abbreviated trait names is given in supplementary material S2.*

Trait	Type	Min.	Median	Mean	Max.	NAs	Unit
PC1	num	-9.71	0.37	0.00	4.84	0	
PC2	num	-6.32	0.44	0.00	2.60	0	
PC3	num	-3.03	0.09	0.00	3.85	0	
PC4	num	-2.60	0.14	0.00	2.40	0	
LAR	num	35.2	65.6	64.96	90.2	84	cm2/g
Cluster	int	1	3	3.478	5	0	-
SLA	num	60.6	101.8	99.23	132.3	84	cm2/g
Stomata	int	1	1	1.257	2	0	-
LeafPers	num	1.80	3	4.274	32.5	5	years
LeafDentate	num	0.0	0.5	0.6701	1.0	16	-
LeafLen	num	2.63	11	12.519	31.25	0	cm
LeafWid	num	0.06	0.12	0.121	0.3	0	cm
LMR	num	0.53	0.672	0.6527	0.787	84	g/g
LeafRigid	num	0.0	1.0	0.7216	1.0	16	-
ConeWid	num	1.5	5.0	5.675	17.5	0	cm
ConeLen	num	3.25	7.5	9.398	40.0	0	cm
DBH	num	15.0	110	125.3	365.0	0	cm
Height	num	500	3000	3365	8000.0	0	cm
Serotinous	int	0	0	0.2035	1	0	-
BarkClass	int	1	3	2.23	3	0	-
GrassStage	int	0	0	0.1171	1	2	-
BranchShedding	int	0	1	0.5258	1	16	-
Bark	num	0.6	3.024	3.039	7.62	59	cm
SeedLen	num	0.35	0.65	0.8277	2.5	0	cm
ResproutCapacity	int	0	0	0.1441	1	2	-
RGR	num	12.8	32.3	31.97	47.4	84	g/g/d
RGRmax	num	21.6	49.7	49.5	75.0	88	g/g/d
SeedWid	num	0.2	0.5	0.5442	1.2	30	cm
SeedMass	num	3.5	35.1	132.89	1278	33	cm
MastI	num	1.00	3.5	3.344	10.0	52	years
WingLen	num	0.0	1.55	1.363	3.125	0	cm
WingWid	num	0.0	0.6	0.5533	1.5	42	cm
BirdDisp	int	0	0	0.3274	1	0	-
WindDisp	int	0	1	0.7876	1	0	-
animalDisp	int	0	0	0.3363	1	0	-
RodentDisp	int	0	0	0.1062	1	0	-
RangeSize	num	1.0	81.0	275	6079	0	cm
Cvalue	num	20.0	24.02	25.04	31.76	95	-
GenomeSize	num	22.1	29.6	29.28	36.9	35	pg-
z.score	num	-18.0	1.5	0.5186	13.4	54	-
invasiveness	int	0	1	0.619	1	92	-
maxAge	num	80.0	500.0	816.2	5000.0	78	years
MinGenTime	num	3.0	10	12.46	40.0	50	years
minAgeSeed	num	1.0	2	1.706	3.0	62	years
NAR	num	0.36	0.56	0.55	0.76	84	g/cm2/d
Gravity	num	0.34	0.45	0.4402	0.57	84	12%MC
DriedWeight	num	25.0	34.0	33.54	44.0	85	kg/m3
Rupture	num	7800	11480	11362	16300	84	MPa
Hardness	num	380	660	645.5	1110	84	N
MeanSeedMass	num	3.6	31.0	136.2	960.0	84	-
Elastic	num	135000	1461000	1498966	2327000	84	GPa
Strength	num	4460	6030	6311	8470	84	MPa
Shrinkage	num	1.10	1.65	1.719	2.9	87	T/R

Table 2: *Statistical summary of all factorial traits used in the analysis of phylogenetic signal. The numbers indicate how many species belong to the respective trait factor.*

Fire Regime	
crown	21
crown surface	7
surface	41
no	41
unknown	2

Dispersal	
wind	89
animal	38
rodent	12
bird	37

Continent	
East America	15
West America	55
East Eurasien	33
West Eurasien	11

Hardiness Zone	
1	6
2	2
3	5
4	3
5	10
6	7
7	13
8	33
9	18
10	14
11	2

continuous traits I used the package phytools (Revell, 2012). I ran the analyses for each trait over all 100 phylogenies to allow for assessing the uncertainty originating from using a specific phylogeny.

1.4 Results

1.4.1 Phylogenetic inference

The inferred, dated phylogeny traced the origin of the genus *Pinus* to 143 My (133 - 162 My; 95% highest posterior probability) in the late Jurassic and early Cretaceous, with a crown age at 86 My (84 - 86 My) when the *Pinus* subgenera *Pinus* and *Strobus* diverged (Fig 1.) in the late Cretaceous. The diversification of subgenus *Pinus* ended in a higher number of extant species (71 spp) than the diversification of subgenus *Strobus* (42 spp). Both subgenera consist mostly of species formed during recent radiations (fewer than 50 My, mostly around the last 20 to 5 My). The phylogeny was highly supported within most of these deeper nodes by having posterior probabilities >0.90 (generally, more than 50% of the nodes show posterior probabilities >0.90). At the crown node of genus *Pinus* and the two outgroup species *Picea* and *Cathaya* there was a lower posterior probability value (0.58). The classification of *P. krempfii* into the section *Quinquefoliae* was highly supported (posterior probability of 1), but it remains unsure if this species is more closely related to *Gerardianae* or to *Strobus*. At lower taxonomic levels I obtained low posterior probabilities in most subsections and slight differences in the positioning for single species as compared to previous studies. Overall, the classification of species to subgenera, sections and subsections highly agreed with previously developed pine phylogenies.

1.4.1.1 subgenus Pinus

Within section *Trifoliae* the subsections *Australes* and *Ponderosae* were not well resolved. The crown node was highly supported, but the younger the nodes, the less supported they were. For example within subsection *Ponderosae*, the clade consisting of *P. torreyana, P. coulteri, P. sabiniana* and *P. jeffreyi* had a crown node that was highly supported by a posterior probability value of one. However, these morphologically very closely related species showed very low support values (0.1 - 0.3) at individual nodes.

In section *Pinus* most of the deeper nodes showed lower support than in section *Trifoliae,* and this was true for both subsections (*Pinus* and *Pinaster*). In my phylogeny, *P. latteri* and *P. merkusii* were clearly sister to the other species in subsection *Pinus*, a placement that was controversial in previous phylogenies.

1.4.1.2 subgenus Strobus

Within subgenus *Strobus*, I obtained both, well supported and insufficiently resolved groups. Subsection *Gerardianae* was clearly classified as a monophyletic group (posterior probability of 1), consisting of the species *P. bungeana, P. gerardiana* and *P. squamata*. *P. krempfii* also was placed in this subsection, although with less clear support (posterior probability of 0.72). Subsection *Strobus* was classified with high support (posterior probability of 1.0), but more than half of the species belonging to this group were not well resolved.

In the section *Parraya,* the subsection *Cembroides* was classified with strong support for monophyly, but most splits below the subsection level were not well supported except for the splits between few sister species. On the contrary the subsections *Balfourianae* and *Nelsoniae* consisting of the four species *P. aristata, P. balfouriana, P. longaeva* and *P. nelsonii* were all well resolved.

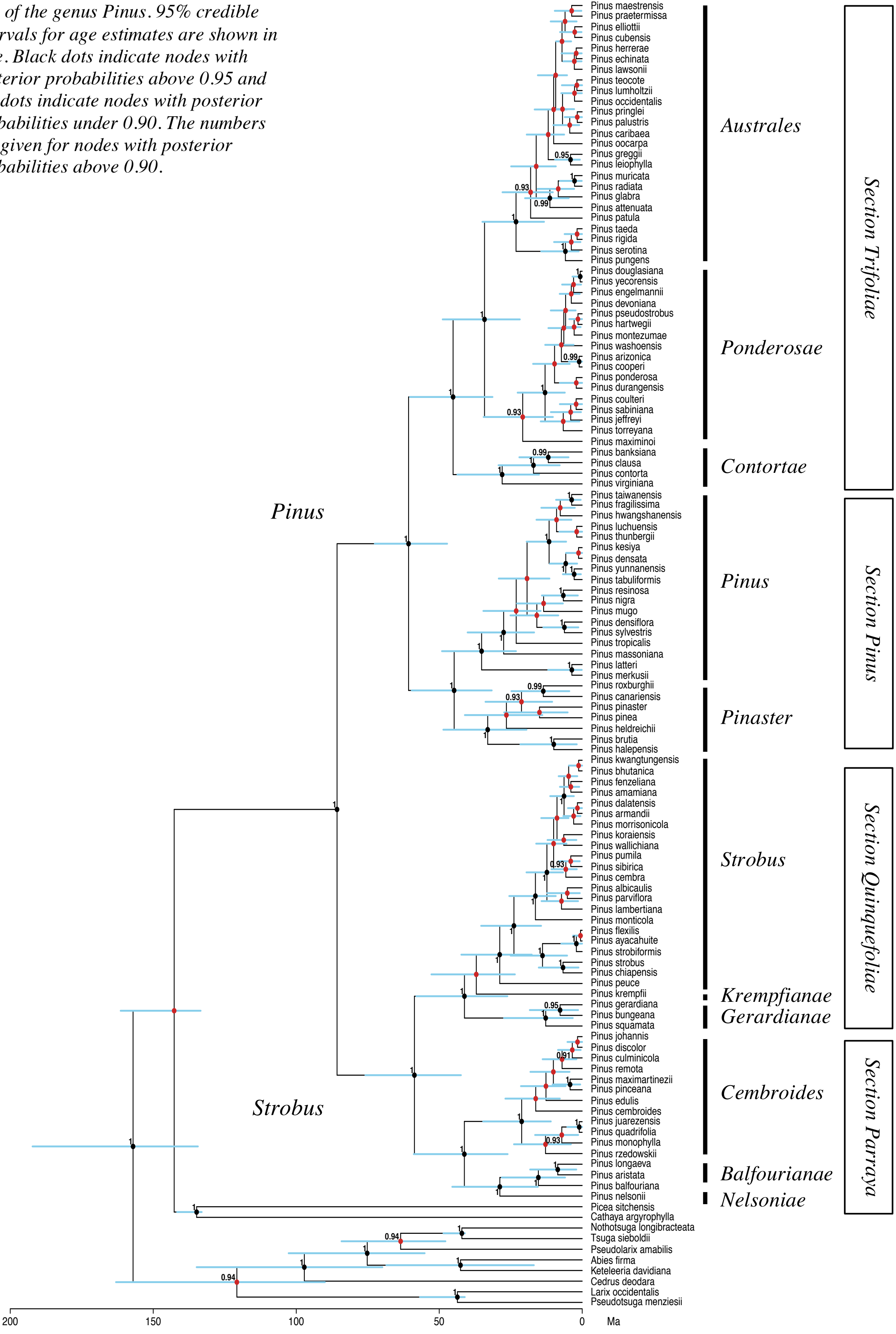
1.4.2 Phylogenetic signal

Figure 2 illustrates the phylogenetic signal of individual traits grouped by functional or morphological characters (climate preferences, leaf traits, cone morphology, tree size, fire adaptation, seed morphology, seed wing morphology, dispersal mode, range size, genome size, invasiveness, life history traits and wood specific traits). The traits are presented in three different colors based on the frequency of covering the 113 species of pines in my phylogeny (green if traits are available for all species, orange if traits are available for most species, and blue for traits I had available only for some species). Generally and consistently among all trait groups, I found strong phylogenetic signal and this signal was statistically significant for almost all traits (non-significant p-values for a trait are indicated by °°). I obtained remarkably high phylogenetic signal for genome size (*Genome*; $\lambda \approx 0.95$), stomata type (*Stoma*), cluster of needles (*Clust*), and seed length (*SLen*) (all: $\lambda > 0.8$). On the contrary, species' range size (*Range*), leaf rigidity (*LRig*), mast year interval (*MastI*), invasiveness (*Inva*), and net assimilation rate (*NAR*) showed no phylogenetic signal. The signal in fire resistance, tree height and wing length showed low phylogenetic, yet statistically significant signal.

Among the climate preferences I got high phylogenetic signal for hardiness zone and PC1-3 ($\lambda > 0.65$) and a lower signal for PC4 ($\lambda \approx 0.5$). Leaf characters also showed high λ-values for most traits, with all traits having $\lambda > 0.8$, except leaf width (*LWid*, $\lambda > 0.6$). In this group low (no) and non-significant values were only found for leaf rigidity (*LRig*, $\lambda \approx 0.0$) and leaf mass ratio (LMR, $\lambda \approx 0.3$). In addition to the first two groups, several other trait groups showed for the majority or for all traits high phylogenetic signal ($\lambda > 0.5$): cone morphology, seed morphology, dispersal mode, and wood specific traits. Several trait groups showed highly variable or moderately high λ-values: tree size, fire adaptation, seed wing morphology, invasiveness, and life history traits.

I found no difference in phylogenetic signals when comparing the different levels of completeness in trait availability among species. However, most of the wood specific traits showed high phylogenetic signal ($\lambda >\approx 0.5$), while the most life history traits revealed rather average signal strength ($\lambda \approx 0.5$). Surprisingly, the two traits representing invasiveness showed highly opposing phylogenetic signal (*Inva,* $\lambda < 0.1$; *Z,* $\lambda > 0.7$). Similarly, the two traits indicating bark thickness showed differing results, depending on being classified (*BarkC*, $\lambda > 0.5$) or tested as continuous variable (*Bark*, $\lambda < 0.3$). All but one (*Rodent*, $\lambda < 0.1$) of the dispersal mode characters revealed high phylogenetic signal ($\lambda \approx 0.7$).

Figure 1. *Maximum clade credibility tree of the genus Pinus. 95% credible intervals for age estimates are shown in blue. Black dots indicate nodes with posterior probabilities above 0.95 and red dots indicate nodes with posterior probabilities under 0.90. The numbers are given for nodes with posterior probabilities above 0.90.*



The phylogenetic signals of the 19 bioclimatic variables are summarized in supplementary material S5.

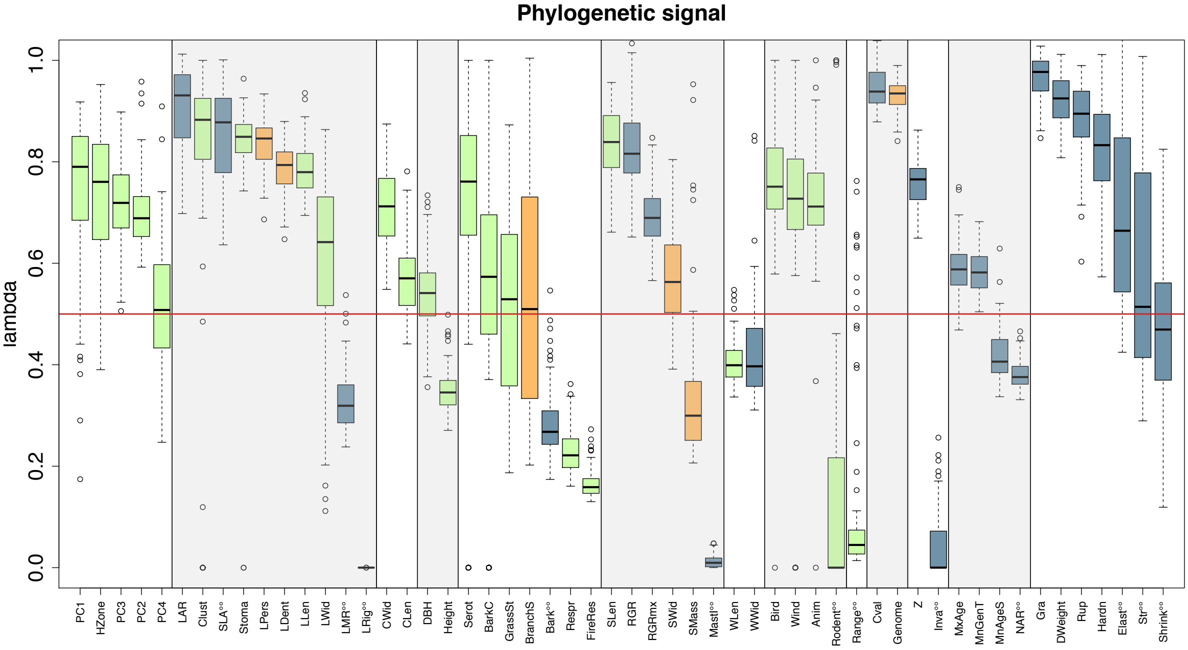


Figure 2. *Boxplots showing the phylogenetic signal strength (Pagel's lambda) for each trait from 100 independent phylogenies. The traits are grouped by morphology or physiology. Traits that are available for all species are given in green color, traits available for most species are given in orange color, and traits only available for few species are given in blue color. From left to right the following trait groups are mapped: (1) climate preferences (PC1-4: axes of principal component analysis, HZone: HardinessZone,), (2) leaf morphology (LAR: relative leaf production rate, Clust: Cluster of needles, SLA: specific leaf area, Stomat: Stomata type, LPers: leaf persistence, LDen: leaf dentate, LLen: leaf length, LWid. leaf length, LMR: leaf mass ratio, LRig: leaf rigid), (3) cone morphology (CWid: cone width, CLen: cone length), (4) tree size (DBH: diameter at breast height, Height: max. tree height), (5) fire adaptation (Serot: serotiny, BarkC: bark classified into 3 thickness groups, GrassSt: grass stage, BranchS: branchshedding, Bark: bark thickness, Respr: resprouting, FireRes: fire resistance), (6) seed morphology (SLen: seed length, RGR: seedling relative growth rate, RGRmax: max seedling relative growth rate, SWid: seed width, SMass: seed mass, MastI: mast year interval), (7) wing morphology (WLen: wing length, WWid: wing width), (8) dispersal mode (Bird: dispersal by birds, Wind: wind dispersal, Anim: dispersal by animals, Rodent: dispersal by rodents), (9) range size (Range: species range size), (10) genome size (Cval: c value, Genome: genome size), (11) invasiveness (Z: z-score measure of potential invasiveness, inva: species' invasiveness), (12) life history traits (MxAge: maximum age, MnGenT: minimum generation time, MnAgeS: minimum age at seed production, NAR: net assimilation rate), (13) wood specific traits (Gra: specific gravity, DWeight: average dried weight, Rup: modulus of rupture, Hardn: Janka hardness, Str: crushing strength, Shrink: shrinkage).*

1.5 Discussion

1.5.1 Phylogenetic inference

The presented maximum credibility tree for *Pinus* is highly similar to previously published phylogenies of the genus *Pinus* (Gernandt *et al*., 2005; He *et al*., 2012; Parks, 2012) and is completely congruent with the broad classification into the major clades at the level of subgenera (*Strobus, Pinus*), of sections (*Pinus, Trifoliae* in subgenus *Pinus*, and *Parraya* and *Quinquefoliae* in subgenus *Strobus*), and of subsections (in *Pinus*: *Australes, Ponderosa, Contortae, Pinus* and *Pinaster*, in *Strobus*:

Strobus, Krempfianae, Gerardianae and Cembroides). Therefore, the built phylogenies in my study provide an admissible basis for the further comparative methods.

Despite the low posterior probability in the split of the genus *Pinus* from the two genera *Picea* and *Cathaya,* the here presented phylogeny is congruent with the ones of He *et al*. (2012) and Leslie *et al*. (2012), but not with the phylogeny of Parks (2012). This difference most likely originates from using fossil calibration in all studies except in the study of Parks (2012), who did not date his phylogeny. In the selection of fossils, I followed most closely Leslie *et al*. (2012), who argued very carefully with regards to the use of the various fossils. The placement of the fossil *Picea burtonii*, which I have also used, is most likely responsible for the positioning of the genera *Picea* and *Cathaya* in close proximity to the genus *Pinus*.

In general, all earlier published phylogenies found similar uncertainties with regards to the positioning of lower taxonomic levels (Gernandt *et al*., 2005; He *et al*., 2012; Parks, 2012). The uncertainty regarding the true evolutionary relationships of these species groups could be due to simultaneous speciation event in time, rapid radiations, and conservative genome evolution, which often leads to insufficient morphological or molecular support (limited sequence variation) for their true branching pattern. On the other hand, it could also be due to conflicting evolutionary histories of different genes, resulting in ambiguous nodes (Nunn, 2011; Parks, 2012). Maybe adding the ycf1 gene, which Parks (2012) identified as a highly informative gene for the *Pinus* phylogeny, would have improved the resolution of some of these lower taxonomic levels. Yet, I chose not to include it, because many nucleotides differed strongly among species, which can lead to uncertainties or conflicts in the positioning of individual species. Further, caution is advised as the ycf1 gene might be a target of positive selection and reveal adaptive incidents rather than neutral genealogies (Parks, 2012). Since my phylogeny is comparable to Parks' (2012) topology and resolution, I believe that including this gene sequence would not much improve the pine phylogeny.

