Supplementary Information for
Tempo and drivers of plant diversification in the European mountain system

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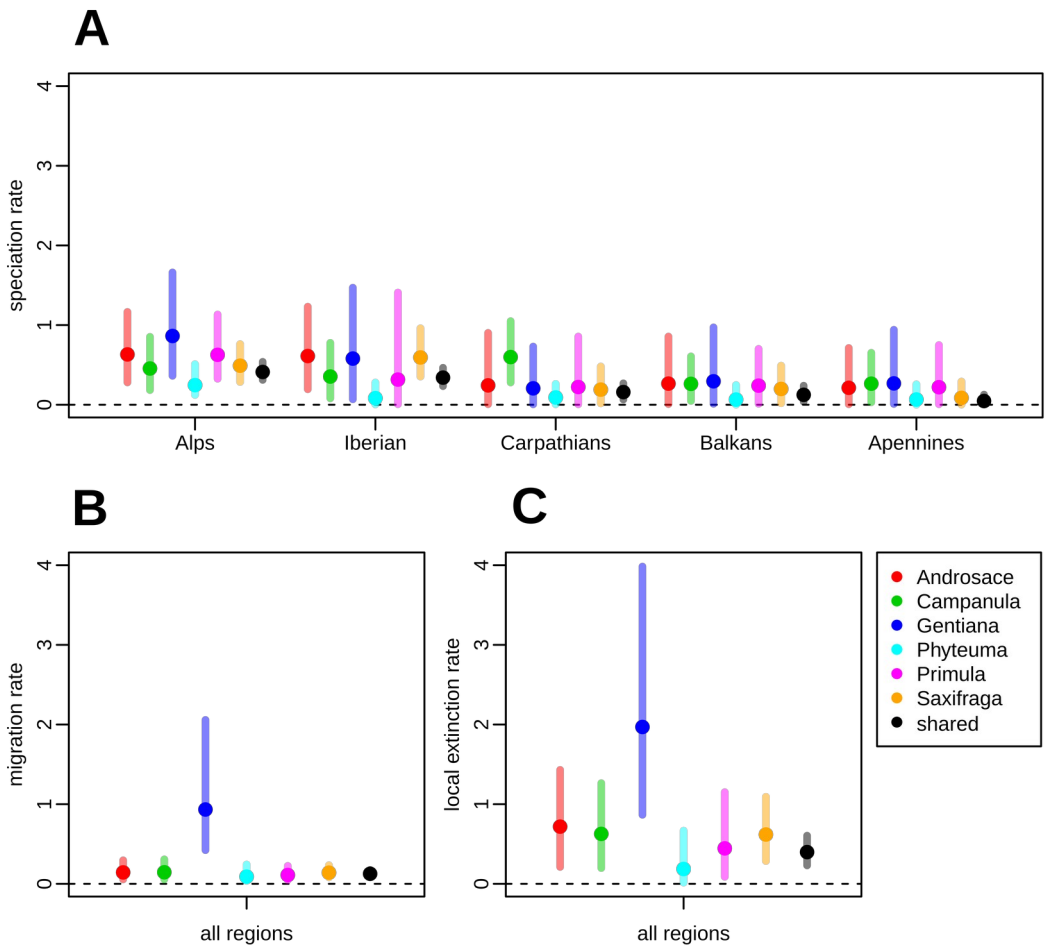
This PDF includes:

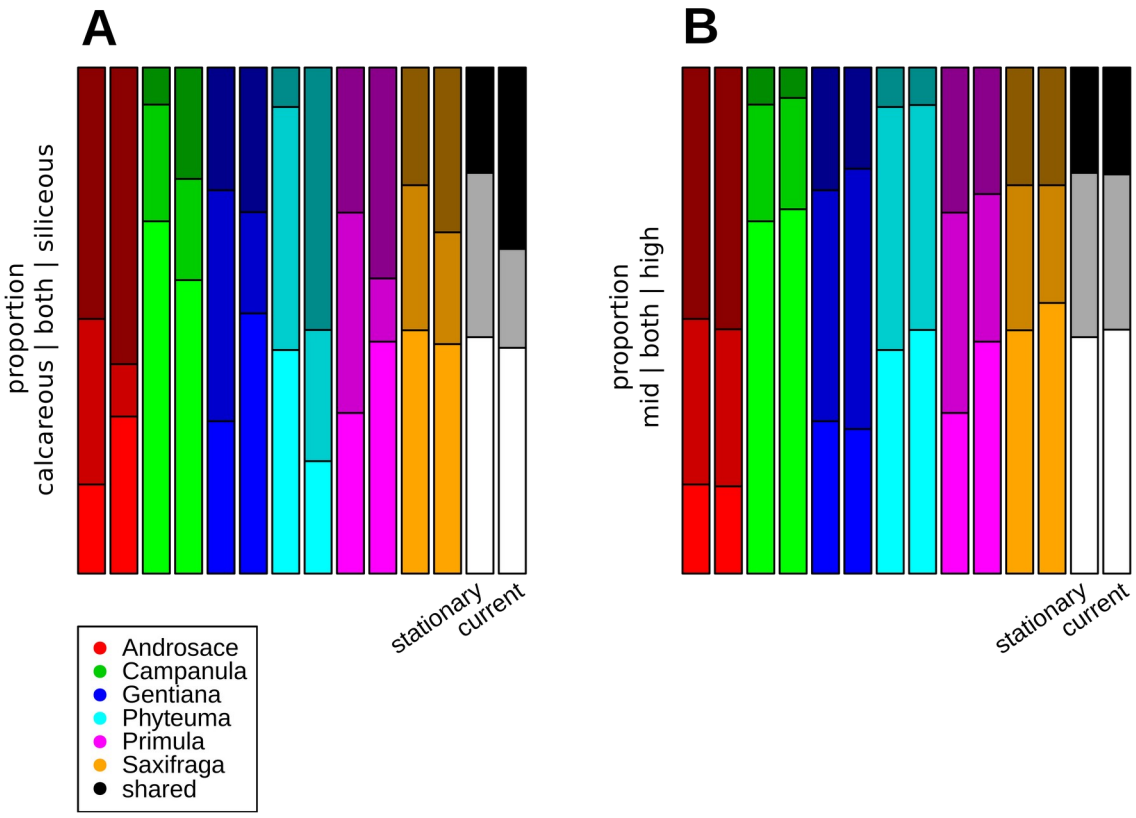
Other supplementary materials for this manuscript include the following:

Supplementary dataset SD1 – Accession table.
Supplementary dataset SD2 – Genomic regions.
Supplementary dataset SD3 – Maximum credibility species trees.
Supplementary dataset SD4 – Ecological and geographic information.
Supplementary dataset SD5 – Alternative maximum credibility species trees.

Supplementary figure SF1: Rates of (A) constant-state speciation across 5 regions of European mountain system, (B) common migration rates between each pair of regions and (C) common extinction rates. The bars indicate 95% credibility interval of Bayesian parameter estimate of ClaSSE model with the best AIC (no state-change speciation, region-specific constant-state speciation rates, single extinction rate, single migration rate).