The topology of my phylogeny resembles more closely the one by Parks (2012) than the one by Gernandt *et al*. (2005). This is surprising on the one hand because I only used eight plastome genes, which is more similar in numbers to Gernandt *et al*.'s (2005) phylogeny (*matK* and *rbcL*) than to Parks (2012) who used the whole plastome genome. On the other hand, I used specifically genes recommended by Parks (2012) since he found them to resolve the *Pinus* phylogeny well. Also, my methodology to develop the phylogeny was more similar to the one used by Parks (MAFFT-based alignment of gene sequences, Bayesian inference) than by Gernandt *et al. (2005)* (manual alignment of gene sequences, most parsimonious tree). Additionally, the resolution of my phylogenies lying between Gerndants *et al.'s* (2005) and Parks' (2012) phylogeny is consistent with the statement of Parks (2012) saying that an extended sequence-matrix leads to increased proportion of highly resolved nodes.

1.5.1.1 subgenus Pinus

In section *Trifoliae*, the topology of my phylogeny closely resembles the one found by Parks (Parks, 2012). In subsection *Ponderosae* my results show a similar classification of single species as in Parks' (2012) phylogeny. Also, in subsection *Ponderosae*, the clade consisting of *P. torreyana, P. coulteri, P. sabiniana* and *P. jeffreyi* reveal the same low resolution as in the phylogeny of Parks (2012). Yet, both my and Parks' (2012) phylogenies show strong support to separate these four morphologically similar species as a monophyletic group. Similar to Gernandt *et al.* (2009), *P. yecorensis* is classified close to *P. douglasiana*, but not in a group together with *P. maximinoi*. In my results, *P. maximinoi* diverge earlier than Gernandt *et al.* (2009) have proposed. This latter species is not included in Parks' phylogeny. In my phylogeny, the subsection *Contortae* in section (*Trifoliae*) results in a highly supported monophyletic group similar to Parks (2012). However, in his phylogeny, the relationship of *P. banksiana* could not be clearly defined, while in my phylogeny this species is clearly placed sister to *P. clausa*.

In my results, *P. latteri* and *P. merkusii* are clearly sister to the other species group of subsection *Pinus,* which is contrary to Parks (2012), where these species are sister to subsection *Pinaster*. Parks (2012) discussed that most studies based on (cone) morphology place these species within subsection *Pinaster* (e.g. Frankis, 1993), while most molecular studies place these species as sister to subsection *Pinus*, albeit typically based on low to moderate support. Interestingly, Parks' (Parks, 2012) placement of these species as sister to subsection *Pinaster* had low support (posterior probability of 0.52), whereas the placement of these species as sister to subsection *Pinus* in my results shows a high support (posterior probability of 1).

1.5.1.2 subgenus Strobus

The resolution within section *Parraya* is similarly resolved in my phylogeny as in the one from Parks (2012). It is primarily the subsections *Balfourinae* and *Nelsoniae* that are well resolved whereas most of the species within subsection *Cembroides* are not well resolved. However, in the phylogeny of Gernandt *et al.* (2005) the split of *P. nelsonii* and subsection *Balfourianae* was not well supported, whereas in subsection *Cembroides* the strength of resolution was similarly low.

1.5.2 Phylogenetic signal

Generally, most of the traits show high phylogenetic signal in *Pinus,* which implies that more closely related species show more similar trait states than species randomly drawn from the tree, as expected under a Brownian motion model of evolution. Traits with a lambda value close to one, as for example genome size, are consistent with Brownian motion model of evolution (Nunn, 2011). Yet, the phylogenetic signal only assesses a pattern rather than an underlying evolutionary process by which closely related species tend to resemble each other (Nunn, 2011). Therefore, one can only make assumptions about the process leading to the observed pattern. For example genome size correlates with the phylogeny to a remarkably high degree. The underlying process of this pattern could be due to the different evolutionary pathway of genome size in the two subgenera. The assumed size of ancestral genome in the genus *Pinus* averages 32 pg and has decreased within the species of subgenus *Pinus,* whereas it remained stable or increased within subgenus *Strobus* (Grotkopp *et al*., 2004). Different studies detected a strong correlation between genome size and seed mass (Grotkopp *et al*., 2004; Beaulieu *et al*., 2007) or genome size and frost resistance (Grime *et al*., 1985; Macgillivray & Grime, 1995). In these analyses, the inclusion of phylogenetic relatedness was key to make correct interpretations of the statistical results. The same also holds for studies analyzing correlated evolution of stomata type, leaf length, seed length, cluster of needles and relative leaf reproduction rate in *Pines,* as these traits show all high phylogenetic signals.

Nevertheless, the analyses to test evolutionary relatedness in the different traits in pines reveal both, conservatism and lability. Traits with low or absent phylogenetic signal like SLA, range size, leaf rigidity or mast year interval for example, do not correlate with the phylogenetic structure and are therefore independent from one another and can be analyzed without accounting for the relationship of species. But caution must be taken by assuming no correlation between these traits and the phylogeny because the low phylogenetic signal could be due to strong stabilizing selection (Nunn, 2011).

1.6 Conclusion

I conclude that it is not necessary to assemble whole plastome genomes to infer reasonably well-resolved pine phylogenies for further phylogenetic comparative analyses in the genus *Pinus*. Because of recent divergence, rapid radiation, and hybridization, which might lead to incomplete lineage sorting, not all species may clearly be distinguished by phylogenetic reconstructions even when using whole plastome sequences. To account for the uncertainty of evolutionary relationships of some species groups, one has to conduct the analyses over numerous inferred phylogenies (obtained through Bayesian methods) instead of assuming and seek one single best phylogeny of pines.

Phylogenetic comparative methods are crucial for analyses of trait relationships in pines as most traits show medium to high phylogenetic signal.

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2 The role of fire in triggering diversification rates in pine species

2.1 Abstract

Plants have been exposed to fire throughout their whole evolutionary history and the role of fire in driving natural selection and therefore its effects on the evolution of adaptation strategies in fire-prone areas has been widely examined and confirmed. Plants have evolved a range of different strategies to successfully colonize fire-prone areas, which has resulted in different life histories. The role of the different strategies on plants' diversification rate has been assessed in several studies either at specific fire-prone sites or in global studies based on few species belonging to different taxonomic groups. However, the role of fire as a driver of diversification in plants stays controversial and remains to be elucidated. Therefore, I investigated in a globally and taxonomically comprehensive assessment using *Pinus* the impact of fire on diversification rates, and I compared the effect of the different plant functional strategies on diversification. I demonstrate that it is likely not only the change in life histories that influences diversification rates but rather the evolution of environmental specialization to tolerate fire regimes, the associated degree of pleiotropic investment costs and its effects on life histories. My results provide a basis for understanding the role of disturbances on species diversification rate linked to the degree of their environmental specialization and the associated costs.

2.2 Introduction

Wildfires frequently occur all over the globe and act as a major force in shaping ecosystems (Pausas & Keeley, 2009). The raise of fire as an important force on earth's ecosystems dates back to the late Devonian, from when the first charcoal records were found (Scott, 2000), or possibly even further back to the Silurian origin of land plants (Keeley *et al.*, 2011). During this long time interval, spanning over 400 Ma, changing oxygen levels in the atmosphere have influenced the fire intensity and frequency (Scott, 2000; He *et al.*, 2012). At the beginning (ca. 400 Ma before present), fires occurred at rather low intensity in the form of surface fires due to the low oxygen content of the atmosphere, burning primarily the smaller living plants, the litter and soil layers (Scott, 2000). However, during the Cretaceous (89 - 96 Ma BP), crown fires substituted these less severe fires by burning also the crowns of the living trees (Scott, 2000; He *et al.*, 2012). The intensity and frequency of these different fire severities (also named "fire regimes") do not only depend on the oxygen levels in the atmosphere but also on the climate (mostly precipitation and temperature) and fuel characteristics (Johnson, 2001).

There is clear evidence that ongoing climate change will increase fire activities in the future, in both intensity and frequency in many places on the globe (Marlon *et al.*, 2009). This likely has a strong impact on the earth's ecosystems, as fire plays an important role in shaping ecosystem patterns and processes (Bowman *et al.*, 2009). Fire disturbances are an integral part of many of the world's biomes and might be at least as important as climate in controlling the global biome distribution (Bond *et al.*, 2005). For example, fire reduces biomass, maintains open vegetation where climate would favor forests (Bond & Keeley, 2005; Bond & Scott, 2010) and preserves the formation and function of fire-prone communities (Bond & Keeley, 2005).

Fire disturbance also acts as an evolutionary pressure and its important role in driving natural selection was shown at different spatial and temporal scales (Pausas & Verdu, 2005; Gomez-Gonzalez *et al.*, 2011; Pausas & Schwilk, 2012; Budde *et al.*, 2013). Differences in fire regimes tend to select different dominant plant traits whereas similar fire regimes tend to select similar dominant plant traits (Bond & Keeley, 2005). Generally for trees and forests, one distinguishes between surface fire regimes and crown fire regimes, which act as different selective forces on tree's trait evolution (He *et al.*, 2012). It is important to mention here that plants in general are rather adapted to these fire regimes (including fire frequency, fire intensity and patterns of fuel consumption) than to fire per se (Agee, 1998; Keeley *et al.*, 2011). The evolution of a fire response trait (often considered as "key innovation") enables species to occupy a new ecological zone and to diversify in the absence of competing taxa, a process in which extinction or speciation rates might trigger diversification in a clade that has evolved such traits (Heard & Hauser, 1995). However, such single evolutionary novelties are never by themselves the single cause for influencing evolutionary rates as evolution and selective pressures always arise in a broader context (Hunter, 1998). In fact, multiple underlying mechanisms of such novel innovations can be causally connected to diversification (Heard & Hauser, 1995).

There are two widely recognized strategies of species fire responses, which both allow for persistence after fire on the population level but results in contrasting population dynamics (Agee, 1998; Verdu *et al.*, 2007; Segarra-Moragues & Ojeda, 2010). "Evaders" (also termed “reseeders”) store seeds in either soil or canopy and release them after fire disturbance, which ensures their persistence in stand-replacing sites through rapid post-fire recruitment (Agee, 1998; Richardson, 2000; Verdu & Pausas, 2007). The life expectancy of evader-species is short (Lamont & Wiens, 2003) caused by frequently returning fire intervals (Segarra-Moragues & Ojeda, 2010). Therefore, these species show early reproduction and release a huge amount of seeds (Verdu *et al.*, 2007), which leads to frequent and high natural selection (Segarra-Moragues & Ojeda, 2010). "Resisters" (also termed “resprouters”) persist in fire-disturbed area through protection of the meristem from heat damage or through resprouting after the disturbance (Richardson, 2000). Resister species gain a higher maximum age (Lamont & Wiens, 2003) and therefore their age at first reproduction is higher than that of evaders. The population turnover in evader-species is higher than in resisters, thus evader-species should undergo more molecular substitution rates per time than resisters and thus end in higher diversification rates (Barraclough & Savolainen, 2001; Verdu *et al.*, 2007; Smith & Donoghue, 2008; Segarra-Moragues & Ojeda, 2010). This correlation was assessed in different studies and resulted in different conclusions. It has been shown several times that fire triggers consistently diversification in reseeders

(Ojeda, 1998; Verdu & Pausas, 2007; Segarra-Moragues & Ojeda, 2010), or at least partially (Litsios et al., 2013). Yet, other studies also showed that fire had no influence on the diversification rate (Verdu *et al.*, 2007). Concisely, the influence of fire regimes on diversification rates still remains controversial.

The genus *Pinus* has evolved during the lower Cretaceous (~150 Ma) and has adapted to many different habitats over the whole Northern hemisphere (Richardson, 2000). Therefore, pines are linked to fire throughout their whole evolutionary history. Pines have diversified into two subgenera by the end of the Mesozoic, namely: subgenus *Strobus* (with one fibrovascular bundle per needle) and subgenus *Pinus* (with two fibrovascular bundles per needle) (Richardson, 2000). The diversification in these two subgenera was shaped by their different evolutionary strategies. The subgenus *Strobus* has adapted to abiotically stressful environments, whereas subgenus *Pinus* has diversified into fire prone environments (Keeley, 2012). The divergent evolutionary history of these two subgenera resulted in different numbers of extant species. Subgenus *Strobus* is comprised of 42 species whereas subgenus *Pinus* consists of 71 extant species.

He *et al.* (2012) described five widely recognized functional traits in pines that are defined as fire response traits, and which are under strong genetic control and are supposed to represent key innovations in the evolution of pines: (1) thick barks have evolved in association with low-intensity surface fires and have allowed species to survive the heat of surface fires (but in fact also to other forms of abiotic stress); (2) serotiny in pines is defined as the retention of mature cones that only open and release seeds with high temperatures generated by fire, which is an adaptation to severe crown fires; (3) branch shedding means that species shed their lower branches once their foliage has burnt off. By this it limits the ability of surface fires to climb into the canopy and is therefore typically linked to surface or low-intensity crown fire adaptation; (4) grass stage (delayed trunk development) is an adaptation to surface fires where the needles protect the apex against fire heat, representing also a (very) low-intensity surface fire adaptation; (5) resprouting capacity is an adaptation to sites of low productivity and comparably high fire frequency, and allows to rapidly regenerate pines after fire damages. The adapative value of these fire response traits are widely accepted and no longer considered as exaptations (adaptive traits that originated in response to some other environmental factor, and then were appropriated for their value in fire-prone landscapes) (Keeley *et al.*, 2011; Budde *et al.*, 2013; Dantas & Pausas, 2013; Hernandez-Serrano *et al.*, in press). To summarize, pines evolved to fire prone environments through either the evading-strategy (serotinous cones) or the resisting-strategy (thick bark, branch shedding, grass stage, resprouting).

Given the congruent spatial and temporal interaction of fire and pines, this genus is an ideal study system to assess the effect of fire response traits on diversification rates. In detail, I ask the following questions: (1) to what degree do fire response traits affect diversification rates (speciation, extinction or character state transition rates), (2) is there a difference in the diversification rate between resisters that show adaptation to low-intensity fires (thick bark, branch shedding, resprouting and grass stage) compared to evaders that show adaptation to high-intensity crown-fires (serotinous cones). No study has yet analyzed such a large tree, and representing the largest genus among gymnosperms for trait evolution effects on diversification rates. To test these questions, I developed a phylogenetic tree using GenBank sequences for eight plastid gene regions, compiled and updated the trait data set of He *et al* (2012), and conducted comparative analyses over the whole pine genus and separately over the subgenus *Pinus* that radiated into fire prone areas.

2.3 Material and Methods

2.3.1 Phylogenetic inference

First, I downloaded eight available plastid gene regions (*matK, rbcL, trnV, ycf2, accD, rpl20, rpoB, rpoC1*) from GenBank (Benson *et al*., 2007) for 113 *Pinus* species and 10 outgroup species (*Picea sitchensis, Cathaya argyrophylla, Abies firma, Keteleeria davidiana, Larix occidentalis, Pseudotsuga menziesii, Nothotsuga longibracteata, Tsuga sieboldii, Cedrus deodara, Pseudolarix amabilis* (see supplementray material S1 for accession numbers). I aligned these sequences by using MAFFT (Katoh *et al*., 2002) and eliminated ambiguous alignments through Gblocks (Talavera & Castresana, 2007) with default settings. I inferred the phylogenetic relationships of the species in a Bayesian framework implemented in BEAST (Drummond & Rambaut, 2007). I ran four Markov Chain Monte Carlo analyses independently for 70×10^7 generations, sampling phylogenies every 10^3 steps. I checked the log-files of each run for convergence in Tracer (Drummond & Rambaut, 2007) and ensured that the effective sample size (ESS) of each parameter exceeded the value of 150. I excluded the first 25% of the trees as burn-in and randomly selected 100 dated trees using logCombiner (Drummond & Rambaut, 2007). The time calibrated trees were calculated following chapter 1 by including fossil calibration. To my knowledge, I sampled all known pine species. Therefore, the fully resolved and rooted phylogenies are assumed to include all extant species.

2.3.2 Diversification rate

I individually used the same five traits as He *et* al. (2012) and therefore compiled the following binary states for all 113 pine species: bark thickness >15 mm (yes/no), serotinous cones (yes/no), grass stage (yes/no), resprouting capacity (yes/no), and branch shedding (yes/no). The distribution of the five traits over the whole genus revealed that serotinous cones, grass stage and resprouting was only developed in species belonging to subspecies *Pinus,* whereas bark thickness and branch shedding was also developed in the subgenus *Strobus*. Therefore, I decided to run the following analyses over the whole phylogeny and separately for the subgenus *Pinus,* but not for the subgenus *Strobus* due to the absence of fire adaptation in this clade.

In order to detect asymmetrical rates of speciation, extinction, or character state change of each of the trait states, I used the BiSSE (Binary State Speciation and Extinction) (Maddison *et al.*, 2007) approach as implemented in the R package diversitree (FitzJohn, 2012; R Development Core Team, 2013). This method simultaneously estimates based on likelihood method (ML) six parameters for each individual analysis, namely: (a) speciation rates (λ_0/ λ_1) for each trait state, (b) extinction rate (μ_0/μ_1) for each trait state, and (c) transition rates (q_{01}/q_{10}) between states. Due to the data structure I used for the ML parameter estimation the "nlminb" optimization method for all traits except for resprouting (where I used the default settings). To take into account phylogenetic uncertainty I ran the analyses within a Bayesian framework for each tree of the entire subset of 100 ultrametric trees. I conducted the BiSSE analyses through Markov chain Monte Carlo (MCMC) simulation for 500 iterations using exponential priors for the rates over the whole phylogeny and separately for the subgenera *Pinus*. I determined the net diversification rate of each trait state by subtracting the specific extinction rate from the corresponding speciation rate. Further, I pooled the posterior distributions of all analyses that have been repeated over the 100 phylogenies and calculated from these pooled posteriors the 95% confidence interval to examine for overlap. Additionally, I tested for significance between the mean values of each of these pooled posterior distributions with a two-sided, unpaired t-test.

2.4 Results

2.4.1 Phylogenetic inference

The inferred phylogenetic trees showed comparable classifications to previous published phylogenies of pines (Gernandt *et al.*, 2005; Parks, 2012). The topology of the phylogenies were generally highly supported with the majority of nodes having posterior probabilities higher than 0.90. The nodes with low posterior probabilities were mostly found within recent speciation events, while the deeper nodes were better supported.

2.4.2 Diversification rate

2.4.2.1 genus Pinus

The probability densities to observe the inferred phylogenies with the existing trait distribution given the estimated values for the speciation-, extinction-, and diversification rate are illustrated in figure 1. Generally, I found significant differences in the estimated mean values of the density distributions of diversification rates when the analyses were conducted over the whole genus. Species with thick bark (average p-value for all 100 selected trees $p<0.001$, for difference in mean between thick/thin bark), branch shedding ($p=0.002$) or grass stage ($p<0.001$), all representing adaptations to low surface fires, showed significantly higher diversification rates than species without these adaptations. The higher diversification rates could be traced to the significantly higher speciation rate in all three traits (bark: p=0.001, branch shedding: p=0.002, grass stage: p=0.008) and the comparatively smaller extinction rates (bark: p<0.001, branch shedding: p=0.138, grass stage: p<0.001), where branch shedding did not show significantly smaller rates. Contrarily, species with serotinous cones (p=0.008) or resprouting capacity (p=0.016) showed significantly lower diversification rates than species without these adaptations. The higher diversification rates resulted from the significantly lower speciation rates in both of these traits: serotiny (p=0.013) and resprouting (p=0.018). The extinction rate for species with serotinous cones was not significantly lower than for species without serotinous cones (p=0.07) whereas species with resprouting capacity had significantly higher extinction rates than species without resprouting capacity (p=0.001). However, despite partly showing clear differences between rates of different trait states and significant p-values of the means, none of these differences exceeded the 95% confidence intervals, which would indicate a clear evidence for difference in these rates (see Litsios *et al.*, 2013).

2.4.2.2 subgenus Pinus

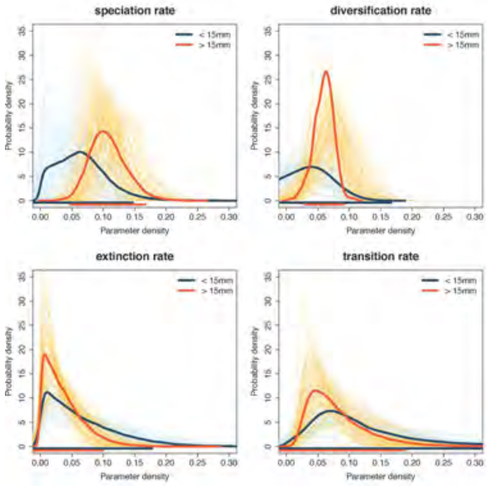
Within the subgenus *Pinus* I found the same pattern as in the genus but with a more pronounced difference in diversification rates between trait states (Fig. 1). Species with a thick bark (p<0.001), branch shedding (p<0.001) showed significantly, or for grass stage (p=0.073) insignificantly, higher diversification rates than species with no adaptations to low surface fires on two of the three traits. I could trace this back to significantly higher speciation rates for fire-adapted species (while extinction rates did not differ clearly). I found an opposing pattern in pines that had evolved serotiny, which is an adaptation to severe crown fires. Species with serotinous cones diversified at significantly lower rates (p<0.001) than species with no serotinous cones. This difference in diversification among serotiny states could be traced back to significantly higher speciation rates of species without serotinous cones (p<0.001), while no significant difference was found in the posterior densities of the extinction rate among species with or without serotinous cones (p=0.09). Species with resprouting capacity, which is an adaptation to high surface fire frequency, tended to show a similar pattern as species with serotinous cones. Species with resprouting ability diversified at significantly slower rates than species with no resprouting capacity (p=0.016).

The transition rates between adapted and non-adapted states differed only significantly for grass stage (p<0.001, resprouting (p=0.003), and to a lesser extent in bark thickness (p<0.001). The switch from species with grass stage to species without grass stage occurred at significantly higher rates than vice versa (p<0.001). A similar but weaker pattern was found for resprouting and bark thickness.

Again and similar to the analysis over the whole genus, despite the partly clear differences between rates of different trait states, none of these differences exceeded the 95% confidence intervals, which would indicate a clear evidence for difference in these rates (see Litsios *et al.*, 2013).

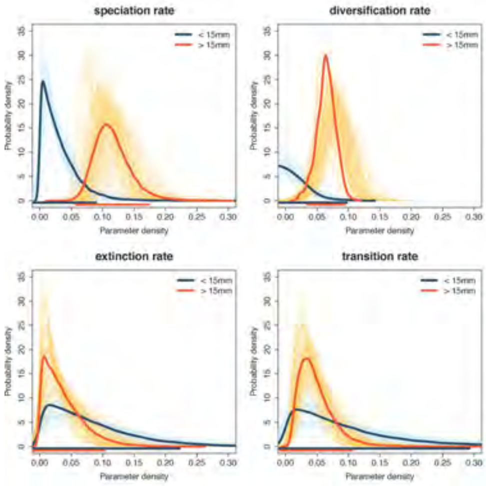
Bark thickness (>15mm) in genus *Pinus*

bark < 15mm: **37**/113
bark > 15mm: **76**/113



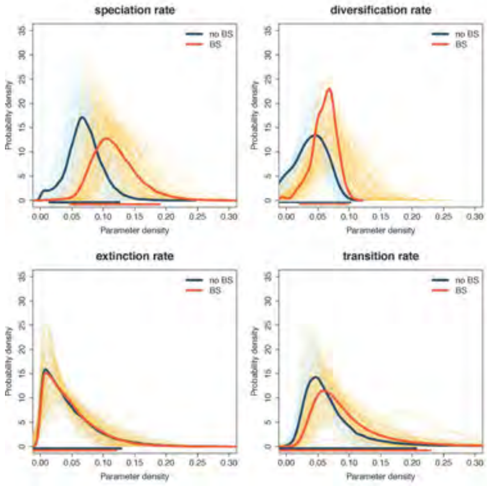
Bark thickness (>15mm) in genus *Pinus*

bark < 15mm: **13**/71
bark > 15mm: **58**/71



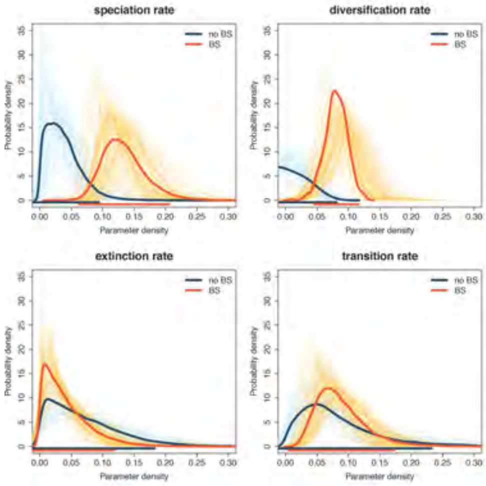
Branch shedding in genus *Pinus*

non branch shedding: **47**/113
branch shedding: : **51**/113



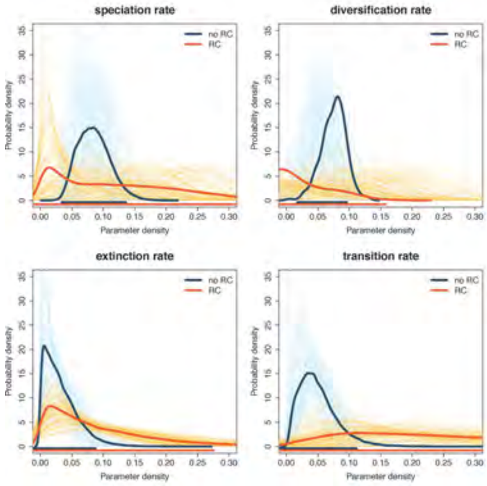
Branch shedding in subgenus *Pinus*

non branch shedding: **22**/71
branch shedding: **43**/71



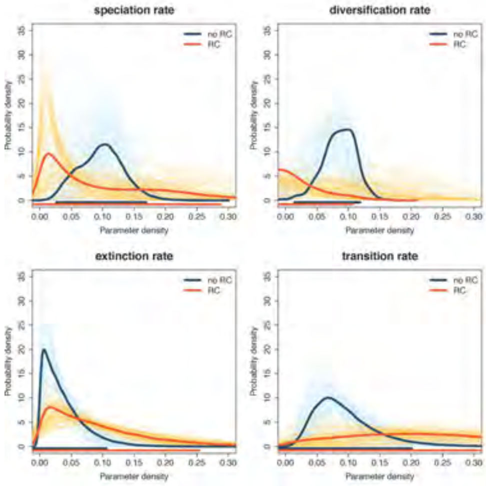
Resprouting in genus *Pinus*

non resprouting: **97**/71
resprouting: **16**/71



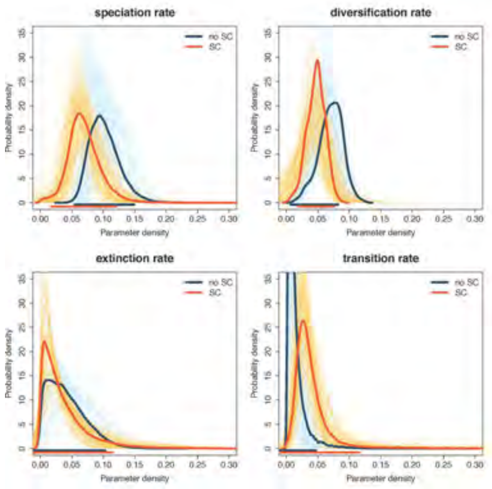
Resprouting in subgenus *Pinus*

non resprouting: **55**/71
resprouting: **16**/71



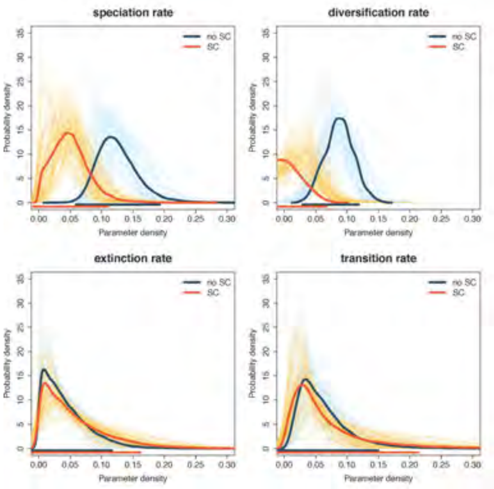
Serotinous cones in genus *Pinus*

non serotinous: **90**/113
serotinous: **23**/113



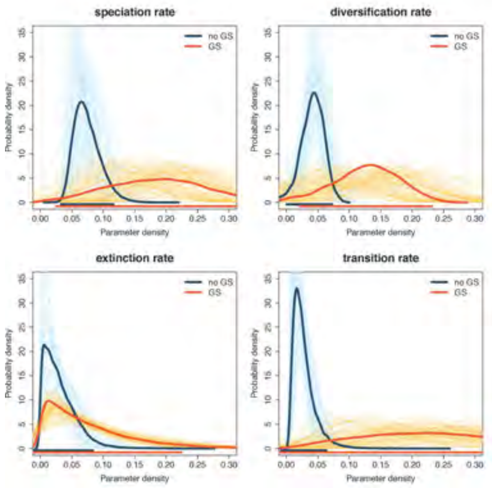
Serotinous cones in subgenus *Pinus*

non serotinous: **48**/71
serotinous: **23**/71



Grass stage in genus *Pinus*

no grass stage: **100**/113
grass stage: **13**/113



Grass stage in subgenus *Pinus*

no grass stage: **58**/71
grass stage: **13**/71

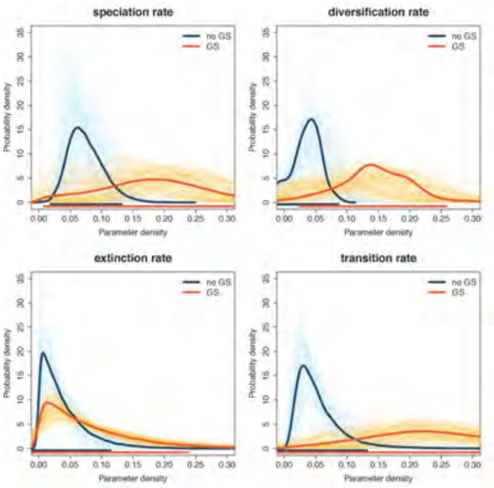


Figure 1: *Posterior probability distributions for speciation- diversification- extinction- and transition rates for each analyzed fire response trait, from top to bottom: bark thickness, branch shedding, resprouting, serotinous cones and grass stage. Left panels show the posterior probability distribution for analyzes conducted over the whole genus Pinus and right panels show it for the subgenus Pinus. The numbers indicate the percentage of species representing the specific trait states. Blue colors indicate the non-adapted trait state (e.g. thin bark), while orange colors indicate the trait adaptation (e.g. thick bark). The thick lines represent the mean over all 100 trees, while the thin lines represent the probability distribution of each individual tree. The blue and orange bars below the probability distribution indicate the 95% credibility interval of the two respective distributions.*

2.5 Discussion

2.5.1 Diversification rate in response to fire adaptations

In my study, I find clear differences in diversification rates in relation to the evolution of fire response traits, primarily in subgenus *Pinus,* and to a lesser extent in the analyses over the whole genus. This suggests that either these examined traits, other traits or characters evolved in parallel, or environmental gradients correlated to these traits have directly or indirectly influenced diversification rates, mainly through increased speciation rates. Previous studies that have analyzed the influence of evolving "evader" versus "resister" traits on diversification reveal conflicting results. In the genus *Erica* species that have evolved as evaders (seeders) show higher within-population genetic diversity and higher among-population differentiation, which is hypothesized to be the basis that leads to a higher speciation and diversification rate (Segarra-Moragues & Ojeda, 2010). Contrary, Verdu *et al.* (2007) show by comparisons of 45 phylogenetically paired congeneric taxa that the rate of molecular mutations within evaders is not higher than within resprouters, which is considered a resister trait. They conclude that seeders (evaders) do not diversify at higher rates than resprouters (resisters). Further, Litsios *et al. (2013)* demonstrate the importance of environmental heterogeneity for increased diversification.

In the subgenus *Pinus*, which has mainly adapted to a range of fire regimes (Keeley, 2012), I find phylogenetic evidences for higher diversification rates associated with traits indicating resister strategies (bark thickness, grass stage, branch shedding). This result supports the hypothesis that key innovations can trigger diversification rates (Heard & Hauser, 1995; Hunter, 1998). But interestingly, both serotiny and resprouting, other key innovations to adapt to fire-prone systems have an inverse effect on the diversification rate. Species with serotinous cones or resprouting capacity diversified at slightly lower rates than non-serotinous or non-resprouting species. Therefore, the general assumption of single novelties triggering diversification rate is not confirmed in the analysis of fire response traits in pines. Yet, key innovations do not directly influence evolutionary rates. Rather the underlying evolutionary mechanisms and demographic processes affect species diversification and one has to consider the broader context influencing evolutionary processes. Several previous studies show that evaders diversify at higher rates than resisters due to the context of divergent life history. Surprisingly, my results show ambiguous results, with three out of four resister traits having higher, and only one having slightly lower diversification rates than species without this adaptation. Furthermore, the only evader trait developed in pines (cone serotiny) shows lower diversification rates than species without this trait, which is again contrary to previously found results mainly in angiosperms. The hypothesis of the correlation between life history and diversification does not seem to hold for pines.

An explanation for the higher diversification rate of resisters than evaders could be that evaders represent a more specialized form of adaptation than the evolution of traits in response to low surface fires. Resister populations persist recurring disturbances, therefore these species are forced to inhabit environments exhibiting a larger range of partly highly variable conditions (Litsios *et al.*, 2013), can rapidly adapt, and are less at risk to undergo extinction. On the contrary, evaders release after each fire disturbance, a huge amount of seeds from which only those germinate that are most suitable for the offered niche space. As a consequence, evaders may more likely be forced to specialize to particular environmental conditions and may thus be more prone to extinction if the environment undergoes huge changes, whereas resisters may have evolved more as generalists that can better survive considerable environmental changes (Litsios *et al.*, 2013; Ozinga *et al.*, 2013). The higher diversification rate of resisters would then be due to their lower extinction rate following environmental change, which is not the case in my study. The evolutionary extinction rates found in my study are not significantly different among trait types. Therefore, my results – despite following the general trend in overall diversification rates – are not in agreement with this hypothesis.

When comparing the results for the genus with those from the subgenus, we see a very similar, but statistically less significant pattern for each fire response trait. This might be due to the fact, that the fire response traits primarily were developed in the subgenus *Pinus*. The subgenus *Strobus* radiated rather into abiotic stressful sites, an effect which I did not analyze here. Therefore, the highest contrasts for developing these key innovations are visible within the *Pinus* subgenus. In subgenus *Strobus*, other adaptations have been developed that likely also influence diversification rates. Therefore, the signal can be expected to be weaker when comparing key innovations within subgenus *Pinus* against all other species of the whole genus.

2.5.2 Diversification rate in response to disturbance, stress and pleiotropic costs

The classification of the five fire response traits analyzed in these study into the two life history strategies "evader" and "resister" might not be the most suitable. In fact, I compare species that are adapted to fire-prone or low productive areas with non-adapted species inhabiting resource rich(er) and (more) productive sites where primarily competition for light is a limiting factor. This is a different approach of comparison than often considered in previous studies where the two life history strategies (evader and resister) are compared against each other within the same fire-prone area. Another possibility to classify and compare the influence of the development of fire response traits on diversification is to differentiate adaptation to varying disturbance intensities. In this case, serotiny and resprouting represent adaptations to severe disturbances and grass stage to very frequent disturbances. Serotinous cones represent an adaptation in response to severe crown fires, whereas resprouting ability is not only an adaptation to high frequency in surface fires, but allows to colonize sites with low productivity due to repeated droughts or with high grazing pressure, both representing severe (primarily frequent) disturbances. On the other hand, bark thickness and branch shedding stand for adaptations to low intensity and low frequency fires (low disturbances). My results indicate with two out of three severe disturbance adaptations that species building adaptations to severe or frequent disturbance show a lower diversification rate due to a lower speciation rate than species without adaptations. On the contrary, species with adaptations to low disturbance reveal higher diversification rates due to higher speciation rates than non-adapted species.

This pattern perfectly aligns with the intermediate disturbance hypothesis (Connell, 1978), which has been postulated to also hold for speciation rates, as demonstrated by an experiment using an aquatic system (Kassen *et al.*, 2004). Moreover, Kassen and colleagues (2004) have hypothesized that this pattern also holds for abiotic stress, a fact that I did not test with my data, except that resprouting capacity is considered also an adaptation to low productivity (which stands for limitations in abiotic constraints, such as low nutrients, low water availability), and thick bark can also be considered to assist in resistance to drought. Figure 2 illustrates, how my results can be brought to a more general concept, building on Kassens' (2004) and my own results and ideas.

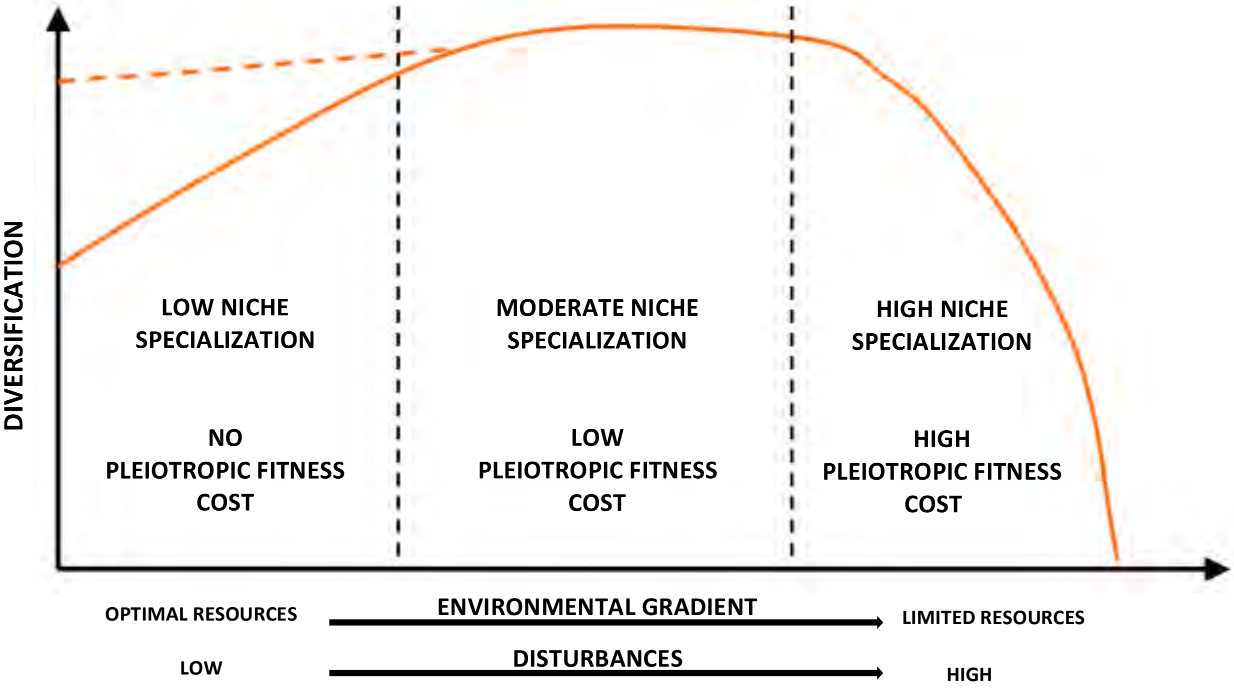


Figure 2. *Model showing the course of diversification along an independent or simultaneously changing environmental gradient of resource availability and disturbances.*

The combination of disturbance intensity/frequency gradients and abiotic stress gradients is well incorporated into the C-S-R plant strategy concept of Grime (1977), which is often also used to classify plants according to their tolerances of stress, disturbance and competition (representing the external factors limiting plants' biomass) in a triangular classification system (Figure 3). Kassen *et al. (2004)* found high diversification (resulting from rapid radiation) at intermediate rates of productivity and disturbance and decreasing diversity towards the extremes caused by pleiotropic fitness costs associated with niche specialization. Therefore, they hypothesized that ecological gradients limit adaptive radiation (thus diversification).