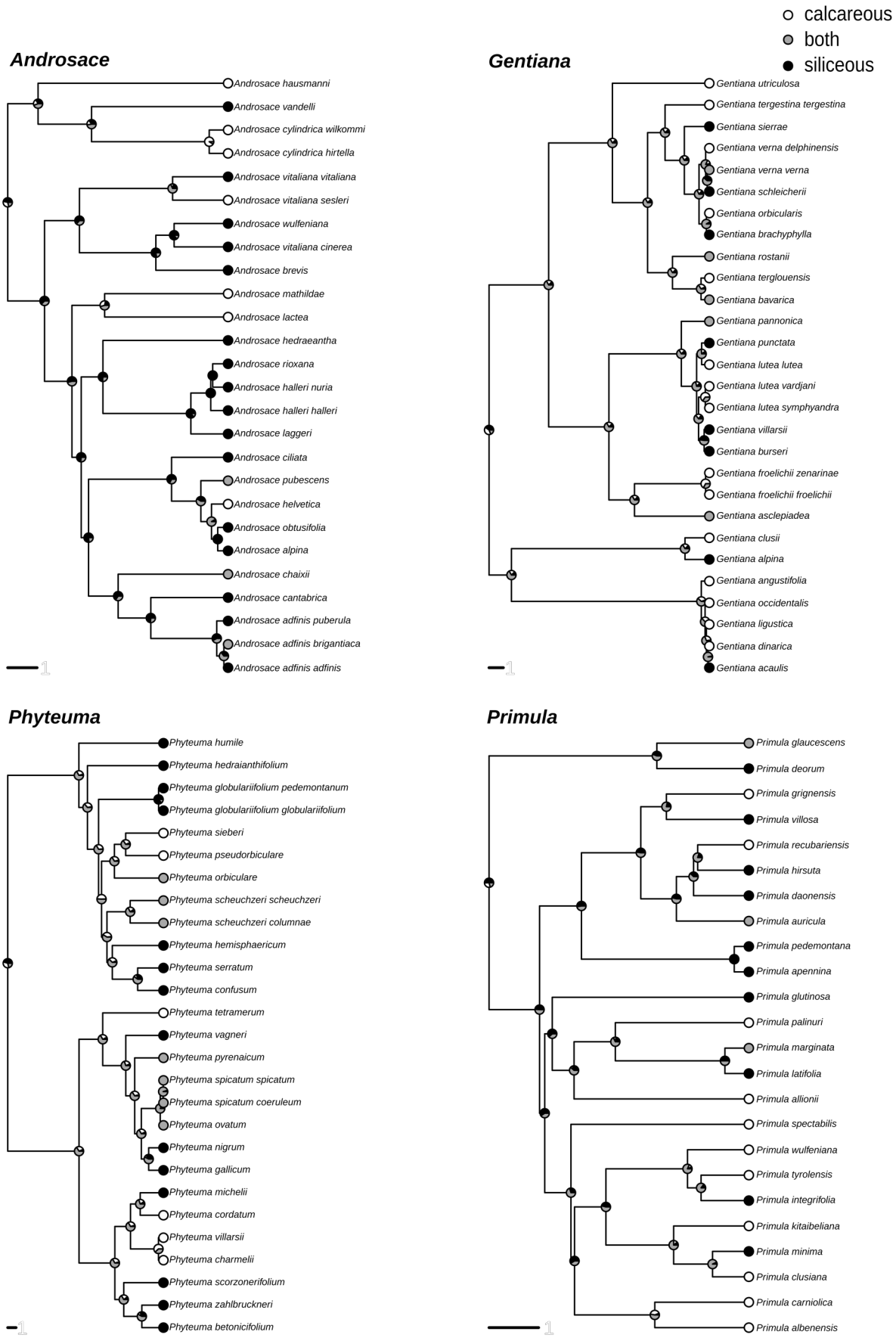


Supplementary figure SF2: Current and stationary proportions of (A) calcareous specialists, siliceous specialists or bedrock generalist species; and (B) high elevation specialists, mid-elevation specialists, and elevation generalist species. The color scheme follows the same one as in Fig. SF1, but includes shading to differentiate niche states. Stationary proportions represent a limit distribution of states of the model for time$\rightarrow\infty$, and are calculated by eigendecomposition of ClaSSE model matrices constructed from mean posterior parameter estimates, with the function *stationary.freq.classe* in R package *diversitree*.



Supplementary figure SF3: Ancestral state estimation of (A) bedrock and (B) elevation niches for the six lineages, based on median posterior parameter estimates from respective ClaSSE models using the marginal reconstruction algorithm provided in the R package *HiSSE*. The bar at the bottom of each phylogeny represents a time interval of 1 Ma.