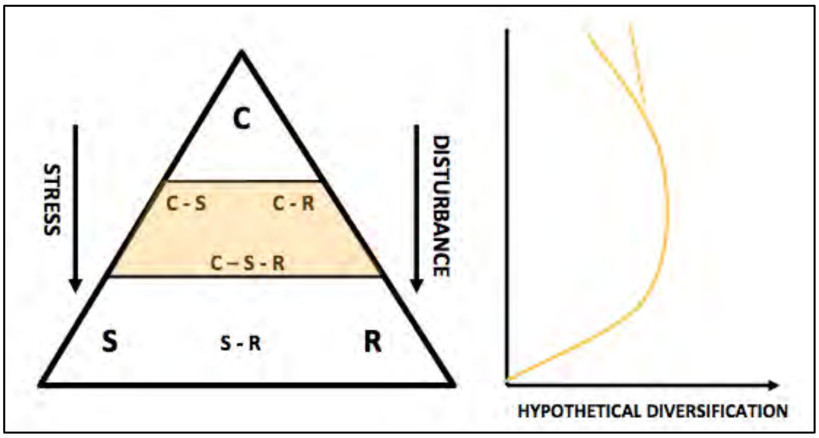


Figure 3. *The triangular illustration on the left side illustrates Grimes' (1977) model for the plant strategies describing the numerous equilibrium between competition, stress and disturbance in vegetation. "C" stands for a resource rich environment with light as the only limiting factor for species growth. "S" represents a shift to stressful and harsh habitats with low resource availability and "R" stands for increased disturbance in intensity and frequency. The right side illustration shows a hypothetical trend for diversification for the different environments and plant strategies.*

Based on Grime's (1977) triangular classification plant's can evolve distinct life strategies based on the external factors limiting plant's biomass. They face an investment-allocation into competition (C), stress-tolerance (S) and ruderal (R) that stands for disturbances. In an optimal and productive environment with high resource availability and no disturbances (strategy "C" in Grime's model in figure 3), only competition (for light) is the limiting factor for species' biomass production. No other adaptations are necessary to compete well under these conditions. As the environment undergoes correlated or independent biotic or abiotic changes (indicated by the arrows from the "C-" to the "S-" and/or the "R-strategy" in figure 3), new ecological opportunities emerge, which leads to rapid radiation into newly available and unexploited niches. In this heterogeneous environment, divergent natural selection and high resource competition lead to high diversification (indicated by the orange shaded zone in figure 3). If the disturbances are more severe or if only very limited resources are available, species have to invest considerably into disturbance or stress avoidance, which leads to high pleiotropic fitness costs due to their specialization into specific niches that require a high degree of adaptation. Extreme disturbance and intense resource limitation leads to strongly diversifying selection favoring niche specialists that enable species to invade an otherwise unavailable habitat but at very high (pleiotropic) fitness costs. These adaptations might be so highly specialized that the diversification rate decreases due to detrimental effects on other important traits for fitness or traits involved in species' metabolic rates.

Therefore, and according to this new view, it is not the choice of the strategy (as evader or resister) that influences diversification. Rather, diversification is influenced by the capability of species to invade heterogeneous environments, and by the degree of specialization needed to adapt to biotically or abiotically disturbed habitats. The higher the degree of specialization, the higher are the pleiotropic investment costs leading to decreased diversification.

The here-proposed view relates to the often-used, classical productivity-diversity hypothesis (Grime, 1973; Almufti *et al.*, 1977; Tilman, 1982). This theory has raised controversy with regards to the shape of this relationship (Adler *et al.*, 2011), where some scientists have proposed a hump-shaped relationship with intermediate productivity relating to highest diversity values (e.g. Rosenzweig & Abramsky, 1993; Huston & Deangelis, 1994). However, some scientists have claimed that other shapes are also possible and have theoretical grounds (Abrams, 1995). My results indicate also that diversity peaks at intermediate, not maximal, resource availability. The results by Adler *et al.* (2011) also give support for this shape for at least some of their analyzed data series, but they also stress the fact that disturbance may play a role when such patterns are found.

2.5.3 Critical evaluation of the analysis pathway

The diversification rates of evader vs. resister traits contradict previous findings. This may indicate a different evolutionary pathway in pines, or it may point to other mechanisms or co-distributed traits or environmental variables that affect these evolutionary patterns (see FitzJohn, (2012). He warned of fallacies using the BiSSE analyses to assess the influence of single traits on diversification because the results can also be biased by a co-distributed trait over the phylogeny, which leads to the same observed patterns and therefore misleading conclusions. Some of the analyzed fire response traits could correlate with another, yet unassessed, trait responsible for changes in speciation rates. I therefore suggest that further studies should also assess trait syndromes (Verdu & Pausas, 2013) rather than only single traits. In doing so one could take into account not only the analyzed fire response traits as in this study, but also include maximum height, age to maturity, longevity and flammability (Budde *et al.*, 2013).

Overall, I assume that environmental variability is the main force influencing the observed diversification pattern in my study system, based on the above-described model and the results of Litsios *et al. (2013)*. I therefore do not assume that a co-distributed trait influences the here observed differences in diversification rate. The influence of environmental gradients on diversification rate can be assessed by mapping climatic or ecological variables onto the phylogenies and to test for a possible correlation with each individual fire response trait or trait syndrome (Barraclough & Nee, 2001). A weakness of categorizing the individual traits or trait syndromes is the fact that it is based on subjective classifications. To overcome such problems of subjective choice, I suggest running the analyses for quantitatively measured traits in order to observe patterns of different effects of these traits on diversification rates. To test the hypothesis that diversification rate depends on the degree of resource limitation in a non-linear fashion, one might conduct the study on continuous traits, preferably on climate data representing stress tolerance (drought tolerance, cold tolerance etc.) using QuaSSE (FitzJohn, 2012). Therefore, this study should be extended to the second ecological stimulus (stress tolerance) of the subgenus *Strobus* by separating out the two main scenarios of ecological stimulus (fire and stress tolerance). One could also test the corresponding syndromes for their specific influence on diversification. Because fire is an older stimulus, one would expect that fire has been a larger component of influencing diversification than stress tolerance.

Further, the here conducted analyses were based on insufficient iterations within the MCMC analyses and I did not sufficiently discard the burn-in period. This resulted in a (higher degree of) overlap of the credibility intervals of the poster densities, despite clear separation in speciation and diversification rates in many cases. Therefore, one needs to run further analyses for many more iterations in order to get an even more convincing result regarding the overlap and significance between trait states rate. Yet, given that the modes of the distributions do not overlap with the other distribution credibility interval, I can already claim that the found differences have a tendency to be higher or lower.

2.5.4 Phylogenetic inference

Barraclough and Nee (2001) stated two issues about using phylogenies for studying speciation. The first deals with the importance of accurate and complete sampling of species belonging to the group of interest. The second is about the status of species included in the phylogenies, which refers to that the number and identity of species depend on the judgment of the taxonomist who described them. The first issue is well covered in this study since I used a complete sampling of all described taxonomic species for the genus *Pinus*. The second issue might not be fully implemented as I simply assume that the single used sample of each taxonomic species does reflect an evolutionary entity. To avoid this fallacy, I could have used more than one sample for each species if it was available in GenBank. Further, the deeper nodes in the phylogenies are supported by high posterior probabilities, whereas the lower nodes showed partly low posterior probabilities. Due to these low posterior probabilities of some species groups I only can hypothesize that the taxonomically defined species in my study represents evolutionary units (Barraclough & Nee, 2001). I reduced all these phylogenetic uncertainties (both topology and branch lengths) by conducting the analyses over each of the 100 randomly sampled trees. Consequently, the inferred phylogenies seem to provide an admissible basis for the comparative analysis, and the ensemble approach of conducting all analyses over a sample of 100 random trees assures that the result is robust with regards to the uncertainties inherent in the developed pine phylogeny.

2.6 Conclusions and outlook

I conclude that fire response traits in pines do not trigger diversification rate simply by representing a key innovation. Rather, it seems to be the degree of environmental specialization required both for adapting to fire and to limited resource availability that affects diversification. My results provide strong support for the significance of biotic and abiotic stress in combination with disturbance rates in constraining diversification. I therefore propose to test the here found patterns by analyzing quantitative traits (using QuaSSE) and by combining these with analyses along disturbance gradients (also using QuaSSE). If successful, it would allow contributing to the productivity-diversity hypothesis, specifically with regards to the nature of the shape of this relationship.

2.7 Acknowledgements

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3 Supplementary material

S1: Accession numbers of gene sequences

S2: Trait Database

S3: Distribution maps of *Pinus* species

S4: Trait distribution over phylogeny

S5: Phylogenetic signal of the 19 bioclimatic variables

S6: Complete List of References

3.1 S1 - Accession numbers of gene sequences

species	Accession	Gene	Author
P. albicaulis	FJ899566	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2009)
P. aristata	FJ899567	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnV,ycf2	(Parks *et al.*, 2009)
P. amamiana	JN854226	accD,matK,rbcL,rpl20,rpoC1,trnV,	(Parks *et al.*, 2012)
P. arizonica	JN854225	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnV	(Parks *et al.*, 2012)
P. armandii	FJ899568	accD,rbcL, rbcL,rpl20,rpoB,rpoC1,trnV	(Parks *et al.*, 2009)
P. armandii	AB161002	matK	(Gernandt *et al.*, 2005)
P. attenuata	FJ899569	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2009)
P. ayacahuite	FJ899570	accD,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2009)
P. ayacahuite	AY497257	matK	(Gernandt *et al.*, 2005)
P. balfouriana	AY115799	matK	(Gernandt *et al.*, 2003)
P. balfouriana	AY115760	rbcL	(Gernandt *et al.*, 2003)
P. balfouriana	AB019880	trnV	(Wang *et al.*, 1999)
P. banksiana	FJ899571	accD,rbcL,rpoB,rpoC1,trnV	(Parks *et al.*, 2009)
P. banksiana	EF440517	matK	(Bouille *et al.*, 2011)
P. bhutanica	DQ353719	rbcL	(Gernandt, 2007)
P. bhutanica	AY497262	matK	(Gernandt *et al.*, 2005)
P. brutia	JN854224	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. bungeana	JN854223	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. canariensis	FJ899572	accD,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2009)
P. canariensis	AB084494	matK	(Geada Lopez, 2002)
P. caribaea	JN854222	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. cembra	AB160985	matK	(Gernandt *et al.*, 2005)
P. cembra	FJ899574	accD,rbcL,rpl20,rpoB,rpoC1,trnv	(Parks *et al.*, 2009)
P. cembroides	JN854220	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. chiapensis	JN854219	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. clausa	JN854217	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. contorta	EU998740	accD,rbcL,rpl20,rpoB,rpoC1,trnv,	(Cronn *et al.*, 2008)
P. contorta	AY497266	matK	(Gernandt *et al.*, 2005)
P. cooperi	DQ353708	matK	(Gernandt, 2007)
P. cooperi	DQ353723	rbcL	(Gernandt, 2007)
P. coulteri	JN854215	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. cubensis	JN854214	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. culminicola	JN854213	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. dalatensis	JN854211	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. densata	JN854209	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. densiflora	JN854210	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv	(Parks *et al.*, 2012)
P. devoniana	JN854208	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. discolor	JN854207	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. douglasiana	JN854205	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. durangensis	AY497276	matK	(Gernandt *et al.*, 2005)
P. durangensis	AY497240	rbcL	(Gernandt *et al.*, 2005)
P. durangensis	DQ159460	trnV	(Eckert & Hall, 2006)
P. echinata	JN854204	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. edulis	JN854203	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. elliottii	JN854202	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. engelmannii	JN854201	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. fenzeliana	JN854212	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. flexilis	FJ899576	accD,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2009)
P. flexilis	AY497258	matK	(Gernandt *et al.*, 2005)
P. fragilissima	JN854200	accD,matK,rbcL,rpl20,rpoB,rpoC1,ycf2	(Parks *et al.*, 2012)
P. gerardiana	EU998741	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Cronn *et al.*, 2008)
P. glabra	JN854199	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. greggii	JN854198	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. halepensis	JN854197	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. hartwegii	JN854206	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. heldreichii	JN854195	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. herrerae	AB080943	matK	(Geada Lopez, 2003)
P. herrerae	AB063386	rbcL	(Geada Lopez *et al.*, 2001)
P. herrerae	AB063602	trnv	(Geada Lopez *et al.*, 2001)
P. herrerae	AM883768	rpoB	(Cowan, 2008)
P. hwangshanensis	JN854194	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. jeffreyi	JN854193	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. johannis	JN854192	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. juarezensis	AY115742	rbcL	(Gernandt *et al.*, 2003)
P. juarezensis	AY115770	matK	(Gernandt *et al.*, 2003)
P. kesiya	JN854191	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. koraiensis	AY228468	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Noh *et al.*, 2007)
P. krempfii	EU998742	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Cronn *et al.*, 2008)

species	Accession	Gene	Author
P. lambertiana	EU998743	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Cronn *et al.*, 2008)
P. latteri	JN854190	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. lawsonii	JN854188	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. leiophylla	JN854218	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. longaeva	EU998744	matK,rbcL,rpl20,rpoB,rpoC1,trnv	(Cronn *et al.*, 2008)
P. luchuensis	AB097780	matK	(Geada Lopez & Harada, 2003)
P. luchuensis	AB097772	rbcL	(Geada Lopez & Harada, 2003)
P. luchuensis	AB097788	trnv	(Geada Lopez & Harada, 2003)
P. lumholtzii	JN854186	accD,matK,rbcL,rpl20,rpoB,rpoC1,ycf2	(Parks *et al.*, 2012)
P. maestrensis	AB080939	matK	(Geada Lopez, 2003)
P. maestrensis	AB063371	rbcL	(Geada Lopez, 2002)
P. maestrensis	AB063587	trnV	(Geada Lopez, 2002)
P. massoniana	JN854185	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. nelsonii	EU998746	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Cronn *et al.*, 2008)
P. nigra	JN854179	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. occidentalis	JN854177	accD,matK,rbcL,rpl20,rpoB,rpoC1,ycf2	(Parks *et al.*, 2012)
P. oocarpa	AB081084	matK	(Geada Lopez, 2003)
P. oocarpa	DQ353726	rbcL	(Gernandt, 2007)
P. oocarpa	AM883774	rpoB	(Cowan, 2008)
P. oocarpa	AB063598	trnv	(Geada Lopez *et al.*, 2001)
P. palustris	JN854176	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. parviflora	FJ899581	matK,rpl20,rpoB,rpoC1.ycf2	(Parks *et al.*, 2009)
P. parviflora	EU269033	rbcL	(Gernandt, 2008)
P. patula	JN854175	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. peuce	FJ899582	accD,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2009)
P. peuce	AY497254	matK	(Gernandt *et al.*, 2005)
P. pinaster	FJ899583	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2009)
P. pinceana	JN854174	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. pinea	JN854173	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. ponderosa	JN854172	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. praetermissa	DQ353711	matK	(Gernandt, 2007)
P. praetermissa	DQ353727	rbcL	(Gernandt, 2007)
P. pringlei	JN854189	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. pseudostrobus	JN854178	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. pumila	JN854168	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. pungens	JN854167	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. quadrifolia	JN854166	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. radiata	JN854165	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. remota	JN854164	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. resinosa	FJ899556	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2009)
P. rigida	JN854163	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. roxburghii	JN854162	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. rzedowskii	FJ899557	accD,matK,rbcL,rpl20,rpoB,rpoC1,ycf2	(Parks *et al.*, 2009)
P. sabiniana	JN854161	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. serotina	JN854160	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. sibirica	FJ899558	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2009)
P. squamata	FJ899559	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2009)
P. strobiformis	JN854159	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. strobus	FJ899560	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2009)
P. sylvestris	JN854158	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. tabuliformis	AY555717	rbcL	(Song *et al.*, 2003)
P. tabuliformis	AB161015	matK	(Gernandt *et al.*, 2005)
P. tabuliformis	AM883727	rpoB	(Cowan, 2008)
P. tabuliformis	AB019884	trnv	(Wang *et al.*, 1999)
P. taeda	FJ899561	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2009)
P. taiwanensis	JN854157	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. teocote	AB097773	rbcL	(Geada Lopez & Harada, 2003)
P. teocote	AB097789	trnv	(Geada Lopez & Harada, 2003)
P. teocote	AB097783	matK	(Geada Lopez & Harada, 2003)
P. thunbergii	FJ899562	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2009)
P. torreyana	FJ899564	accD,rbcL,rpl20,rpoB,rpoC1,trnv	(Parks *et al.*, 2009)
P. torreyana	AY497273	matK	(Gernandt *et al.*, 2005)
P. tropicalis	JN854156	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. virginiana	JN854155	accD,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. virginiana	AB080923	matK	(Geada Lopez, 2003)
P. wallichiana	JN854154	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. washoensis	DQ353706	matK	(Gernandt, 2007)
P. washoensis	DQ353721	rbcL	(Gernandt, 2007)
P. yecorensis	JN854152	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. yunnanensis	JN854151	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)

species	**Accession**	**Gene**	**Author**
P. kwangtungensis	JN854153	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. lambertiana	EU998743	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Cronn *et al.*, 2008)
P. latteri	JN854190	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. lawsonii	JN854188	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. leiophylla	JN854218	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. longaeva	EU998744	matK,rbcL,rpl20,rpoB,rpoC1,trnv	(Cronn *et al.*, 2008)
P. luchuensis	AB097780	matK	(Geada Lopez & Harada, 2003)
P. luchuensis	AB097772	rbcL	(Geada Lopez & Harada, 2003)
P. luchuensis	AB097788	trnv	(Geada Lopez & Harada, 2003)
P. lumholtzii	JN854186	accD,matK,rbcL,rpl20,rpoB,rpoC1,ycf2	(Parks *et al.*, 2012)
P. maestrensis	AB080939	matK	(Geada Lopez, 2003)
P. maestrensis	AB063371	rbcL	(Geada Lopez, 2002)
P. maestrensis	AB063587	trnV	(Geada Lopez, 2002)
P. massoniana	JN854185	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. nelsonii	EU998746	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Cronn *et al.*, 2008)
P. nigra	JN854179	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. occidentalis	JN854177	accD,matK,rbcL,rpl20,rpoB,rpoC1,ycf2	(Parks *et al.*, 2012)
P. oocarpa	AB081084	matK	(Geada Lopez, 2003)
P. oocarpa	DQ353726	rbcL	(Gernandt, 2007)
P. oocarpa	AM883774	rpoB	(Cowan, 2008)
P. oocarpa	AB063598	trnv	(Geada Lopez *et al.*, 2001)
P. palustris	JN854176	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. parviflora	FJ899581	matK,rpl20,rpoB,rpoC1.ycf2	(Parks *et al.*, 2009)
P. parviflora	EU269033	rbcL	(Gernandt, 2008)
P. patula	JN854175	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. peuce	FJ899582	accD,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2009)
P. peuce	AY497254	matK	(Gernandt *et al.*, 2005)
P. pinaster	FJ899583	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2009)
P. pinceana	JN854174	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. pinea	JN854173	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. ponderosa	JN854172	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. praetermissa	DQ353711	matK	(Gernandt, 2007)
P. praetermissa	DQ353727	rbcL	(Gernandt, 2007)
P. pringlei	JN854189	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. pseudostrobus	JN854178	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. pumila	JN854168	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. pungens	JN854167	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. quadrifolia	JN854166	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. radiata	JN854165	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. remota	JN854164	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. resinosa	FJ899556	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2009)
P. rigida	JN854163	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. roxburghii	JN854162	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. rzedowskii	FJ899557	accD,matK,rbcL,rpl20,rpoB,rpoC1,ycf2	(Parks *et al.*, 2009)
P. sabiniana	JN854161	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. serotina	JN854160	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. sibirica	FJ899558	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2009)
P. squamata	FJ899559	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2009)
P. strobiformis	JN854159	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. strobus	FJ899560	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2009)
P. sylvestris	JN854158	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. tabuliformis	AY555717	rbcL	(Song *et al.*, 2003)
P. tabuliformis	AB161015	matK	(Gernandt *et al.*, 2005)
P. tabuliformis	AM883727	rpoB	(Cowan, 2008)
P. tabuliformis	AB019884	trnv	(Wang *et al.*, 1999)
P. taeda	FJ899561	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2009)
P. taiwanensis	JN854157	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. teocote	AB097773	rbcL	(Geada Lopez & Harada, 2003)
P. teocote	AB097789	trnv	(Geada Lopez & Harada, 2003)
P. teocote	AB097783	matK	(Geada Lopez & Harada, 2003)
P. thunbergii	FJ899562	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2009)
P. torreyana	FJ899564	accD,rbcL,rpl20,rpoB,rpoC1,trnv	(Parks *et al.*, 2009)
P. torreyana	AY497273	matK	(Gernandt *et al.*, 2005)
P. tropicalis	JN854156	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. virginiana	JN854155	accD,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. virginiana	AB080923	matK	(Geada Lopez, 2003)
P. wallichiana	JN854154	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. washoensis	DQ353706	matK	(Gernandt, 2007)
P. washoensis	DQ353721	rbcL	(Gernandt, 2007)
P. yecorensis	JN854152	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
P. yunnanensis	JN854151	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)

species	Accession	Gene	Author
Abies firma	JQ512507	rbcL	(Shin & Kim, 2012)
Abies firma	FJ899565	matK,rpoB,rpoC1,ycf2	(Parks *et al.*, 2009)
Cathaya argyrophylla	AB547400	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Lin *et al.*, 2010)
Cedrus deodora	AB480043	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Lin *et al.*, 2010)
Keteleeria davidiana	AP010820	accD,matK,rbcL,rpl20,rpoB,rpoC1,ycf2	(Wu *et al.*, 2009)
Larix occidentalis	FJ899578	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2009)
Nothotsuga	AF145459	rbcL	(Wang & Sang, 1999)
Nothotsuga	AF143437	matK	(Wang & Sang, 1999)
Picea sitchensis	EU998739	accD,matK,rbcL	(Cronn *et al.*, 2008)
Pseudolarix amabilis	AF143432	matK	(Wang *et al.*, 2000)
Pseudolarix amabilis	AB019829	rbcL	(Wang *et al.*, 1999)
Pseudolarix amabilis	AB019903	trnv	(Wang *et al.*, 1999)
Pseudotsuga menziesii	JN854170	accD,matK,rbcL,rpl20,rpoB,rpoC1,trnv,ycf2	(Parks *et al.*, 2012)
Tsuga sieboldii	JQ512629	rbcL	(Shin & Kim, 2012)
Tsuga sieboldii	JQ512505	matK	(Shin & Kim, 2012)

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3.2 S2 - Trait database

	climate variables					*tree characteristics*		
Species	**PC1**	**PC2**	**PC3**	**PC4**	**HZone**	**Range**	**DBH**	**Height**
Pinus_albicaulis	-4.96	-0.34	-0.20	-2.02	2	394	200	2050
Pinus_aristata	3.11	-6.12	1.12	0.06	3	65	120	2000
Pinus_amamiana	-4.06	1.02	-0.89	0.66	9	2	200	3000
Pinus_arizonica	0.46	2.19	-0.23	1.45	8	90	120	3550
Pinus_armandii	-0.52	0.00	2.36	0.11	7	286	150	4250
Pinus_attenuata	-1.05	0.56	-1.13	-2.15	7	57	80	3000
Pinus_ayacahuite	3.19	1.74	1.03	-0.29	7	62	200	5000
Pinus_balfouriana	-1.95	0.91	-1.11	-1.91	5	10	255	2350
Pinus_banksiana	-6.76	-1.18	1.91	1.30	2	2102	80	2700
Pinus_bhutanica	-0.80	0.04	3.72	-1.14	9	40	65	2500
Pinus_brutia	-1.43	0.48	-1.52	-1.30	7	141	210	3000
Pinus_bungeana	-2.33	0.10	1.79	1.22	5	20	165	3000
Pinus_canariensis	0.24	1.85	-0.63	-2.32	9	1	225	4250
Pinus_caribaea	4.75	-1.27	-0.97	-0.65	10	81	100	4500
Pinus_cembra	-3.20	-2.83	0.86	-1.99	1	87	150	2500
Pinus_cembroides	0.24	2.31	-0.56	1.65	8	205	50	2250
Pinus_chiapensis	4.12	0.37	0.48	-0.33	10	31	150	4000
Pinus_clausa	2.80	-1.94	-1.34	1.02	7	49	50	2100
Pinus_contorta	-5.21	-0.26	0.81	-0.96	7	1355	200	5000
Pinus_cooperi	0.84	1.79	0.77	0.32	7	37	110	3500
Pinus_coulteri	-0.73	2.56	-1.47	-0.57	8	33	100	2500
Pinus_cubensis	4.11	-0.83	-1.58	-0.39	11	6	100	3500
Pinus_culminicola	-0.14	2.23	-1.25	-0.08	7	1	37.5	750
Pinus_dalatensis	4.71	0.27	1.32	-0.29	10	3	150	4000
Pinus_densata	-0.26	-0.11	2.38	-0.01	6	111	130	3000
Pinus_densiflora	-0.65	-3.15	1.43	0.95	5	321	165	3500
Pinus_devoniana	2.36	2.14	0.80	0.15	9	88	100	3000
Pinus_discolor	0.24	2.31	-0.56	1.65	8	205	50	1500
Pinus_douglasiana	3.17	1.77	1.06	0.53	10	32	100	4500
Pinus_durangensis	0.64	1.92	0.58	0.71	8	68	100	4000
Pinus_echinata	-0.23	-2.98	-2.82	0.86	6	560	140	4100
Pinus_edulis	-2.61	1.45	-1.08	1.97	5	262	115	2050
Pinus_elliottii	1.67	-2.58	-2.18	1.16	9	151	95	3600
Pinus_engelmannii	0.46	2.30	-0.13	1.45	8	110	95	3100
Pinus_fenzeliana	1.85	-2.86	0.34	0.87	9	7	100	5000
Pinus_flexilis	-4.53	0.65	-0.30	0.50	3	335	185	2300
Pinus_fragilissima	4.06	-3.73	3.63	-1.51	9	8	120	3000
Pinus_gerardiana	-4.42	0.44	0.49	-1.37	7	42	100	2500
Pinus_glabra	1.24	-3.09	-2.94	1.02	8	129	100	3750
Pinus_greggii	0.52	1.90	-0.21	-0.13	8	22	80	2500
Pinus_halepensis	-0.90	0.53	-1.84	-0.89	8	279	100	3000
Pinus_hartwegii	1.81	1.65	1.22	-0.68	8	51	100	3000
Pinus_heldreichii	-2.05	-2.00	-1.52	-2.27	5	25	200	3000
Pinus_herrerae	1.33	1.99	0.85	0.40	10	50	100	3500
Pinus_hwangshanensi	0.67	-3.32	0.42	0.95	7	36	100	4500
Pinus_jeffreyi	-1.80	1.49	-1.38	-1.14	8	104	200	5500
Pinus_johannis	0.39	2.17	-1.32	1.70	8	34	50	500
Pinus_juarezensis	-1.09	2.52	-1.76	0.14	8	11	50	1500
Pinus_kesiya	3.24	-0.13	1.99	0.42	9	162	100	4500
Pinus_koraiensis	-5.26	-1.03	2.95	2.40	3	427	125	5000
Pinus_krempfii	3.75	0.40	0.29	-1.13	10	4	225	4000
Pinus_kwangtungensi	1.09	-0.39	1.76	0.09	5	2	150	3000
Pinus_lambertiana	-1.84	1.16	-1.17	-1.63	7	116	365	8000
Pinus_latteri	4.84	-0.04	1.17	0.39	9	50	200	3000
Pinus_lawsonii	2.70	2.02	1.09	-0.13	10	41	77.5	3000
Pinus_leiophylla	0.70	2.32	0.09	0.96	9	170	87.5	3500
Pinus_longaeva	-3.77	1.35	-1.59	0.60	4	39	350	1600
Pinus_luchuensis	3.83	-6.32	-2.33	-0.89	9	4	80	2250
Pinus_lumholtzii	1.44	1.99	0.74	0.58	8	74	70	2000
Pinus_maestrensis	4.11	-0.83	-1.58	-0.39	11	6	100	3000
Pinus_massoniana	0.98	-2.50	0.51	1.06	7	602	150	4500
Pinus_maximartinezii	2.38	2.56	0.54	1.47	10	1	55	1750
Pinus_maximinoi	2.36	2.14	0.80	0.15	10	88	100	5000
Pinus_merkusii	4.17	0.25	0.98	0.44	10	102	200	3750
Pinus_monophylla	-3.18	1.72	-1.92	0.86	6	150	90	2000
Pinus_montezumae	2.11	1.96	0.74	-0.17	9	86	100	3250
Pinus_monticola	-3.56	-0.48	-0.69	-2.59	4	322	340	7250
Pinus_morrisonicola	4.60	-5.78	0.88	-0.93	8	6	150	3500
Pinus_mugo	-2.77	-1.98	0.10	-1.19	1	249	100	1500
Pinus_muricata	-0.54	2.57	-0.72	-1.97	8	15	120	3000

	climate variables					*tree characteristics*		
Species	**PC1**	**PC2**	**PC3**	**PC4**	**HZone**	**Range**	**DBH**	**Height**
Pinus_nelsonii	0.71	2.20	-0.82	0.73	8	8	30	1000
Pinus_nigra	-2.01	-0.22	-1.35	-1.20	5	404	194.5	5000
Pinus_occidentalis	4.38	-0.29	-1.21	-0.15	10	21	135	4250
Pinus_oocarpa	3.80	1.41	0.67	0.03	9	189	125	4500
Pinus_palustris	1.02	-3.12	-2.84	1.13	8	282	120	4700
Pinus_parviflora	-0.51	-4.51	0.47	0.32	5	108	125	2500
Pinus_patula	1.22	1.52	0.78	-0.79	8	15	100	4000
Pinus_peuce	-2.84	-1.33	-0.72	-2.38	5	5	100	3000
Pinus_pinaster	-1.30	0.17	-1.52	-1.29	8	213	150	4000
Pinus_pinceana	0.50	2.56	-0.84	0.96	9	20	30	1200
Pinus_pinea	-0.87	0.51	-1.68	-1.12	8	156	125	2750
Pinus_ponderosa	-3.30	1.21	-0.71	0.39	3	851	265	7350
Pinus_praetermissa	2.91	1.39	0.77	0.52	9	44	30	2000
Pinus_pringlei	3.48	2.03	0.91	0.08	9	38	100	2500
Pinus_pseudostrobus	3.14	1.44	0.60	0.02	9	141	125	4750
Pinus_pumila	-9.72	-1.06	3.44	1.45	1	3617	15	600
Pinus_pungens	-1.85	-3.00	-1.73	0.95	6	84	70	2250
Pinus_quadrifolia	-1.09	2.52	-1.76	0.14	8	11	60	1550
Pinus_radiata	-0.78	2.60	-0.44	-2.41	8	5	210	3650
Pinus_remota	0.37	1.87	-1.37	1.81	8	44	40	900
Pinus_resinosa	-4.59	-2.53	0.09	0.74	3	787	125	3750
Pinus_rigida	-2.30	-3.23	-1.50	0.82	4	306	115	3000
Pinus_roxburghii	0.80	-0.78	1.67	-0.18	9	97	75	5500
Pinus_rzedowskii	3.58	2.33	0.54	0.42	10	10	90	4000
Pinus_sabiniana	-0.92	1.66	-1.60	-0.83	8	65	125	3750
Pinus_serotina	0.82	-2.79	-2.43	1.34	8	183	60	2000
Pinus_sibirica	-7.59	-1.10	2.16	1.64	1	3384	180	4000
Pinus_squamata	-2.21	0.86	3.85	-1.22	8	2	60	2000
Pinus_strobiformis	0.00	2.16	-0.29	1.33	8	148	125	3250
Pinus_strobus	-3.99	-2.78	-0.33	0.61	1	1182	190	6350
Pinus_sylvestris	-4.54	-1.31	0.90	-0.53	1	6079	160	4000
Pinus_tabuliformis	-3.00	0.44	2.18	1.42	5	290	120	2750
Pinus_taeda	0.59	-3.07	-3.02	0.94	7	431	155	4500
Pinus_taiwanensis	4.06	-3.73	3.63	-1.51	8	8	110	5000
Pinus_teocote	1.63	1.95	0.54	0.18	8	132	77.5	2500
Pinus_thunbergii	0.49	-4.20	0.68	0.63	6	122	200	3750
Pinus_torreyana	0.14	2.42	-0.67	-1.96	8	4	150	3150
Pinus_tropicalis	4.43	-0.81	-0.71	-0.02	10	9	100	3000
Pinus_virginiana	-1.07	-3.04	-2.35	0.90	6	304	75	3000
Pinus_wallichiana	-2.60	0.16	1.82	-1.37	8	168	150	7000
Pinus_washoensis	-3.22	2.05	-1.50	-0.25	6	3	100	6000
Pinus_yecorensis	2.65	1.31	0.34	1.09	10	21	95	3000
Pinus_yunnanensis	0.87	0.11	2.31	-0.22	8	173	100	3000

	leaf morphology							
Species	**Length**	**Width**	**Cluster**	**Persist**	**Stomata**	**SLA**	**LAR**	**LMR**
Pinus_albicaulis	5.125	0.125	5	8	1	NA	NA	NA
Pinus_aristata	3.625	0.09	5	18.5	2	NA	NA	NA
Pinus_amamiana	6.5	0.09	5	3	2	NA	NA	NA
Pinus_arizonica	12.75	0.135	5	3.5	1	NA	NA	NA
Pinus_armandii	10.75	0.125	5	3	2	NA	NA	NA
Pinus_attenuata	12.25	0.125	3	4	1	NA	NA	NA
Pinus_ayacahuite	13.25	0.085	5	3	2	NA	NA	NA
Pinus_balfouriana	2.875	0.12	5	30	2	NA	NA	NA
Pinus_banksiana	3.125	0.175	2	3	1	132.	77.	0.588
Pinus_bhutanica	19.5	0.1	5	2	2	NA	NA	NA
Pinus_brutia	14	0.125	2	3	1	NA	NA	NA
Pinus_bungeana	7.75	0.2	3	5	1	NA	NA	NA
Pinus_canariensis	25	0.175	3	2.5	1	92.4	64.	0.693
Pinus_caribaea	20.25	0.16	3	3	1	99.4	53.	0.532
Pinus_cembra	7.75	0.125	5	5	2	60.6	35.	0.581
Pinus_cembroides	4.25	0.085	3	5	1	NA	NA	NA
Pinus_chiapensis	9	0.09	5	3	2	NA	NA	NA
Pinus_clausa	6.5	0.125	2	4	1	NA	NA	NA
Pinus_contorta	5	0.135	2	6.5	1	117.	69.	0.596
Pinus_cooperi	8	0.115	5	3	1	NA	NA	NA
Pinus_coulteri	22.5	0.205	3	4	1	85.6	53.	0.628
Pinus_cubensis	6.825	0.105	2	3	1	NA	NA	NA
Pinus_culminicola	4	0.11	5	4	2	NA	NA	NA
Pinus_dalatensis	7.25	0.08	5	3	2	NA	NA	NA
Pinus_densata	11	0.125	2	3	1	NA	NA	NA
Pinus_densiflora	9.25	0.1	2	3	1	NA	NA	NA
Pinus_devoniana	31.25	0.135	5	3	1	NA	NA	NA
Pinus_discolor	4.25	0.1	3	NA	2	NA	NA	NA
Pinus_douglasiana	27.75	0.095	5	2.75	1	NA	NA	NA
Pinus_durangensis	19.25	0.1	5	2.75	1	NA	NA	NA
Pinus_echinata	8.75	0.1	2	5	1	NA	NA	NA
Pinus_edulis	3.125	0.12	2	7.5	1	NA	NA	NA
Pinus_elliottii	19.5	0.135	3	3	1	114	66.	0.588
Pinus_engelmannii	28.75	0.175	3	3	1	NA	NA	NA
Pinus_fenzeliana	11	0.125	5	NA	2	NA	NA	NA
Pinus_flexilis	6.125	0.1	5	6	1	86.1	48.	0.562
Pinus_fragilissima	18	0.11	2	3	1	NA	NA	NA
Pinus_gerardiana	7.75	0.2	3	3	1	NA	NA	NA
Pinus_glabra	6.25	0.095	2	3	1	130	90.	0.694
Pinus_greggii	11.75	0.11	3	4	1	NA	NA	NA
Pinus_halepensis	10.25	0.075	2	3	1	104	65.	0.632
Pinus_hartwegii	13.5	0.135	5	3	1	NA	NA	NA
Pinus_heldreichii	7.875	0.15	2	6	1	NA	NA	NA
Pinus_herrerae	16.25	0.08	3	3	1	NA	NA	NA
Pinus_hwangshanensi	13.5	0.08	2	3.5	1	NA	NA	NA
Pinus_jeffreyi	19.25	0.17	3	6	1	87	53	0.609
Pinus_johannis	4	0.105	3	NA	2	NA	NA	NA
Pinus_juarezensis	4	0.1	5	4	2	NA	NA	NA
Pinus_kesiya	17	0.06	3	2	1	NA	NA	NA
Pinus_koraiensis	9.75	0.1	5	3	2	NA	NA	NA
Pinus_krempfii	4.75	0.3	2	6	1	NA	NA	NA
Pinus_kwangtungensi	5.25	0.125	5	NA	2	NA	NA	NA
Pinus_lambertiana	6.25	0.115	5	4	1	68.7	41.	0.599
Pinus_latteri	20	0.15	2	1.8	1	NA	NA	NA
Pinus_lawsonii	17	0.125	4	3	1	NA	NA	NA
Pinus_leiophylla	10.5	0.09	5	3	1	NA	NA	NA
Pinus_longaeva	2.625	0.1	5	32.5	2	NA	NA	NA
Pinus_luchuensis	13.25	0.085	2	3	1	NA	NA	NA
Pinus_lumholtzii	25.75	0.135	3	2	1	NA	NA	NA
Pinus_maestrensis	12.5	0.105	2	3	1	NA	NA	NA
Pinus_massoniana	16.5	0.1	2	2	1	NA	NA	NA
Pinus_maximartinezii	8.75	0.06	5	2	2	NA	NA	NA
Pinus_maximinoi	25.75	0.08	5	2.75	1	NA	NA	NA
Pinus_merkusii	19.25	0.1	2	2	1	NA	NA	NA
Pinus_monophylla	4.625	0.17	1	9	1	NA	NA	NA
Pinus_montezumae	21.25	0.105	5	3	1	NA	NA	NA
Pinus_monticola	7.5	0.085	5	4	2	NA	NA	NA
Pinus_morrisonicola	6.5	0.08	5	4	2	NA	NA	NA
Pinus_mugo	4.75	0.185	2	8.5	1	NA	NA	NA
Pinus_muricata	12.5	0.165	2	3	1	127.	85.	0.674

	leaf morphology							
Species	**Length**	**Width**	**Cluster**	**Persist**	**Stomata**	**SLA**	**LAR**	**LMR**
Pinus_nelsonii	6.25	0.075	3	3	1	NA	NA	NA
Pinus_nigra	11.25	0.15	2	4	1	88.1	65.	0.742
Pinus_occidentalis	16.75	0.13	4	3	1	NA	NA	NA
Pinus_oocarpa	20.25	0.12	4	2.5	1	NA	NA	NA
Pinus_palustris	28.75	0.15	3	2	1	74.5	58.	0.787
Pinus_parviflora	5.25	0.085	5	4.5	2	NA	NA	NA
Pinus_patula	20	0.08	3	3	1	121.	85.	0.702
Pinus_peuce	8.25	0.06	5	4	2	NA	NA	NA
Pinus_pinaster	16.25	0.175	2	3	1	86.9	59.	0.682
Pinus_pinceana	8.75	0.1	3	3	2	NA	NA	NA
Pinus_pinea	10.75	0.16	2	4	1	75.1	50.	0.672
Pinus_ponderosa	18.75	0.15	3	4.5	1	96.6	59.	0.612
Pinus_praetermissa	12.5	0.065	5	3	1	NA	NA	NA
Pinus_pringlei	21.5	0.125	3	3	1	NA	NA	NA
Pinus_pseudostrobus	25	0.105	5	3	1	NA	NA	NA
Pinus_pumila	5.25	0.1	5	4	2	NA	NA	NA
Pinus_pungens	6.25	0.125	2	3	1	NA	NA	NA
Pinus_quadrifolia	3.5	0.125	5	4	2	NA	NA	NA
Pinus_radiata	11.5	0.135	2	3.5	1	118.	79.	0.676
Pinus_remota	3.75	0.095	2	5	1	NA	NA	NA
Pinus_resinosa	14.5	0.12	2	4	1	102.	74	0.723
Pinus_rigida	10.25	0.135	3	3	1	101.	74.	0.735
Pinus_roxburghii	26.25	0.145	3	2.5	1	NA	NA	NA
Pinus_rzedowskii	8	0.07	5	3	2	NA	NA	NA
Pinus_sabiniana	23.25	0.15	3	4	1	78.6	48.	0.613
Pinus_serotina	17.5	0.14	3	3	1	NA	NA	NA
Pinus_sibirica	8.5	0.145	5	4.5	2	NA	NA	NA
Pinus_squamata	13	0.09	5	NA	1	NA	NA	NA
Pinus_strobiformis	8	0.095	5	5	2	NA	NA	NA
Pinus_strobus	8	0.085	5	3	1	118.	80.	0.679
Pinus_sylvestris	5.5	0.15	2	3	1	112.	83	0.736
Pinus_tabuliformis	11.5	0.125	2	3	1	NA	NA	NA
Pinus_taeda	14.75	0.175	3	3	1	104.	69.	0.663
Pinus_taiwanensis	12.5	0.085	2	3	1	NA	NA	NA
Pinus_teocote	12.5	0.12	3	3	1	NA	NA	NA
Pinus_thunbergii	10	0.15	2	3.5	1	110.	75.	0.681
Pinus_torreyana	22	0.2	5	4	1	73.7	40.	0.545
Pinus_tropicalis	25	0.15	2	2.5	1	NA	NA	NA
Pinus_virginiana	6	0.125	2	4	1	108.	76.	0.704
Pinus_wallichiana	19.5	0.1	5	3.5	2	NA	NA	NA
Pinus_washoensis	12.5	0.15	3	6	1	NA	NA	NA
Pinus_yecorensis	27.5	0.1	5	3	1	NA	NA	NA
Pinus_yunnanensis	15.5	0.11	3	3	1	NA	NA	NA