A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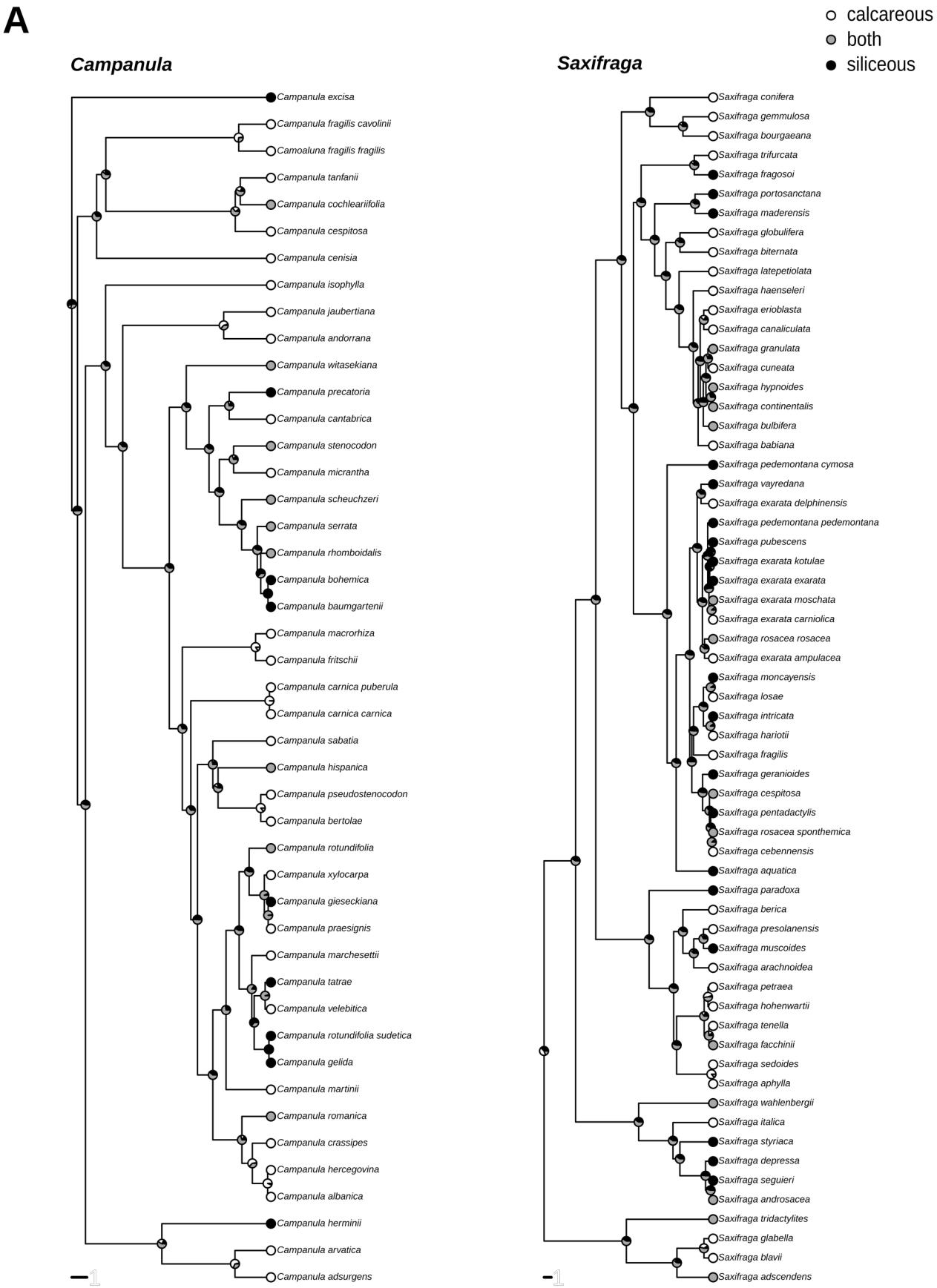
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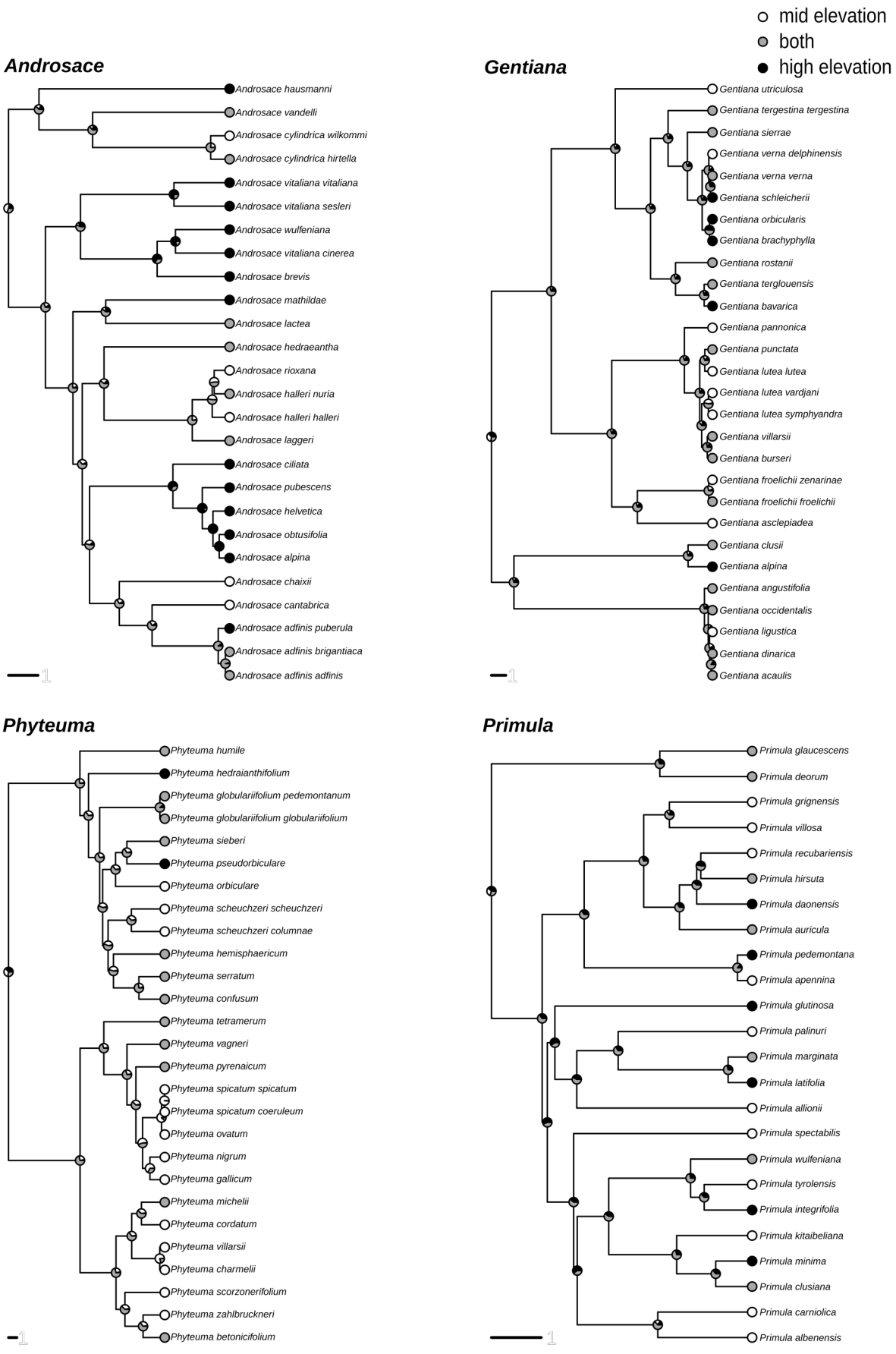
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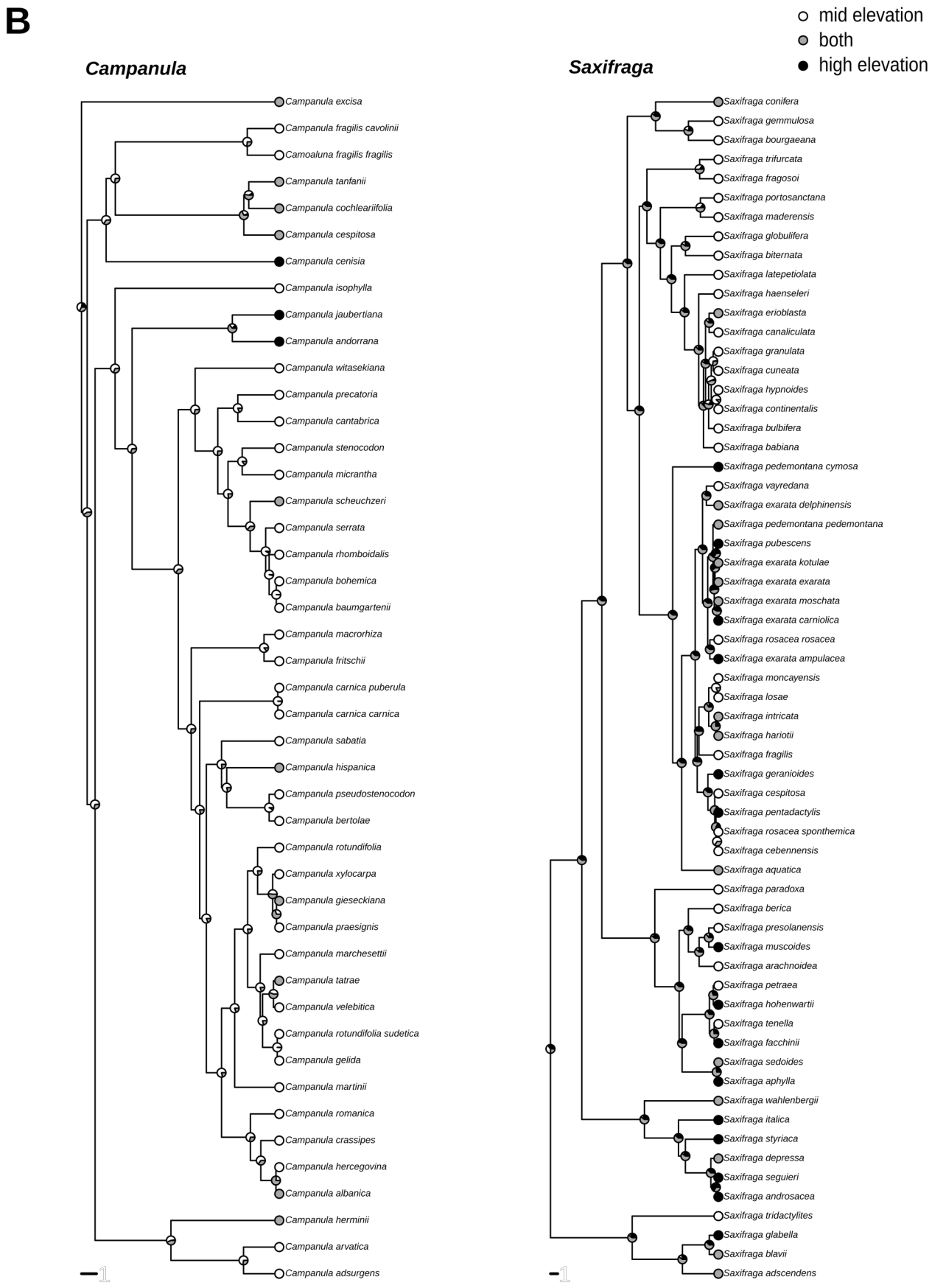
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Supplementary note SN1 – The PhyloAlps consortium