	cone size		*wing size*		*dispersal mode*			
species	**Width**	**Length**	**Width**	**Length**	**Bird**	**Wind**	**Animal**	**Rodent**
Pinus_albicaulis	5.5	6.55	0	0	1	0	1	1
Pinus_aristata	5	8.5	NA	1.15	1	1	1	0
Pinus_amamiana	3.5	6	NA	0.075	1	0	1	0
Pinus_arizonica	4.75	7.5	0.6	1.6	0	1	0	0
Pinus_armandii	6.5	11	NA	0.25	1	0	1	0
Pinus_attenuata	4.75	12	0.6	1.55	0	1	0	0
Pinus_ayacahuite	11	31.25	1	2.375	1	1	1	0
Pinus_balfouriana	5	7.75	NA	1.3	0	1	0	0
Pinus_banksiana	1.5	4.625	NA	1.1	0	1	0	0
Pinus_bhutanica	6	16	0.85	1.925	0	1	0	0
Pinus_brutia	6.5	8.5	0.95	1.7	1	1	1	0
Pinus_bungeana	4.5	5.625	NA	0.4	1	0	1	0
Pinus_canariensis	5.8	14.25	NA	2.55	0	1	0	0
Pinus_caribaea	5	9.25	0.65	1.63	0	1	0	0
Pinus_cembra	5	6.75	0	0	1	0	1	1
Pinus_cembroides	4.5	4	0	0	1	0	1	0
Pinus_chiapensis	5.5	12	NA	2.25	0	1	0	0
Pinus_clausa	3.2	6	NA	1.75	1	1	1	1
Pinus_contorta	2.5	4	NA	1.1	1	1	1	0
Pinus_cooperi	5	7.5	NA	2.25	0	1	0	0
Pinus_coulteri	17.5	26.25	1.4	2.4	0	1	0	0
Pinus_cubensis	4.25	5.5	0.55	1.475	0	1	0	0
Pinus_culminicola	4	3.625	0	0	1	0	1	0
Pinus_dalatensis	7	13.875	NA	2.125	0	1	0	0
Pinus_densata	5.5	5	NA	1.75	0	1	0	0
Pinus_densiflora	2	4.375	0.6	1.425	0	1	0	0
Pinus_devoniana	11.5	25	1.25	2.825	0	1	0	0
Pinus_discolor	3	3.5	NA	0.075	1	0	1	1
Pinus_douglasiana	6	8.5	0.8	2.175	0	1	0	0
Pinus_durangensis	5	7.5	0.75	1.575	0	1	0	0
Pinus_echinata	2.5	5.5	NA	1.425	0	1	0	0
Pinus_edulis	4.5	4.25	0	0	1	0	1	0
Pinus_elliottii	5	12	NA	2.075	1	1	1	0
Pinus_engelmannii	8	12	0.85	2.15	0	1	0	0
Pinus_fenzeliana	4.5	10	0	0	1	0	1	0
Pinus_flexilis	5	10.75	0	0	1	0	1	0
Pinus_fragilissima	6.5	7.5	0.6	1.8	0	1	0	0
Pinus_gerardiana	9.5	16.75	NA	0.45	1	0	1	0
Pinus_glabra	2.5	5.5	NA	1.275	0	1	0	0
Pinus_greggii	6	11.5	0.675	1.675	0	1	0	0
Pinus_halepensis	4	8	1	1.975	0	1	0	0
Pinus_hartwegii	6.5	10	0.95	1.675	0	1	0	0
Pinus_heldreichii	5	7.75	NA	2	0	1	0	0
Pinus_herrerae	2.75	3.625	0.4	0.65	0	1	0	0
Pinus_hwangshanensi	3.75	4.5	0.55	1.75	0	1	0	0
Pinus_jeffreyi	11.5	17.5	1	2.2	1	1	1	1
Pinus_johannis	3	4.5	NA	0.075	1	0	1	1
Pinus_juarezensis	5.75	4.25	NA	0.15	1	0	1	1
Pinus_kesiya	3.5	6	0.7	1.575	0	1	0	0
Pinus_koraiensis	7	10.75	0	0	1	0	1	1
Pinus_krempfii	4	7	0.45	1.26	0	1	0	0
Pinus_kwangtungensi	4.25	6	0.6	0.9	0	1	0	0
Pinus_lambertiana	11.5	40	1.35	2.5	0	1	0	0
Pinus_latteri	6.5	8	NA	1.75	0	1	0	0
Pinus_lawsonii	5	6.5	0.55	1.35	0	1	0	0
Pinus_leiophylla	4.75	6	0.6	1.325	0	1	0	0
Pinus_longaeva	5	7.875	NA	1.125	1	1	1	0
Pinus_luchuensis	2.75	4.125	NA	1.05	0	1	0	0
Pinus_lumholtzii	3.75	4.75	0.5	1.15	0	1	0	0
Pinus_maestrensis	4.25	5.5	0.55	1.475	0	1	0	0
Pinus_massoniana	3.75	5.75	0.6	1.825	0	1	0	0
Pinus_maximartinezii	11	21	0	0	1	0	1	0
Pinus_maximinoi	6	7.5	0.6	1.825	0	1	0	0
Pinus_merkusii	6	7.75	0	2.175	0	1	0	0
Pinus_monophylla	5.75	5.5	0	0	1	0	1	0
Pinus_montezumae	7.5	14.5	0.95	2.15	0	1	0	0
Pinus_monticola	3.5	17.5	NA	2.225	0	1	0	0
Pinus_morrisonicola	5.5	8.5	0.65	1.75	0	1	0	0
Pinus_mugo	3.25	4	NA	1.2	0	1	0	0
Pinus_muricata	4.5	6.5	0.65	1.65	0	1	0	0

	cone size		*wing size*		*dispersal mode*			
species	**Width**	**Length**	**Width**	**Length**	**Bird**	**Wind**	**Animal**	**Rodent**
Pinus_nelsonii	4.75	9.75	0	0	1	0	1	0
Pinus_nigra	3	7	NA	1.85	0	1	0	0
Pinus_occidentalis	5	7.25	0.5	1.375	0	1	0	0
Pinus_oocarpa	6	5.5	0.6	1.35	0	1	0	0
Pinus_palustris	10	21.25	1.1	3.125	0	1	0	0
Pinus_parviflora	4	7	0.86	1.075	1	1	1	0
Pinus_patula	5.25	8	0.65	1.625	0	1	0	0
Pinus_peuce	2.5	11.5	0	1.575	1	1	1	0
Pinus_pinaster	6.5	14.25	0.85	2.6	1	1	1	0
Pinus_pinceana	4.75	7.5	0	0	1	0	1	0
Pinus_pinea	9	10.5	NA	1	1	1	1	1
Pinus_ponderosa	4	9.25	0.7	1.8	1	1	1	0
Pinus_praetermissa	7	5.875	0.65	1.625	0	1	0	0
Pinus_pringlei	4.75	6.5	0.7	1.55	0	1	0	0
Pinus_pseudostrobus	9.5	12	0.85	2.2	0	1	0	0
Pinus_pumila	2.75	3.875	0	0	1	0	1	0
Pinus_pungens	5	7.25	NA	1.925	0	1	0	0
Pinus_quadrifolia	5.75	5	0	0	1	0	1	1
Pinus_radiata	8	10.25	0.85	1.975	0	1	0	0
Pinus_remota	4.5	3.25	0	0	1	0	1	0
Pinus_resinosa	2.6	5.125	NA	1.575	0	1	0	0
Pinus_rigida	7	6	NA	1.75	0	1	0	0
Pinus_roxburghii	9.5	13.75	0.9	2.25	0	1	0	0
Pinus_rzedowskii	7.25	12.5	1.5	2.625	0	1	0	0
Pinus_sabiniana	17.5	20.5	NA	1	0	1	0	0
Pinus_serotina	8	8	NA	1.75	0	1	0	0
Pinus_sibirica	5	8.75	0	0	1	0	1	0
Pinus_squamata	5.5	9	NA	1.5	0	1	0	0
Pinus_strobiformis	9	20.5	0	0	1	0	1	1
Pinus_strobus	6	14	NA	2.275	0	1	1	1
Pinus_sylvestris	4.5	4.5	0.55	1.25	0	1	0	0
Pinus_tabuliformis	6.25	6.25	0.6	1.375	0	1	0	0
Pinus_taeda	9	8.75	NA	1.85	0	1	0	0
Pinus_taiwanensis	3.75	5.75	NA	1.5	0	1	0	0
Pinus_teocote	3.75	5.5	0.7	1.375	0	1	0	0
Pinus_thunbergii	3.75	5.125	NA	1.25	0	1	0	0
Pinus_torreyana	12.5	13.75	NA	1.125	0	1	0	0
Pinus_tropicalis	4.75	7	0.55	1.3875	0	1	0	0
Pinus_virginiana	2.7	5.625	NA	1.775	0	1	0	0
Pinus_wallichiana	3.5	23.75	0.9	2.375	0	1	0	0
Pinus_washoensis	6.5	8.5	NA	1.6	0	1	0	0
Pinus_yecorensis	5	10.25	NA	2.05	0	1	0	0
Pinus_yunnanensis	4	7.25	0.5	1.375	0	1	0	0

	fire response						
species	**Serotiny**	**BarkC**	**Grass Stage**	**Branch**	**Bark**	**Resprout**	**FireRes**
Pinus_albicaulis	0	1	0	0	1.27	0	1
Pinus_aristata	0	2	0	0	1.575	0	0
Pinus_amamiana	0	1	0	0	1.5	0	0
Pinus_arizonica	0	3	0	1	5	0	1
Pinus_armandii	0	1	0	0	1.5	0	0
Pinus_attenuata	1	1	0	0	0.965	0	1
Pinus_ayacahuite	0	3	0	0	NA	0	0
Pinus_balfouriana	0	2	0	1	1.575	0	1
Pinus_banksiana	1	1	0	1	1.27	0	1
Pinus_bhutanica	0	1	0	0	NA	0	0
Pinus_brutia	1	3	0	0	4.445	0	1
Pinus_bungeana	0	1	0	0	NA	0	0
Pinus_canariensis	1	3	0	0	3	1	1
Pinus_caribaea	0	3	0	1	NA	1	1
Pinus_cembra	0	1	0	0	NA	0	0
Pinus_cembroides	0	1	0	1	1.27	0	1
Pinus_chiapensis	0	2	0	0	NA	0	1
Pinus_clausa	1	1	0	0	1.016	0	1
Pinus_contorta	1	1	0	0	1.016	0	1
Pinus_cooperi	0	3	0	1	NA	0	1
Pinus_coulteri	1	2	0	0	1.75	0	1
Pinus_cubensis	0	3	0	1	NA	0	1
Pinus_culminicola	0	1	0	0	NA	0	0
Pinus_dalatensis	0	3	0	0	NA	0	0
Pinus_densata	0	3	0	1	NA	0	0
Pinus_densiflora	0	1	0	0	NA	0	1
Pinus_devoniana	0	3	1	1	NA	0	1
Pinus_discolor	0	1	0	0	NA	0	0
Pinus_douglasiana	0	3	1	1	NA	0	1
Pinus_durangensis	0	3	1	1	NA	0	1
Pinus_echinata	0	2	0	1	2.083	1	1
Pinus_edulis	0	2	0	0	1.575	0	0
Pinus_elliottii	0	3	1	1	3.048	0	1
Pinus_engelmannii	0	3	1	1	4.445	0	1
Pinus_fenzeliana	0	1	0	0	NA	0	0
Pinus_flexilis	0	3	0	1	3.81	0	1
Pinus_fragilissima	0	3	0	1	3	0	0
Pinus_gerardiana	0	1	0	0	NA	0	0
Pinus_glabra	0	3	0	0	3.09	0	0
Pinus_greggii	1	3	0	0	NA	0	1
Pinus_halepensis	1	3	0	0	3.81	0	1
Pinus_hartwegii	0	3	1	1	NA	1	0
Pinus_heldreichii	0	3	1	1	3.2	0	0
Pinus_herrerae	0	3	0	1	NA	0	0
Pinus_hwangshanensi	0	1	0	0	NA	0	0
Pinus_jeffreyi	0	3	0	1	7.62	0	0
Pinus_johannis	0	1	0	0	NA	0	0
Pinus_juarezensis	0	3	0		NA	0	0
Pinus_kesiya	0	3	0	1	NA	0	1
Pinus_koraiensis	0	3	0	1	NA	0	1
Pinus_krempfii	0	1	0	0	NA	0	0
Pinus_kwangtungensi	0	1	0	0	0.6	0	0
Pinus_lambertiana	0	3	0	1	6.985	0	0
Pinus_latteri	0	3	1	1	3.81	0	1
Pinus_lawsonii	0	3	0	1	NA	0	0
Pinus_leiophylla	1	3	0	1	6.985	1	1
Pinus_longaeva	0	1	0	0	NA	0	0
Pinus_luchuensis	0	3	0	0	NA	0	0
Pinus_lumholtzii	0	3	0	1	NA	0	0
Pinus_maestrensis	0	3	0	1	NA	0	1
Pinus_massoniana	0	3	0	1	NA	1	0
Pinus_maximartinezii	0	1	0	0	NA	0	0
Pinus_maximinoi	0	1	0	0	NA	0	0
Pinus_merkusii	0	3	1	1	3.81	0	1
Pinus_monophylla	0	2	0	0	1.905	0	0
Pinus_montezumae	0	3	1	1	NA	0	0
Pinus_monticola	0	3	0	1	3.175	0	0
Pinus_morrisonicola	0	1	0	0	NA	0	0
Pinus_mugo	0	1	0	0	3	0	0
Pinus_muricata	1	3	0	0	6.35	0	1

	fire response						
species	**Serotiny**	**BarkC**	**Grass Stage**	**Branch**	**Bark**	**Resprout**	**FireRes**
Pinus_nelsonii	0	1	0	0	NA	0	0
Pinus_nigra	0	2	0	0	3.1	0	0
Pinus_occidentalis	0	3	0	0	NA	1	0
Pinus_oocarpa	1	3	0	1	NA	1	1
Pinus_palustris	0	3	1	0	2.794	0	1
Pinus_parviflora	0	1	0	1	NA	0	1
Pinus_patula	1	3	0	NA	NA	1	0
Pinus_peuce	0	1	0	NA	NA	0	0
Pinus_pinaster	1	3	0	NA	3.175	0	0
Pinus_pinceana	0	1	0	1	NA	0	0
Pinus_pinea	0	3	0	NA	3.3	0	1
Pinus_ponderosa	0	3	0	1	7.62	0	1
Pinus_praetermissa	0	3	0	1	NA	0	0
Pinus_pringlei	1	3	0	1	NA	1	0
Pinus_pseudostrobus	0	3	0	1	NA	0	1
Pinus_pumila	0	1	0	1	NA	0	0
Pinus_pungens	1	1	0	NA	1.905	0	1
Pinus_quadrifolia	0	1	0	NA	1.524	0	0
Pinus_radiata	1	3	0	NA	4.445	0	1
Pinus_remota	0	2	0	NA	NA	0	0
Pinus_resinosa	0	3	0	NA	4.445	0	1
Pinus_rigida	1	3	0	1	3.048	1	1
Pinus_roxburghii	1	3	0	NA	3.5	1	1
Pinus_rzedowskii	0	2	0	NA	NA	0	1
Pinus_sabiniana	0	2	0	NA	1.75	0	1
Pinus_serotina	1	1	0	1	1.575	1	1
Pinus_sibirica	0	2	0	NA	1.651	0	0
Pinus_squamata	0	3	0	NA	NA	0	0
Pinus_strobiformis	0	1	0	1	1.05	0	0
Pinus_strobus	0	3	0	0	3.175	0	1
Pinus_sylvestris	0	3	0	1	3.175	0	0
Pinus_tabuliformis	0	1	0	1	NA	0	0
Pinus_taeda	0	3	0	1	3.505	0	0
Pinus_taiwanensis	0	1	0	0	NA	0	0
Pinus_teocote	0	3	0	1	NA	1	0
Pinus_thunbergii	0	3	0	1	NA	0	0
Pinus_torreyana	1	2	0	0	1	0	0
Pinus_tropicalis	0	3	1	0	NA	0	1
Pinus_virginiana	1	1	0	1	1.27	1	0
Pinus_wallichiana	0	3	0	0	NA	0	0
Pinus_washoensis	0	3	0	0	7.62	0	0
Pinus_yecorensis	0	3	0	1	NA	0	0
Pinus_yunnanensis	1	3	1	0	NA	1	0

	seed character					
species	**Length**	**Width**	**Mass**	**RGR**	**RGRmax**	**MastI**
Pinus_albicaulis	0.9	0.55	150.7	NA	NA	4
Pinus_aristata	0.55	0.35	22.1	NA	NA	5.5
Pinus_amamiana	1.1	0.5	NA	NA	NA	NA
Pinus_arizonica	0.6	0.4	43	NA	NA	2.5
Pinus_armandii	1.15	0.8	262.8	NA	NA	5
Pinus_attenuata	0.6	0.4	16.4	NA	NA	1
Pinus_ayacahuite	1.15	0.75	48	NA	NA	1.5
Pinus_balfouriana	0.85	0.5	22.9	NA	NA	5.5
Pinus_banksiana	0.4	0.2	3.7	38.6	NA	3.5
Pinus_bhutanica	0.7	0.45	NA	NA	NA	NA
Pinus_brutia	0.75	0.5	38.9	NA	NA	1
Pinus_bungeana	0.925	0.55	117.8	NA	NA	NA
Pinus_canariensis	1.2	0.65	101.5	33.7	47	3.5
Pinus_caribaea	0.575	0.3	17.3	28.7	NA	5.5
Pinus_cembra	1.25	0.7	264.3	12.8	22	4.5
Pinus_cembroides	1.3	0.8	345	NA	NA	6.5
Pinus_chiapensis	0.65	0.3	16.1	NA	NA	NA
Pinus_clausa	0.5	0.2	6	NA	NA	1.5
Pinus_contorta	0.45	0.3	3.5	36.5	51.9	1
Pinus_cooperi	0.4	0.4	NA	NA	NA	NA
Pinus_coulteri	1.5	0.85	319	32	49.2	4.5
Pinus_cubensis	0.6	0.325	NA	NA	NA	NA
Pinus_culminicola	0.6	0.45	25	NA	NA	NA
Pinus_dalatensis	0.7	NA	NA	NA	NA	NA
Pinus_densata	0.525	NA	NA	NA	NA	NA
Pinus_densiflora	0.5	0.4	8.7	NA	NA	2
Pinus_devoniana	0.7	0.6	33	NA	NA	NA
Pinus_discolor	1.2	NA	NA	NA	NA	NA
Pinus_douglasiana	0.575	0.325	NA	NA	NA	NA
Pinus_durangensis	0.625	0.425	41.6	NA	NA	10
Pinus_echinata	0.65	0.4	9.9	NA	NA	6.5
Pinus_edulis	1.25	0.75	268.5	NA	NA	3.5
Pinus_elliottii	0.65	0.4	35.2	31.6	NA	3
Pinus_engelmannii	0.65	0.48	41	NA	NA	3.5
Pinus_fenzeliana	1.1	0.65	NA	NA	NA	NA
Pinus_flexilis	1.25	0.9	119.8	20.4	21.6	3
Pinus_fragilissima	0.55	0.3	NA	NA	NA	NA
Pinus_gerardiana	2.25	1	412.3	NA	NA	3.5
Pinus_glabra	0.6	0.35	9.2	36.6	53.6	1
Pinus_greggii	0.65	0.35	14.1	NA	NA	NA
Pinus_halepensis	0.6	0.45	19.7	38.3	51.3	1
Pinus_hartwegii	0.55	0.5	NA	NA	NA	NA
Pinus_heldreichii	0.65	0.5	23.7	NA	NA	NA
Pinus_herrerae	0.35	0.25	5	NA	NA	NA
Pinus_hwangshanensi	0.6	NA	NA	NA	NA	NA
Pinus_jeffreyi	1.55	0.6	114.5	26.6	38.5	3
Pinus_johannis	1.25	1	379.8	NA	NA	NA
Pinus_juarezensis	1.475	0.7	NA	NA	NA	NA
Pinus_kesiya	0.55	0.4	16.8	NA	NA	1
Pinus_koraiensis	1.55	0.8	487.5	NA	NA	4
Pinus_krempfii	0.4	NA	NA	NA	NA	NA
Pinus_kwangtungensi	1	NA	NA	NA	NA	NA
Pinus_lambertiana	1.5	0.8	225.1	18.4	29.2	4
Pinus_latteri	1	0.4	NA	NA	NA	NA
Pinus_lawsonii	0.45	NA	NA	NA	NA	NA
Pinus_leiophylla	0.4	NA	11.8	NA	NA	NA
Pinus_longaeva	0.65	0.4	NA	NA	NA	NA
Pinus_luchuensis	0.35	NA	NA	NA	NA	NA
Pinus_lumholtzii	0.4	NA	NA	NA	NA	NA
Pinus_maestrensis	0.6	0.325	NA	NA	NA	NA
Pinus_massoniana	0.525	NA	NA	NA	NA	NA
Pinus_maximartinezii	2.35	NA	1278	NA	NA	4.5
Pinus_maximinoi	0.55	0.35	NA	NA	NA	NA
Pinus_merkusii	0.65	0.45	34.3	NA	NA	1.5
Pinus_monophylla	1.55	1	403.4	NA	NA	1.5
Pinus_montezumae	0.6	0.45	27.4	NA	NA	NA
Pinus_monticola	0.65	NA	16.9	NA	NA	5
Pinus_morrisonicola	0.8	0.4	NA	NA	NA	NA
Pinus_mugo	0.5	NA	6.6	NA	NA	1
Pinus_muricata	0.65	0.375	9.6	47.4	62.5	2.5

	seed character					
species	**Length**	**Width**	**Mass**	**RGR**	**RGRmax**	**MastI**
Pinus_nelsonii	30	1000	482	NA	NA	2.5
Pinus_nigra	194.5	5000	19.2	29.3	60.1	3.5
Pinus_occidentalis	135	4250	NA	NA	NA	NA
Pinus_oocarpa	125	4500	15.5	NA	NA	NA
Pinus_palustris	120	4700	86.5	32.3	34.2	6
Pinus_parviflora	125	2500	116.3	NA	NA	4.5
Pinus_patula	100	4000	8.3	41.9	70.3	1
Pinus_peuce	100	3000	51.6	NA	NA	1
Pinus_pinaster	150	4000	50.4	38.9	49.7	1
Pinus_pinceana	30	1200	254	NA	NA	NA
Pinus_pinea	125	2750	757.9	25.7	38.6	6
Pinus_ponderosa	265	7350	38.1	30	41.7	3.5
Pinus_praetermissa	30	2000	NA	NA	NA	NA
Pinus_pringlei	100	2500	14	NA	NA	NA
Pinus_pseudostrobus	125	4750	NA	NA	NA	NA
Pinus_pumila	15	600	78.8	NA	NA	3
Pinus_pungens	70	2250	12.6	NA	NA	NA
Pinus_quadrifolia	60	1550	379	NA	NA	NA
Pinus_radiata	210	3650	31	45.8	71.1	1
Pinus_remota	40	900	NA	NA	NA	NA
Pinus_resinosa	125	3750	9.1	27.7	56	5
Pinus_rigida	115	3000	7.2	36.2	58.8	6.5
Pinus_roxburghii	75	5500	104.3	NA	NA	3
Pinus_rzedowskii	90	4000	56	NA	NA	4
Pinus_sabiniana	125	3750	706	20.3	27	3
Pinus_serotina	60	2000	8.2	NA	NA	1
Pinus_sibirica	180	4000	NA	NA	NA	NA
Pinus_squamata	60	2000	NA	NA	NA	NA
Pinus_strobiformis	125	3250	268.3	NA	NA	3.5
Pinus_strobus	190	6350	17.2	28.7	38.7	6.5
Pinus_sylvestris	160	4000	7.5	42.4	71.7	3.5
Pinus_tabuliformis	120	2750	36	NA	NA	NA
Pinus_taeda	155	4500	25.6	33.9	75	8
Pinus_taiwanensis	110	5000	9.7	NA	NA	NA
Pinus_teocote	77.5	2500	NA	NA	NA	NA
Pinus_thunbergii	200	3750	14.7	35.7	47.8	1
Pinus_torreyana	150	3150	933.5	18.6	NA	1
Pinus_tropicalis	100	3000	35	NA	NA	NA
Pinus_virginiana	75	3000	8.2	38.2	69.9	1
Pinus_wallichiana	150	7000	49.8	NA	NA	2.5
Pinus_washoensis	100	6000	62.3	NA	NA	NA
Pinus_yecorensis	95	3000	NA	NA	NA	NA
Pinus_yunnanensis	100	3000	NA	NA	NA	NA

	life history characters							
species	**Cval**	**Genome**	**Z**	**Inva**	**mxAge**	**mnGen**	**mnAgeSeed**	**NAR**
Pinus_albicaulis	NA	30.9	-6.1	NA	1267	20	2	NA
Pinus_aristata	NA	29.1	-2.9	NA	2435	20	2	NA
Pinus_amamiana	NA	NA	NA	NA	NA	NA	NA	NA
Pinus_arizonica	NA	26.2	1.5	NA	400	15	NA	NA
Pinus_armandii	NA	35.5	-9.6	NA	NA	20	2	NA
Pinus_attenuata	22.09	26.8	11.1	NA	80	5	1	NA
Pinus_ayacahuite	NA	36	8.7	NA	NA	5	NA	NA
Pinus_balfouriana	NA	29.9	-3	NA	2500	20	2	NA
Pinus_banksiana	NA	22.2	11.6	1	246	3	1	0.57
Pinus_bhutanica	NA	NA	NA	NA	NA	NA	NA	NA
Pinus_brutia	NA	33	8.1	NA	NA	7	1	NA
Pinus_bungeana	NA	33.4	NA	NA	NA	NA	NA	NA
Pinus_canariensis	NA	33.4	-1.8	NA	NA	15	2	0.6
Pinus_caribaea	NA	25.5	1.3	NA	NA	12	NA	0.54
Pinus_cembra	NA	32	-9.1	0	1000	20	3	0.36
Pinus_cembroides	NA	33.9	-10.4	NA	NA	15	NA	NA
Pinus_chiapensis	NA	32.3	NA	NA	NA	10	NA	NA
Pinus_clausa	19.94	23.4	11.5	NA	100	5	1	NA
Pinus_contorta	NA	22.1	13.4	1	628	4	1	0.54
Pinus_cooperi	NA	NA	NA	NA	NA	NA	NA	NA
Pinus_coulteri	28.33	31.5	-3.7	0	NA	8	2	0.66
Pinus_cubensis	NA	NA	NA	NA	NA	NA	NA	NA
Pinus_culminicola	NA	30.1	NA	NA	NA	NA	NA	NA
Pinus_dalatensis	NA	NA	NA	NA	NA	NA	NA	NA
Pinus_densata	NA	NA	NA	NA	NA	NA	NA	NA
Pinus_densiflora	NA	26.4	2	NA	NA	20	2	NA
Pinus_devoniana	NA	27.7	NA	NA	NA	NA	NA	NA
Pinus_discolor	NA	NA	NA	NA	NA	NA	3	NA
Pinus_douglasiana	NA	NA	NA	NA	NA	NA	NA	NA
Pinus_durangensis	NA	26.5	-2.6	NA	NA	8	NA	NA
Pinus_echinata	21.73	24.8	5.6	NA	324	5	1	NA
Pinus_edulis	NA	32.9	-10.1	NA	1101	25	3	NA
Pinus_elliottii	22.36	24.9	5.4	1	NA	8	1	0.51
Pinus_engelmannii	NA	26.6	-5	NA	NA	28	3	NA
Pinus_fenzeliana	NA	NA	NA	NA	NA	NA	NA	NA
Pinus_flexilis	29.58	32.7	-4.1	0	1697	20	3	0.45
Pinus_fragilissima	NA	NA	NA	NA	NA	NA	NA	NA
Pinus_gerardiana	NA	36.9	-13.7	NA	300	28	NA	NA
Pinus_glabra	NA	24	8.1	NA	NA	10	2	0.56
Pinus_greggii	NA	24	NA	NA	NA	5	NA	NA
Pinus_halepensis	NA	32.3	9.2	1	NA	7	2	0.6
Pinus_hartwegii	NA	NA	NA	NA	450	NA	NA	NA
Pinus_heldreichii	NA	33.5	NA	NA	963	NA	NA	NA
Pinus_herrerae	NA	24.6	NA	NA	NA	10	NA	NA
Pinus_hwangshanensi	NA	NA	NA	NA	NA	NA	NA	NA
Pinus_jeffreyi	24.91	29.2	2.4	NA	813	8	1	0.57
Pinus_johannis	NA	32.9	NA	NA	NA	NA	NA	NA
Pinus_juarezensis	NA	NA	NA	NA	NA	NA	NA	NA
Pinus_kesiya	NA	29.3	11	NA	NA	5	1	NA
Pinus_koraiensis	NA	33.2	-9.9	NA	NA	15	2	NA
Pinus_krempfii	NA	NA	NA	NA	NA	NA	NA	NA
Pinus_kwangtungensi	NA	NA	NA	NA	NA	NA	NA	NA
Pinus_lambertiana	31.76	34.2	-15	0	800	40	3	0.5
Pinus_latteri	NA	NA	NA	NA	NA	NA	NA	NA
Pinus_lawsonii	NA	NA	NA	NA	NA	NA	NA	NA
Pinus_leiophylla	NA	24.8	NA	NA	NA	NA	3	NA
Pinus_longaeva	NA	NA	NA	NA	5000	NA	NA	NA
Pinus_luchuensis	NA	NA	NA	NA	NA	NA	NA	NA
Pinus_lumholtzii	NA	NA	NA	NA	NA	NA	NA	NA
Pinus_maestrensis	NA	NA	NA	NA	NA	NA	NA	NA
Pinus_massoniana	NA	NA	NA	NA	NA	NA	NA	NA
Pinus_maximartinezii	NA	31.2	-18	NA	NA	13	NA	NA
Pinus_maximinoi	NA	NA	NA	NA	NA	NA	NA	NA
Pinus_merkusii	NA	33.3	5.8	NA	NA	10	NA	NA
Pinus_monophylla	27.36	32.8	-8.3	NA	900	20	2	NA
Pinus_montezumae	NA	27.3	NA	NA	NA	NA	NA	NA
Pinus_monticola	29.3	31.5	3.1	NA	707	10	1	NA
Pinus_morrisonicola	NA	NA	NA	NA	NA	NA	NA	NA
Pinus_mugo	NA	25.9	5.7	NA	NA	15	2	NA
Pinus_muricata	NA	24.5	10	1	NA	5	1	0.76

	life history characters							
species	**Cval**	**Genome**	**Z**	**Inva**	**mxAge**	**mnGen**	**mnAgeSeed**	**NAR**
Pinus_nelsonii	NA	36.1	-9.2	NA	NA	17	NA	NA
Pinus_nigra	NA	26.9	1.8	1	NA	15	2	0.48
Pinus_occidentalis	NA	NA	NA	NA	NA	NA	NA	NA
Pinus_oocarpa	NA	25.2	NA	NA	NA	5	NA	NA
Pinus_palustris	23.04	25.9	-6.4	0	460	20	NA	0.67
Pinus_parviflora	NA	31.9	NA	NA	NA	NA	NA	NA
Pinus_patula	NA	24.8	8.2	1	NA	10	NA	0.6
Pinus_peuce	NA	34	5.5	NA	NA	10	2	NA
Pinus_pinaster	NA	30.9	8.3	1	NA	6	1	0.66
Pinus_pinceana	NA	32	NA	NA	NA	NA	NA	NA
Pinus_pinea	NA	30.4	-15.5	NA	150	15	1	0.57
Pinus_ponderosa	NA	25.9	0.7	1	980	15	2	0.58
Pinus_praetermissa	NA	NA	NA	NA	NA	NA	NA	NA
Pinus_pringlei	NA	25.8	NA	NA	NA	NA	NA	NA
Pinus_pseudostrobus	NA	NA	NA	NA	NA	NA	NA	NA
Pinus_pumila	NA	31.1	-4.1	NA	NA	23	NA	NA
Pinus_pungens	NA	NA	NA	NA	232	NA	1	NA
Pinus_quadrifolia	NA	NA	NA	NA	200	NA	NA	NA
Pinus_radiata	23.12	26.4	10.1	1	NA	5	1	0.61
Pinus_remota	NA	NA	NA	NA	NA	NA	NA	NA
Pinus_resinosa	NA	28.5	-1.3	0	500	20	NA	0.46
Pinus_rigida	NA	25.5	3.6	NA	351	8	1	0.53
Pinus_roxburghii	NA	35.3	-1.3	NA	NA	15	2	NA
Pinus_rzedowskii	NA	32.8	NA	NA	NA	NA	NA	NA
Pinus_sabiniana	28.35	32.3	-8.9	0	NA	10	2	0.46
Pinus_serotina	21.02	23.6	12.7	NA	NA	4	1	NA
Pinus_sibirica	NA	NA	NA	NA	629	NA	3	NA
Pinus_squamata	NA	NA	NA	NA	NA	NA	NA	NA
Pinus_strobiformis	NA	35.4	-5.8	NA	599	15	NA	NA
Pinus_strobus	29.04	31.3	5	1	450	5	1	0.43
Pinus_sylvestris	NA	25.9	9.2	1	1244	5	1	0.6
Pinus_tabuliformis	NA	29.3	NA	NA	NA	NA	1	NA
Pinus_taeda	22.14	24.8	2.8	1	300	5	1	0.5
Pinus_taiwanensis	NA	27.9	NA	NA	NA	NA	NA	NA
Pinus_teocote	NA	NA	NA	NA	NA	NA	NA	NA
Pinus_thunbergii	NA	27.3	10.4	NA	NA	6	1	0.56
Pinus_torreyana	26.33	31.3	-10.4	0	150	12	2	0.48
Pinus_tropicalis	NA	30.5	NA	NA	NA	NA	NA	NA
Pinus_virginiana	20.35	22.5	11.8	NA	200	5	1	0.54
Pinus_wallichiana	NA	30.2	1.2	NA	410	15	2	NA
Pinus_washoensis	NA	26.8	NA	NA	NA	NA	2	NA
Pinus_yecorensis	NA	NA	NA	NA	NA	NA	NA	NA
Pinus_yunnanensis	NA	NA	NA	NA	NA	NA	NA	NA

	wood characters						
species	**Grav**	**DWeight**	**Rupture**	**Hardn**	**Elast**	**Str**	**shrink**
Pinus_albicaulis	NA	NA	NA	NA	NA	20	2
Pinus_aristata	NA	NA	NA	NA	NA	20	2
Pinus_amamiana	NA	NA	NA	NA	NA	NA	NA
Pinus_arizonica	NA	NA	NA	NA	NA	15	NA
Pinus_armandii	NA	NA	NA	NA	NA	20	2
Pinus_attenuata	NA	NA	NA	NA	NA	5	1
Pinus_ayacahuite	NA	NA	NA	NA	NA	5	NA
Pinus_balfouriana	NA	NA	NA	NA	NA	20	2
Pinus_banksiana	0.4	31	9900	570	135000	3	1
Pinus_bhutanica	NA	NA	NA	NA	NA	NA	NA
Pinus_brutia	NA	NA	NA	NA	NA	7	1
Pinus_bungeana	NA	NA	NA	NA	NA	NA	NA
Pinus_canariensis	NA	NA	NA	NA	NA	15	2
Pinus_caribaea	0.51	NA	13340	1110	1745000	12	NA
Pinus_cembra	NA	NA	NA	NA	NA	20	3
Pinus_cembroides	NA	NA	NA	NA	NA	15	NA
Pinus_chiapensis	NA	NA	NA	NA	NA	10	NA
Pinus_clausa	0.46	34	11600	730	1410000	5	1
Pinus_contorta	0.38	29	9400	480	1340000	4	1
Pinus_cooperi	NA	NA	NA	NA	NA	NA	NA
Pinus_coulteri	NA	NA	NA	NA	NA	8	2
Pinus_cubensis	NA	NA	NA	NA	NA	NA	NA
Pinus_culminicola	NA	NA	NA	NA	NA	NA	NA
Pinus_dalatensis	NA	NA	NA	NA	NA	NA	NA
Pinus_densata	NA	NA	NA	NA	NA	NA	NA
Pinus_densiflora	NA	NA	NA	NA	NA	20	2
Pinus_devoniana	NA	NA	NA	NA	NA	NA	NA
Pinus_discolor	NA	NA	NA	NA	NA	NA	3
Pinus_douglasiana	NA	NA	NA	NA	NA	NA	NA
Pinus_durangensis	NA	NA	NA	NA	NA	8	NA
Pinus_echinata	0.47	35	13100	690	1750000	5	1
Pinus_edulis	0.5	37	7800	860	1140000	25	3
Pinus_elliottii	0.54	41	16300	760	1980000	8	1
Pinus_engelmannii	NA	NA	NA	NA	NA	28	3
Pinus_fenzeliana	NA	NA	NA	NA	NA	NA	NA
Pinus_flexilis	0.37	28	9100	430	1170000	20	3
Pinus_fragilissima	NA	NA	NA	NA	NA	NA	NA
Pinus_gerardiana	NA	NA	NA	NA	NA	28	NA
Pinus_glabra	0.41	32	10400	660	1230000	10	2
Pinus_greggii	NA	NA	NA	NA	NA	5	NA
Pinus_halepensis	NA	NA	NA	NA	NA	7	2
Pinus_hartwegii	NA	NA	NA	NA	NA	NA	NA
Pinus_heldreichii	NA	NA	NA	NA	NA	NA	NA
Pinus_herrerae	NA	NA	NA	NA	NA	10	NA
Pinus_hwangshanensi	NA	NA	NA	NA	NA	NA	NA
Pinus_jeffreyi	0.37	28	9300	500	1240000	8	1
Pinus_johannis	NA	NA	NA	NA	NA	NA	NA
Pinus_juarezensis	NA	NA	NA	NA	NA	NA	NA
Pinus_kesiya	0.45	38	12610	670	1776000	5	1
Pinus_koraiensis	NA	NA	NA	NA	NA	15	2
Pinus_krempfii	NA	NA	NA	NA	NA	NA	NA
Pinus_kwangtungensi	NA	NA	NA	NA	NA	NA	NA
Pinus_lambertiana	0.34	25	8200	380	1190000	40	3
Pinus_latteri	NA	NA	NA	NA	NA	NA	NA
Pinus_lawsonii	NA	NA	NA	NA	NA	NA	NA
Pinus_leiophylla	NA	NA	NA	NA	NA	NA	3
Pinus_longaeva	NA	NA	NA	NA	NA	NA	NA
Pinus_luchuensis	NA	NA	NA	NA	NA	NA	NA
Pinus_lumholtzii	NA	NA	NA	NA	NA	NA	NA
Pinus_maestrensis	NA	NA	NA	NA	NA	NA	NA
Pinus_massoniana	NA	NA	NA	NA	NA	NA	NA
Pinus_maximartinezii	NA	NA	NA	NA	NA	13	NA
Pinus_maximinoi	NA	NA	NA	NA	NA	NA	NA
Pinus_merkusii	0.57	44	15750	870	2327000	10	NA
Pinus_monophylla	NA	NA	NA	NA	NA	20	2
Pinus_montezumae	NA	NA	NA	NA	NA	NA	NA
Pinus_monticola	0.35	27	9700	420	1460000	10	1
Pinus_morrisonicola	NA	NA	NA	NA	NA	NA	NA
Pinus_mugo	NA	NA	NA	NA	NA	15	2
Pinus_muricata	NA	NA	NA	NA	NA	5	1