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  Bogdan Hurdu, Mihai Puscas

Supplementary methods SM1 – Phylogenetic analyses and molecular dating calibrations

Coding and non-coding alignments for each of the four families were used to estimate dated phylogenies in BEAST 2[1]. Non-coding alignments and each codon position in coding alignments were modeled with separate averaging-site models as implemented in bModeltest[2]. Four independent runs were performed for 100 M generations applying a Yule tree prior and log-normal clock and a burn-in of 30%. We evaluated convergence both visually and by checking whether the efective sample size (ESS) was >100 for all the parameters. We used TreeAnnotator to generate maximum credibility trees (MCC).

The plant fossil record used for dating calibration may allow multiple interpretations in some cases. For consistency with literature, we specifically used the interpretations mirroring previous influential studies on the respective families[3–6] for the downstream analyses presented in the main text. To test the robustness of this choice, we however reran the phylogenetic analyses with alternative dating calibration where necessary, and explored the differences. The dating calibrations were applied as the uniform priors, because we consider that the paucity of fossil for all the families does not allow for more informative priors.

For Campanulaceae, in accordance with Mansion et al. 2011[3], we defined the following calibration bounds:

- crown age of *C. carpatica+C. pulla+C.pyramidalis* to 16.5-56 Ma BP. The minimum bound is based on fossil seed of *C. palaeopyramidalis*[7]. The maximum bound is based on inferred split between *Codonopsis* and *Campanula*[8].
- root of Campanulaceae to 16.5-56 Ma BP.

For Gentianaceae , in accordance with Favre et al. 2016[4], we defined the following bounds:

- crown age of *Gentiana+Gentianopsis+Lomatogonium+Swertia* to 5-100 Ma BP. The minimum bound is based on fossil seeds of *Gentiana*[9]. The maximum bound is based on the conservative estimate from Rybzcinski et al. 2014[10].
- root of Gentianaceae to 33.6-100 Ma BP. The minimum bound is based on fossil pollen of *Lisianthus*[11].

Alternatively, the the fossil seed of *Gentiana*[9] may be attributed specifically to *G. cruciata* section, and the respective prior would thus refer to crown age of *Gentiana cruciata+Gentiana pneumonanthe*. Similarly, the root prior may alternatively be restricted to 40-50 Ma BP, based on estimate for this divergence event from Merckx et al. 2013[12]. These changes in dating calibration result in very similar maximum credibility dates within the ingroup with slightly lower uncertainty, e.g. the crown age of the three ingroup *Gentiana* clades would be 14.3 Ma (95% CI 8.9-20.7 Ma) instead of 15.4 Ma (95% CI 6.4-28.5 Ma). For the used and the alternative maximum credibility phylogeny of *Gentiana*, see Supplementary dataset SD3 and SD5, respectively.

For Primulaceae , in accordance with Xing and Ree 2017[5], we defined the following bounds:

- crown age of *Cortusa+Hottonia+Primula+Soldanella* to 15.97-72 Ma BP. The minimum bound is based on fossil seeds of *Primula rosiae*[13]. The maximum bound is based on primuloid fossil flower that cannot be attributed directly to Primulaceae[14].
- crown age of *Androsace+Cortusa+Douglasia+Hottonia+Primula+Soldanella* to 5.3-72 Ma BP. The minimum bound is based on fossil seeds of *Androsace*[15].
- crown age of *Anagallis+Androsace+Cortusa+Douglasia+Hottonia+Lysimachia+Primula+ Soldanella+Trientalis* to 28-72 Ma BP. The minimum bound is based on fossil seed attributable to Primuloideae.[16].
- root of Primulaceae to 48.6-72 Ma BP. The minimum bound is based on fossils of *Ardisia*[17].

Alternatively, the fossil seed of Primuloideae[16] could be attributed to *Lysimachia* as in Boucher 2016[18], and the respective prior would thus refer to the crown age of *Lysimachia+Cyclamen.* This change in calibration results in very similar dates within the ingroups, e.g. crown age of *Primula* sect. *auriculata* 5.1 Ma (95% CI 3.0-7.5 Ma) instead of 5.2 Ma (95% CI 3.2-7.9 Ma) and crown age of *Androsace* sect. *aretia* 7.3 Ma (95% CI 4.5-10.9 Ma) instead of 7.5 Ma (95% CI 4.7-10.7 Ma). For the used and the alternative maximum credibility phylogeny of *Primula* and *Androsace*, see Supplementary dataset SD3 and SD5, respectively.

For Saxifragaceae+Grossulariaceae, we restricted, in accordance with Ebersbach et al. 2017[6] the following bounds:

- crown age of *Ribes* to 14.5-125 Ma BP. The minimum age is based on fossil leaves of *Ribes webbii* attributable to *Ribes* group *Calobotrya*[19]. The maximum age is based on earliest angiosperm fossil evidence[20].
- root of Saxifragaceae+Grossulariaceae to 42-125 Ma BP. Minimum age is based on fossil leaves of *Ribes axelrodii*[19].

Alternatively, the root age of Saxifragaceae+Grossulariaceae could be secondary-calibrated by maximum credibility interval from Ebersbach et al. 2017[6], who have more extensive taxon sampling than our study, to 74-93 Ma BP. Such strategy would result in slightly older maximum credibility dates of the ingroup with lower uncertainty, e.g. crown age of *Saxifraga* sect. *Saxifraga* 27.2 Ma (95% CI 18.9-36.1 Ma) instead of 23.2 Ma (95% CI 12.5-38.1 Ma). For the used and the alternative maximum credibility phylogeny of *Saxifraga*, see Supplementary dataset SD3 and SD5, respectively.

Supplementary methods SM2 – Multi-clade time-dependent diversification model R vignette

Introduction

This vignette aims to demonstrate the multi-clade time-dependent diversification model used in the paper. The main idea behind this method is that the analyzed phylogenies are *n* observations of shared diversification process and the likelihood of observing them together is thus a product of individual likelihood functions of each phylogeny.

$$L_{altogether}(x) = \prod_{i=1}^{n} L_i(x)$$

This product likelihood function can be searched for optimal estimate of diversification parameters shared by all the phylogenies. On a technical side, this approach is implemented by modifying the likelihood expressions in the functions *fit_bd* and *fit_env* of the *RPANDA* package[21] in R.

Here we use simulated phylogenies from time-constant birth-death process and a birth-death process with speciation rate dependent on past temperatures to test whether the parameter estimates of single lineage and shared diversification models match those of the generating process. Apart from that, we also explore whether the AIC comparison is useful approach to check if the shared model fits the data better than a set of single-lineage models. Our results show that the parameters of both shared and single-lineage diversification models as we used them throughout the paper can be unambiguously identified, addressing thus the recent criticism of diversification models[22].

Birth-death model

Here we generate a set of 6 phylogenetic trees using a birth death model with constant diversification rates reflecting those detected in the mountain plants dataset (lambda=0.4019096 and mu=0.2594446) over 10 Ma.

```
library(RPANDA)
## Loading required package: picante
## Loading required package: ape
## Loading required package: vegan
## Loading required package: permute
## Loading required package: lattice
## This is vegan 2.5-6
## Loading required package: nlme
library(geiger)
library(pspline)

lambdabd=0.4019096
mubd=0.2594446

rbdtreesim=function(lambdabd,mubd){rbdtree(lambdabd,mubd,10)}
tbdlist=mapply(rbdtreesim, rep(lambdabd,6),rep(mubd,6),SIMPLIFY = F)
```

Then, we define a function for estimating shared parameters of birth-death process across multiple phylogenies. The function is a modification of *fit_bd* from *RPANDA*, the critical part with the product likelihood function is found between the # lines.

```
fit_bdmulti=function (phylolist, tot_timelist, f.lamb, f.mu, lamb_par, mu_par,
flist,
          meth = "Nelder-Mead", cst.lamb = FALSE, cst.mu = FALSE, expo.lamb =
FALSE,
          expo.mu = FALSE, fix.mu = FALSE, dt = 0, cond = "crown")
{
  #the calculation of total n for aicc
  ntiplist=lapply(phylolist,Ntip)
  nobs=Reduce("+",ntiplist)

  if (fix.mu == FALSE) {
    init <- c(lamb_par, mu_par)
    p <- length(init)
    optimLH <- function(init) {
      lamb_par <- init[1:length(lamb_par)]
      mu_par <- init[(1 + length(lamb_par)):length(init)]
      f.lamb.par <- function(t) {
        abs(f.lamb(t, lamb_par))
      }
      f.mu.par <- function(t) {
        abs(f.mu(t, mu_par))
      }

#############################################################################
#####
      #the LH is now a sum of likelihoods for different trees, each tree can
have a
      #different total age (tot_time) and sampling proportion (f)
      lhsinpar=function(phylo, tot_time, f){
        likelihood_bd(phylo, tot_time, f.lamb.par,
                      f.mu.par, f, cst.lamb = cst.lamb, cst.mu = cst.mu,
                      expo.lamb = expo.lamb, expo.mu = expo.mu, dt = dt,
                      cond = cond)
      }
      likelihoodlist=mapply(lhsinpar, phylolist, tot_timelist, flist)
      LH=Reduce("+",likelihoodlist)

      return(-LH)

#############################################################################
#####
    }
    temp <- suppressWarnings(optim(init, optimLH, method = meth))
    lamb.par <- temp$par[1:length(lamb_par)]
    mu.par <- temp$par[(1 + length(lamb_par)):length(init)]
    f.lamb.par <- function(t) {
      f.lamb(t, lamb.par)
    }
    f.mu.par <- function(t) {
      f.mu(t, mu.par)
    }
    res <- list(model = "birth death", LH = -temp$value,
                aicc = 2 * temp$value + 2 * p + (2 * p * (p + 1))
                /(nobs -  p - 1), lamb_par = lamb.par, mu_par = mu.par,
                f.lamb = Vectorize(f.lamb.par), f.mu = Vectorize(f.mu.par))
```

```
  }
  else {
    init <- c(lamb_par)
    p <- length(init)
    optimLH <- function(init) {
      lamb_par <- init[1:length(lamb_par)]
      f.lamb.par <- function(t) {
        abs(f.lamb(t, lamb_par))
      }
      f.mu.par <- function(t) {
        abs(f.mu(t, mu_par))
      }

##############################################################################
#####
      #the LH is now a sum of likelihoods for different trees, each tree can
have a
      #different total age (tot_time) and sampling proportion (f)
      lhsinpar=function(phylo, tot_time, f){
        likelihood_bd(phylo, tot_time, f.lamb.par,
                      f.mu.par, f, cst.lamb = cst.lamb, cst.mu = cst.mu,
                      expo.lamb = expo.lamb, expo.mu = expo.mu, dt = dt,
                      cond = cond)
        }
      likelihoodlist=mapply(lhsinpar, phylolist, tot_timelist, flist)
      LH=Reduce("+",likelihoodlist)

      return(-LH)

##############################################################################
#####
    }
    temp <- suppressWarnings(optim(init, optimLH, method = meth))
    lamb.par <- temp$par[1:length(lamb_par)]
    f.lamb.par <- function(t) {
      f.lamb(t, lamb.par)
    }
    f.mu.par <- function(t) {
      f.mu(t, mu_par)
    }
    res <- list(model = "birth.death", LH = -temp$value,
                aicc = 2 * temp$value + 2 * p + (2 * p * (p + 1))
                /(nobs - p - 1), lamb_par = lamb.par, f.lamb =
Vectorize(f.lamb.par))
  }
  class(res) <- "fit.bd"
  return(res)
}
```