	wood characters						
species	**Grav**	**DWeight**	**Rupture**	**Hardn**	**Elast**	**Str**	**shrink**
Pinus_nelsonii	NA	NA	NA	NA	NA	NA	NA
Pinus_nigra	0.39	30	9340	660	1568000	NA	NA
Pinus_occidentalis	NA	NA	NA	NA	NA	NA	NA
Pinus_oocarpa	0.55	44	14720	950	2209000	NA	NA
Pinus_palustris	0.54	41	14500	870	1980000	NA	NA
Pinus_parviflora	NA	NA	NA	NA	NA	NA	NA
Pinus_patula	0.45	36	11500	550	1463000	NA	NA
Pinus_peuce	NA	NA	NA	NA	NA	NA	NA
Pinus_pinaster	0.39	31	10590	390	1238000	566	1.8
Pinus_pinceana	NA	NA	NA	NA	NA	NA	NA
Pinus_pinea	NA	NA	NA	NA	NA	NA	NA
Pinus_ponderosa	0.38	28	9400	460	1290000	NA	NA
Pinus_praetermissa	NA	NA	NA	NA	NA	NA	NA
Pinus_pringlei	NA	NA	NA	NA	NA	789	1.2
Pinus_pseudostrobus	NA	NA	NA	NA	NA	NA	NA
Pinus_pumila	NA	NA	NA	NA	NA	NA	NA
Pinus_pungens	0.49	36	11600	730	1550000	NA	NA
Pinus_quadrifolia	NA	NA	NA	NA	NA	692	1.9
Pinus_radiata	0.41	32	11480	710	1458000	537	1.6
Pinus_remota	NA	NA	NA	NA	NA	NA	NA
Pinus_resinosa	0.41	34	11000	560	1630000	NA	NA
Pinus_rigida	0.47	34	10800	620	1430000	NA	NA
Pinus_roxburghii	NA	NA	NA	NA	NA	NA	NA
Pinus_rzedowskii	NA	NA	NA	NA	NA	NA	NA
Pinus_sabiniana	NA	NA	NA	NA	NA	NA	NA
Pinus_serotina	0.51	38	11600	740	1750000	NA	NA
Pinus_sibirica	NA	NA	NA	NA	NA	NA	NA
Pinus_squamata	NA	NA	NA	NA	NA	NA	NA
Pinus_strobiformis	NA	NA	NA	NA	NA	NA	NA
Pinus_strobus	0.34	25	8600	380	1240000	NA	NA
Pinus_sylvestris	0.39	34	12080	540	1461000	727	1.7
Pinus_tabuliformis	NA	NA	NA	NA	NA	640	1.1
Pinus_taeda	0.47	35	12800	690	1790000	814	1.4
Pinus_taiwanensis	NA	NA	NA	NA	NA	NA	NA
Pinus_teocote	NA	NA	NA	NA	NA	NA	NA
Pinus_thunbergii	NA	NA	NA	NA	NA	529	2.1
Pinus_torreyana	NA	NA	NA	NA	NA	NA	NA
Pinus_tropicalis	NA	NA	NA	NA	NA	NA	NA
Pinus_virginiana	0.45	32	13000	740	1520000	565	NA
Pinus_wallichiana	NA	NA	NA	NA	NA	NA	NA
Pinus_washoensis	NA	NA	NA	NA	NA	NA	NA
Pinus_yecorensis	NA	NA	NA	NA	NA	NA	NA
Pinus_yunnanensis	NA	NA	NA	NA	NA	NA	NA

3.3 S3 - Species distribution maps

Pinus albicaulis

Pinus aristata

Pinus arizonica

Pinus armandii

Pinus attenuata

Pinus ayacahuite

Pinus balfouriana

Pinus banksiana

Pinus bhutanica

Pinus brutia


Pinus bungeana


Pinus canariensis


Pinus caribaea


Pinus cembra


Pinus cembroides

Pinus chiapensis

Pinus clausa

Pinus contorta

Pinus cooperi

Pinus coulteri


Pinus cubensis


Pinus culminicola


Pinus dalatensis


Pinus densata


Pinus densiflora


Pinus devoniana


Pinus discolor


Pinus douglasiana


Pinus durangensis


Pinus echinata


Pinus edulis


Pinus elliottii


Pinus engelmannii


Pinus fenzeliana


Pinus flexilis


Pinus fragilissima


Pinus gerardiana


Pinus glabra


Pinus greggii


Pinus halepensis

Pinus hartwegii

Pinus heldreichii

Pinus herrerae

Pinus hwangshanensis

Pinus jeffreyi


Pinus johannis


Pinus juarezensis


Pinus kesiya


Pinus krempfii


Pinus koraiensis

Pinus kwangtungensis

Pinus lambertiana

Pinus latteri

Pinus lawsonii

Pinus leiophylla

Pinus longaeva

Pinus luchuensis

Pinus lumholtzii

Pinus maestrensis

Pinus massoniana

Pinus maximartinezii

Pinus maximinoi

Pinus merkusii

Pinus monophylla

Pinus montezumae


Pinus monticola


Pinus morrisonicola


Pinus mugo


Pinus muricata


Pinus nelsonii


Pinus nigra


Pinus occidentalis


Pinus oocarpa


Pinus palustris


Pinus parviflora


Pinus patula


Pinus peuce


Pinus pinaster


Pinus pinceana


Pinus pinea

Pinus ponderosa

Pinus praetermissa

Pinus pringlei

Pinus pseudostrobus

Pinus pumila


Pinus pungens


Pinus quadrifolia


Pinus radiata


Pinus remota


Pinus resinosa


Pinus rigida


Pinus roxburghii


Pinus rzedowskii


Pinus sabiniana


Pinus serotina


Pinus sibirica


Pinus squamata


Pinus strobiformis


Pinus strobus


Pinus sylvestris


Pinus tabuliformis


Pinus taeda


Pinus taiwanensis


Pinus teocote


Pinus thunbergii

Pinus torreyana

Pinus tropicalis

Pinus virginiana

Pinus wallichiana

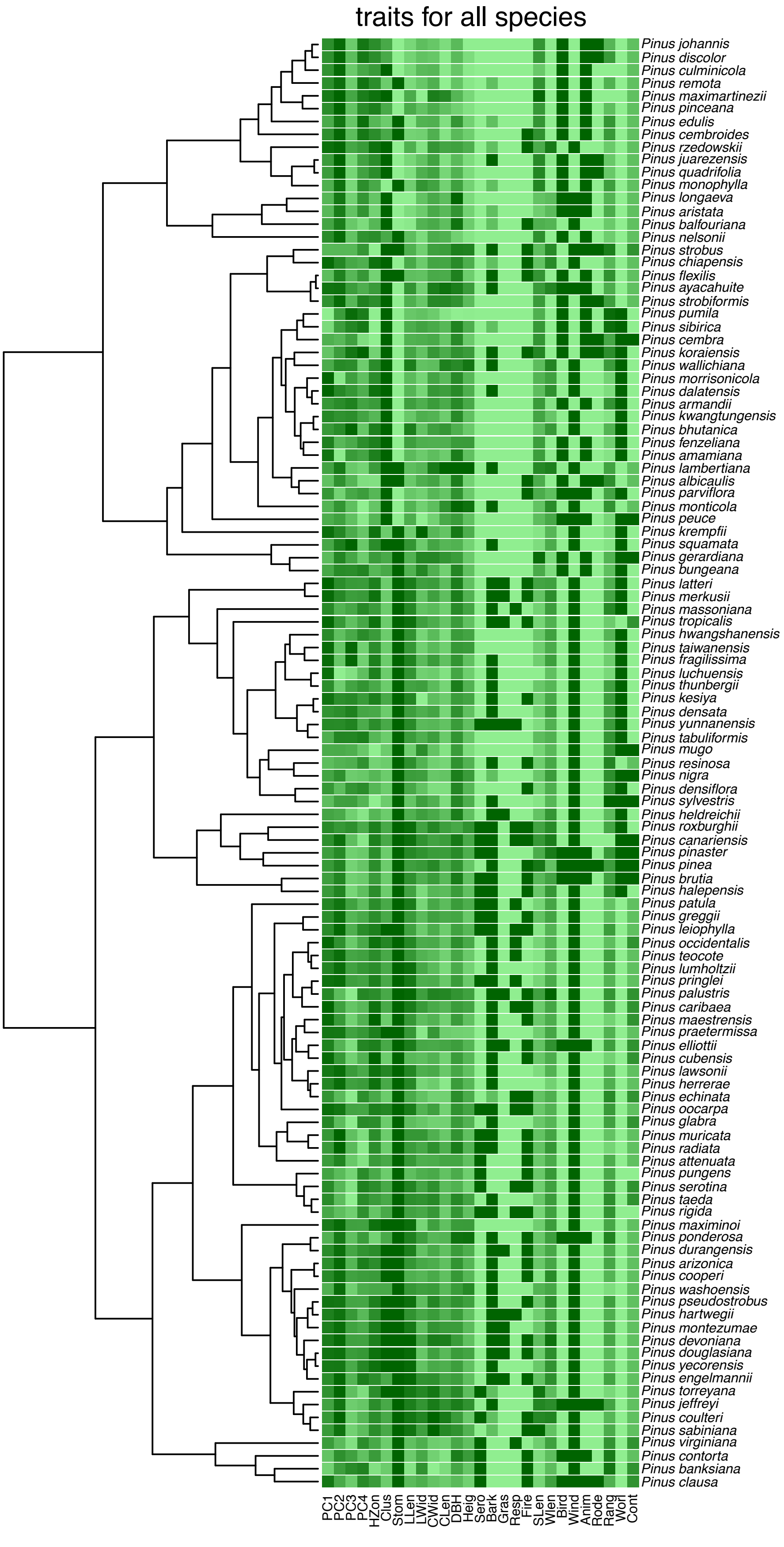
Pinus wangii


Pinus washoensis

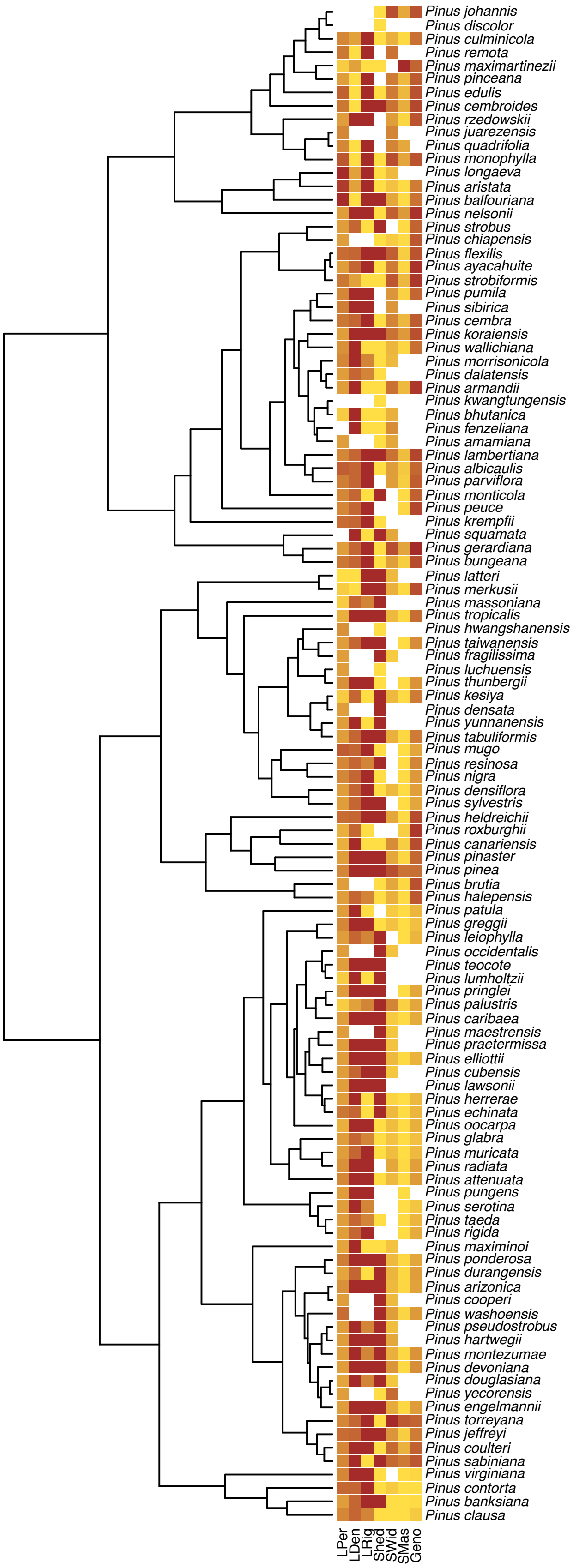

Pinus yecorensis

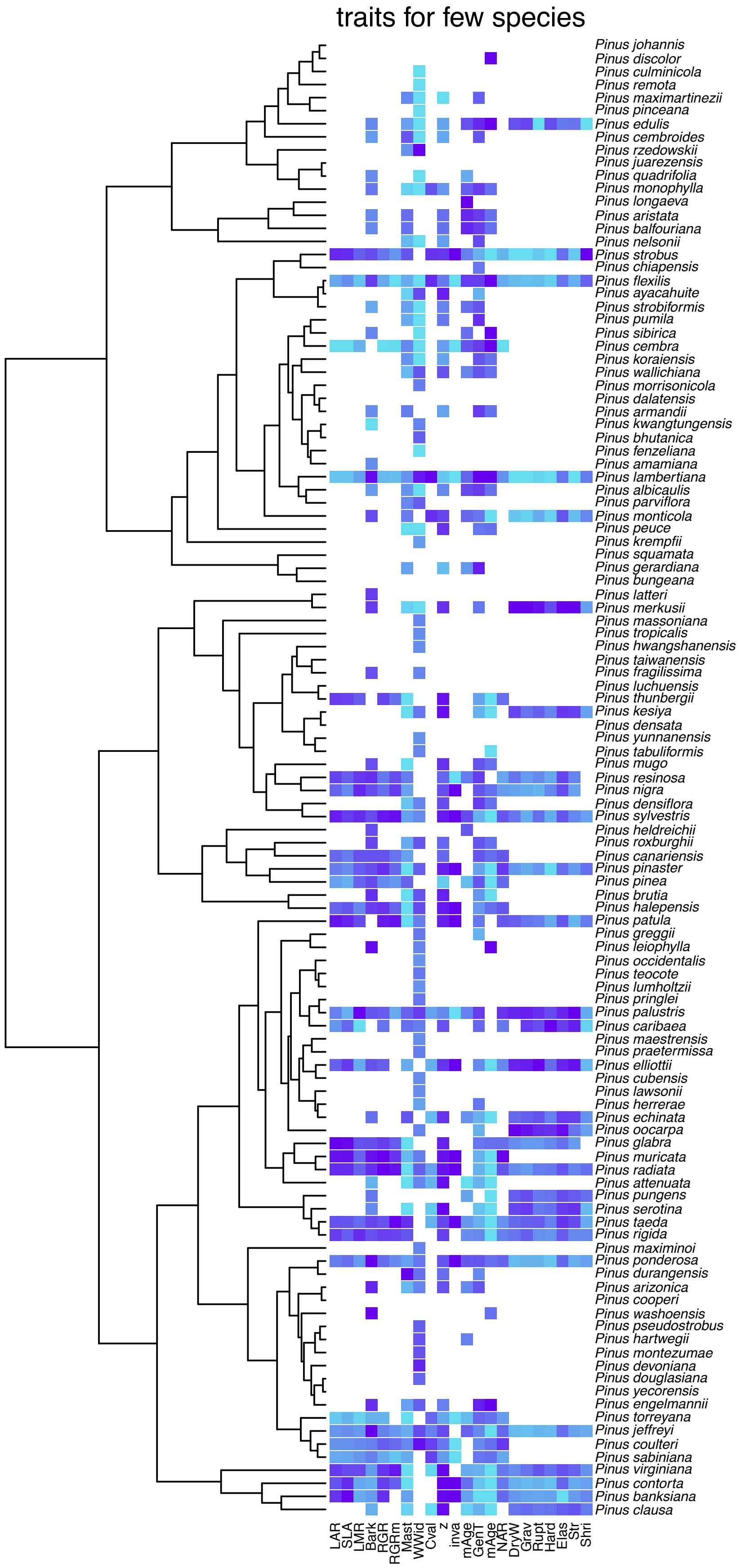

Pinus yunnanensis

3.4 S4 – Trait distribution over phylogeny



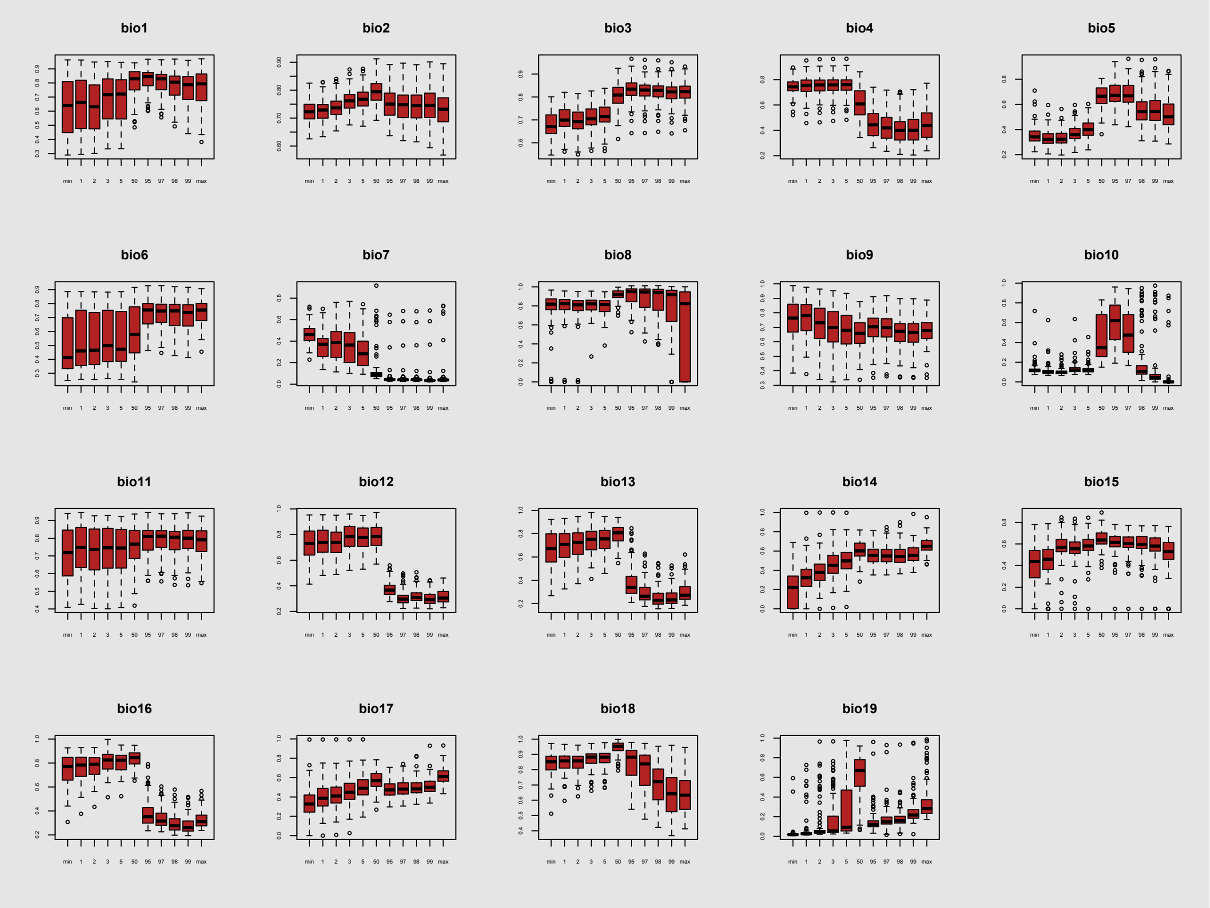
traits for most species





traits for few species

3.5 S5 - Phylogenetic signal of 19 bioclim variables



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