In the next step, we fit the model with shared parameters across the phylogenies.

```
#get total time for each tree
tot_timebdfn=function(phylo){max(node.age(phylo)$ages)}
tot_timebdlist=lapply(tbdlist,tot_timebdfn)

#list of sampling proportion
fbdlist=as.list(rep(1,6))

#starting points for ML search
lamb_parbd<-c(runif(1,0,1))
mu_parbd<-c(runif(1,0,lamb_parbd[1]/2))

#functions of time dependence (constant)
f.lambbd <-function(t,y){y[1]}
f.mubd<-function(t,y){y[1]}

#fit
multibd=fit_bdmulti(tbdlist, tot_timebdlist,
                    f.lamb=f.lambbd,f.mu=f.mubd,
                    lamb_par=lamb_parbd,mu_par=mu_parbd,
                    cst.lamb =T,cst.mu = T,
                    fbdlist, dt=1e-3)

multilambbd=abs(multibd$lamb_par)
multimubd=abs(multibd$mu_par)
multiLHbd=multibd$LH
```

For comparison, we then fit the diversification model on each tree separately.

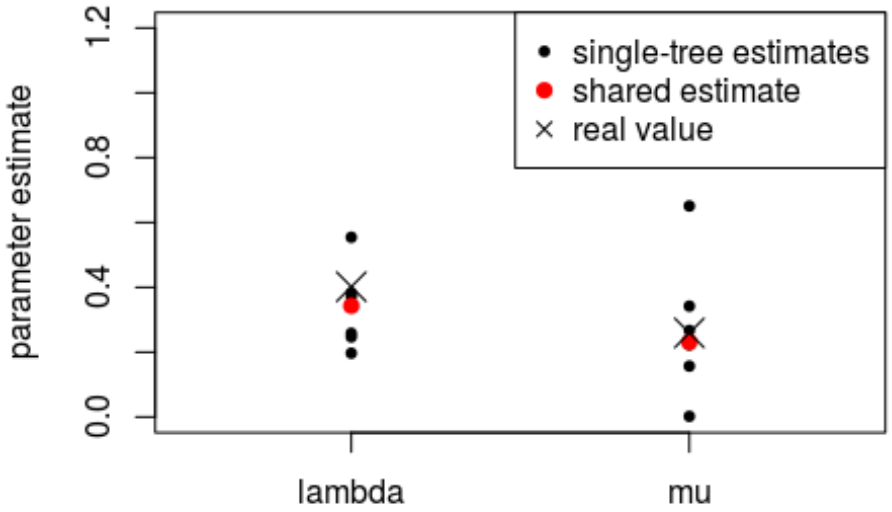
```
# fit
ferbd=function(phylo, tot_time){
    fit_bd(phylo,tot_time,
           f.lamb=f.lambbd,f.mu=f.mubd,
           lamb_par=lamb_parbd,mu_par=mu_parbd,
           cst.lamb = T,cst.mu = T,
           f=1, dt=1e-3)
  }
singlebd=mapply(ferbd,tbdlist,tot_timebdlist)


#vectorize model characteristics from a list
singlelambbd=rep(0,6)
singlemubd=rep(0,6)
singleLHbd=rep(0,6)

for(i in 1:6){
  tempres=singlebd[,i]
  singlelambbd[i]=abs(tempres$lamb_par[1])
  singlemubd[i]=abs(tempres$mu_par[1])
  singleLHbd[i]=tempres$LH
}
```

The plot showing the parameter estimates reflects that shared estimates of speciation and extinction rates closely match the original values, with single-tree estimates being scattered around with larger variance. The aggregation of estimates around the original values suggests that both shared and single-tree model are identifiable from the generated data.

```
plot(c(singlelambbd,singlemubd)~c(rep(1,6),rep(2,6)),
     xlim=c(0.5,2.5),ylim=c(0,1.2),xlab="",ylab="parameter estimate", pch=20,
xaxt="n")
axis(1, at = c(1,2), labels = c("lambda", "mu"))
points(1,multilambbd, col="red", pch=19)
points(2,multimubd, col="red", pch=19)
points(1,lambdabd, pch=4,cex=2)
points(2,mubd, pch=4,cex=2)
legend(x='topright', legend=c("single-tree estimates", "shared estimate", "real
value"), col=c("black", "red", "black"), pch=c(20,19,4))
```



We can also compare the AIC of the shared multi-clade model to the AIC of a set of single-tree models to check whether all the trees can be well explained by a single set of parameters. The AIC of a set of single-tree models can be obtained based on the fact that optimizing multiple functions separately yields the same results as optimizing a sum of them, each having different parameters. Based on this, such AIC can be calculated from the sum of log-likelihoods and model parameters of the single-tree models. The resulting AIC of the shared multi-clade model is lower than the AIC of the set of single-tree models, reflecting that the dataset was indeed simulated using one shared set of parameters.

```
aicmultibd=-2*(multiLHbd-2)
aicsinglebd=-2*(sum(singleLHbd)-2*6)

aicmultibd
## [1] 364.4781
aicsinglebd
## [1] 377.2007
```

Environment-dependent model

Here we generate a set of 6 phylogenetic trees using a birth death model with temperature dependent speciation rate. We use here the estimated diversification rates for *Primula*, which is the lineage for which we detected strongest dependence of diversification on past temperatures. The diversification process runs for 5.5 Ma and is controlled by the following parameters: baseline speciation rate lambda=0.1409249, exponential temperature dependence of speciation rate alpha=0.3602235 and extinction rate mu=9.859543e-08.

```
lambdaenv=0.1409249
alphaenv=0.3602235
muenv=9.859543e-08

data(InfTemp)

renvtreesim=function(lambdaenv,muenv,alphaenv){
  f.lamb = function(t, x, y) {y[1] * exp(x * y[2])}
  f.mu = function(t, x, y) {y[1]}
  sim_env_bd(InfTemp, f.lamb, f.mu, lamb_par = c(lambdaenv, alphaenv), mu_par =
muenv,
             time.stop = 5.5, return.all.extinct = F, prune.extinct = T)$tree
  }

tenvlist=mapply(renvtreesim,
rep(lambdaenv,6),rep(muenv,6),rep(alphaenv,6),SIMPLIFY = F)
```

We define a function *fit_envmulti* which is a shared-parameter equivalent of *fit_env* from *RPANDA* and serves as a wrapper of *fit_bdmulti* used in the previous example.

```
fit_envmulti=function (phylolist, env_data, tot_timelist, f.lamb, f.mu,
lamb_par,
          mu_par, df = NULL, flist, meth = "Nelder-Mead", cst.lamb = FALSE,
          cst.mu = FALSE, expo.lamb = FALSE, expo.mu = FALSE, fix.mu = FALSE,
          dt = 0, cond = "crown")
{
  if (is.null(df)) {
    df <- smooth.spline(x = env_data[, 1], env_data[, 2])$df
  }
  spline_result <- sm.spline(env_data[, 1], env_data[, 2],
                             df = df)
  env_func <- function(t) {
    predict(spline_result, t)
  }
  lower_bound_control <- 0.1
  upper_bound_control <- 0.1
  lower_bound <- min(env_data[, 1])
  upper_bound <- max(env_data[, 1])
  time_tabulated <- seq(from = lower_bound * (1 - lower_bound_control),
                        to = upper_bound * (1 + upper_bound_control), length.out
= 1 +
                          1e+06)
  env_tabulated <- env_func(time_tabulated)
  env_func_tab <- function(t) {
    b <- upper_bound * (1 + upper_bound_control)
    a <- lower_bound * (1 - lower_bound_control)
    n <- length(env_tabulated) - 1
    index <- 1 + as.integer((t - a) * n/(b - a))
    return(env_tabulated[index])
  }
  f.lamb.env <- function(t, y) {
    f.lamb(t, env_func_tab(t), y)
  }
  f.mu.env <- function(t, y) {
    f.mu(t, env_func_tab(t), y)
  }
  ####################################
  #here we use fit_bdmulti instead of fit_bd
  res <- fit_bdmulti(phylolist, tot_timelist, f.lamb.env, f.mu.env, lamb_par,
                mu_par, flist, meth=meth, cst.lamb, cst.mu, expo.lamb, expo.mu,
                fix.mu, dt, cond)
  ####################################
  res$model <- "environmental birth death"
  res$f.lamb <- function(t) {
    f.lamb(t, env_func_tab(t), res$lamb_par)
  }
  if (fix.mu == FALSE) {
    res$f.mu <- function(t) {
      f.mu(t, env_func_tab(t), res$mu_par)
    }
  }
  class(res) <- "fit.env"
  return(res)
}
```

Now we fit the environment-dependent model with shared parameters on the data.

```
#get total time for each tree
tot_timeenvfn=function(phylo){max(node.age(phylo)$ages)}
tot_timeenvlist=lapply(tenvlist,tot_timeenvfn)

#list of sampling proportion
fenvlist=as.list(rep(1,6))

#starting points for ML search
lamb_parenv<-c(runif(1,0,1),runif(1,0,1))
mu_parenv<-c(runif(1,0,lamb_parenv[1]/2))

#functions of time dependence (exponential and constant)
f.lambenv <-function(t,x,y){y[1] * exp(y[2] * x)}
f.muenv <-function(t,x,y){y[1]}

#fit
multienv=fit_envmulti(tenvlist, InfTemp, tot_timeenvlist,
                      f.lamb=f.lambenv,f.mu=f.muenv,
                      lamb_par=lamb_parenv,mu_par=mu_parenv,
                      cst.lamb = F,cst.mu = T,
                      flist=fenvlist, dt=1e-3)

multilambenv=abs(multienv$lamb_par[1])
multialphaenv=multienv$lamb_par[2]
multimuenv=abs(multienv$mu_par[1])
multiLHenv=multienv$LH
```

For comparison, we then fit the diversification model on each tree separately.

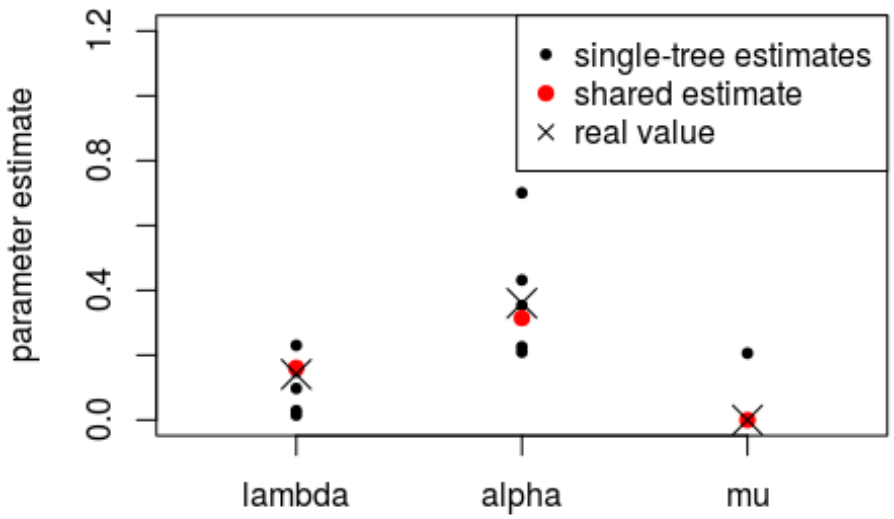
```
# fit
ferenv=function(phylo, tot_time){
  fit_env(phylo,InfTemp, tot_time,
          f.lamb=f.lambenv,f.mu=f.muenv,
          lamb_par=lamb_parenv,mu_par=mu_parenv,
          cst.lamb = F,cst.mu = T,
          f=1, dt=1e-3)
}
singleenv=mapply(ferenv,tenvlist,tot_timeenvlist)

#vectorize model characteristics from a list
singlelambenv=rep(0,6)
singlealphaenv=rep(0,6)
singlemuenv=rep(0,6)
singleLHenv=rep(0,6)

for(i in 1:6){
  tempres=singleenv[,i]
  singlelambenv[i]=abs(tempres$lamb_par[1])
  singlealphaenv[i]=tempres$lamb_par[2]
  singlemuenv[i]=abs(tempres$mu_par[1])
  singleLHenv[i]=tempres$LH
}
```

The plot of the parameter estimates suggests that the shared estimates of speciation, extinction rate and temperature-dependence of speciation closely match the original values, with single tree estimates being scattered around with larger variance. The aggregation of estimates around the original values suggests that also the environment-dependent diversification models are identifiable from the generated data.

```
plot(c(singlelambenv,singlealphaenv,singlemuenv)~c(rep(1,6),rep(2,6),rep(3,6)),
     xlim=c(0.5,3.5),ylim=c(0,1.2),xlab="",ylab="parameter estimate", pch=20,
xaxt="n")
axis(1, at = c(1,2,3), labels = c("lambda", "alpha", "mu"))
points(1,multilambenv, col="red", pch=19)
points(2,multialphaenv, col="red", pch=19)
points(3,multimuenv, col="red", pch=19)
points(1,lambdaenv, pch=4,cex=2)
points(2,alphaenv, pch=4,cex=2)
points(3,muenv, pch=4,cex=2)
legend(x='topright', legend=c("single-tree estimates", "shared estimate", "real
value"),
       col=c("black", "red", "black"), pch=c(20,19,4))
```



We then compare the AIC of the shared multi-clade model with the AIC of the set of single-tree models to check whether all the trees can be well explained by a single set of parameters. As it is shown below, the AIC of the shared multi-clade model is lower than the AIC of the set of single-tree models, reflecting that the environment-dependent set of trees was indeed generated using one shared set of parameters.

```
aicmultienv=-2*(multiLHbd-3)
aicsingleenv=-2*(sum(singleLHbd)-3*6)

aicmultienv
## [1] 366.4781
aicsingleenv
## [1] 389.2007
```

Supplementary methods SM3 – Sensitivity analysis of temperature-dependent diversification models

In this appendix we perform a sensitivity analyses of temperature-dependent speciation models used in the main text, i.e. we explore type II errors of these models using simulated phylogenies with different strength of temperature dependence of speciation rate. Mirroring the analytical structure of the main text, we first analyze the sensitivity of single-lineage models and then of a multi-clade model operating on sets of 6 lineages.

Single-lineage models

To test the sensitivity of single lineage models, we simulated 700 phylogenies resembling the observed dataset, but with varying degree of temperature dependence of speciation rate. The speciation rate was dependent on temperature according to the equation $lambda*e^{alpha*t}$, where *t* is past reconstructed global temperature in °C[23]; and extinction was controlled by temperature-constant rate parameter *mu*. The phylogenies were simulated using randomly generated values of baseline speciation rate *lambda* and extinction rate *mu* corresponding to the maximum likelihood estimates from observed data, that is *lambda* between 0 and 1.35 and *mu* between 0 and value of respective *lambda*. Moreover, the simulations were conditioned to generate trees with crown age between 40 Ma BP and 3.2 Ma BP and having between 23 and 86 extant species, again reflecting the characteristics of the observed dataset. Such phylogenies were simulated 100 times for each value of temperature dependence of speciation *alpha* of 0, 0.1, 0.2, 0.3, 0.4, 0.5 and 0.6. *alpha*=0 represents independence of speciation on temperature, whereas *alpha*=0.6 represents a drop of Quaternary (2.6 Ma BP to present, mean global temperature 2 °C) speciation rate to approximately 24% of pre-Quaternary (5.2-2.6 Ma BP, mean global temperature 4.4 °C) level. The simulations were performed using *sim_env_bd* function from package RPANDA[21].

We fitted each of the simulated phylogenetic trees with constant birth death model and a temperature-dependent speciation model, and compared the AIC of the fits (AICdiff=AICbirthdeath-AICtempdep). In line with the main text, we evaluated sensitivity to two different types of result: "substantially supported" were the results where AICdiff>2, which corresponds to temperature-dependent model outperforming birth-death model even after addition of one completely non-informative parameter to the temperature-dependent model[24]; "marginally supported" were the results where AICdiff>0, which corresponds to at least slightly better informational performance of temperature-dependent model.

Our results (Fig. SM3.1) indicate that the single lineage models are sensitive to values of *alpha*=0.4 and higher, where the model properly identifies 69% of simulated phylogenies when referring to substantially supported result, and 82% of simulated phylogenies when referring to marginally supported result. Also for *alpha*=0.3, the phylogenies were properly categorized at least as marginally supported in 56% of cases. *alpha*=0.4 approximately corresponds to drop of Quaternary speciation rate to 38% of pre-Quaternary level, and *alpha*=0.3 to drop of Quaternary speciation rate to 50% of pre-Quaternary level

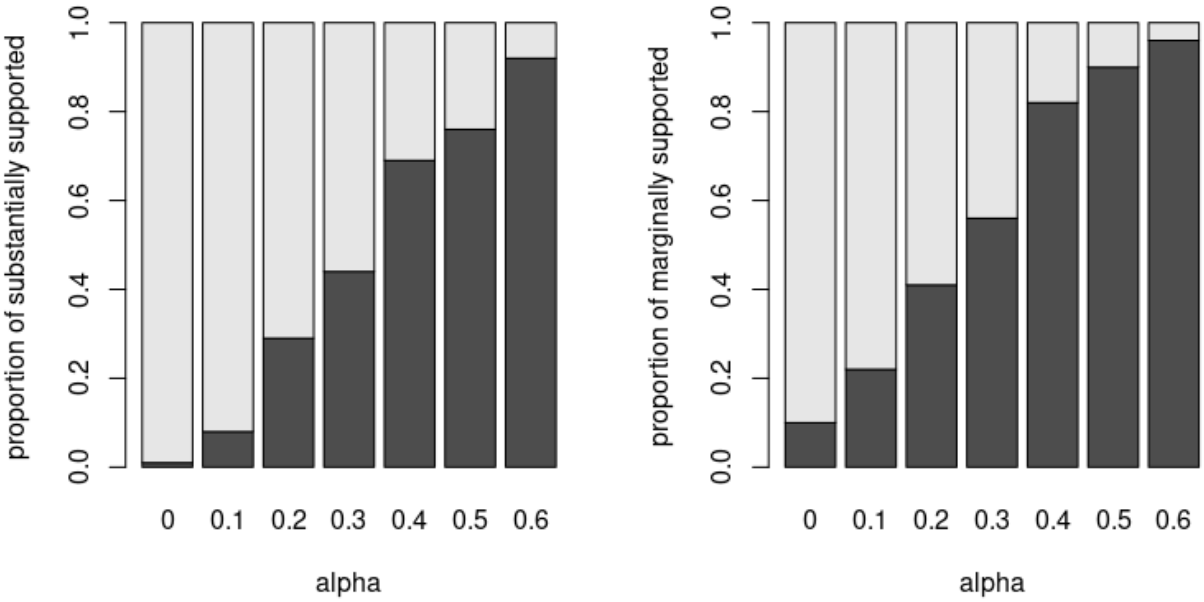


Fig. SM3.1 Sensitivity of single-lineage temperature-dependent models: The left panel shows proportion of phylogenies identified as substantially supported as temperature-dependent (AICdiff>2), and the right panel shows the proportion of phylogenies identified as marginally temperature-dependent (AICdiff>0), for different values of temperature-dependence parameter *alpha*.

Multi-clade model

To explore sensitivity of multi-clade temperature-dependent diversification model, we simulated sets of 6 phylogenies, each of these sextuplets for 700 times. Similarly as for single-lineage models, phylogenies were simulated with exponentially temperature-dependent speciation, with sextuplet-specific randomly generated *lambda* between 0 and 1.35, *mu* between 0 and *lambda*; and were conditioned to crown age between 40 Ma BP and 3.2 Ma BP and 23 to 86 extant species. The sextuplets were simulated 100 times for each value of temperature dependence of speciation *alpha* of 0, 0.1, 0.2, 0.3, 0.4, 0.5 and 0.6. Substantial and marginal support for temperature-dependence was evaluated in the same way as as in the single-lineage models, using the multi-clade model described in the main text and Supplementary methods SM2.

The multi-clade model (Fig. SM3.2) was sensitive to values of *alpha* higher than 0.2, 67% of simulations with *alpha*=0.2 showed substantial support for temperature-dependent model, and 74% showed marginal support for temperature-dependent model. For *alpha*=0.3, the sensitivity was above 90% in both cases. *alpha*=0.2 approximately corresponds to drop of Quaternary speciation rate to 63% of pre-Quaternary level.

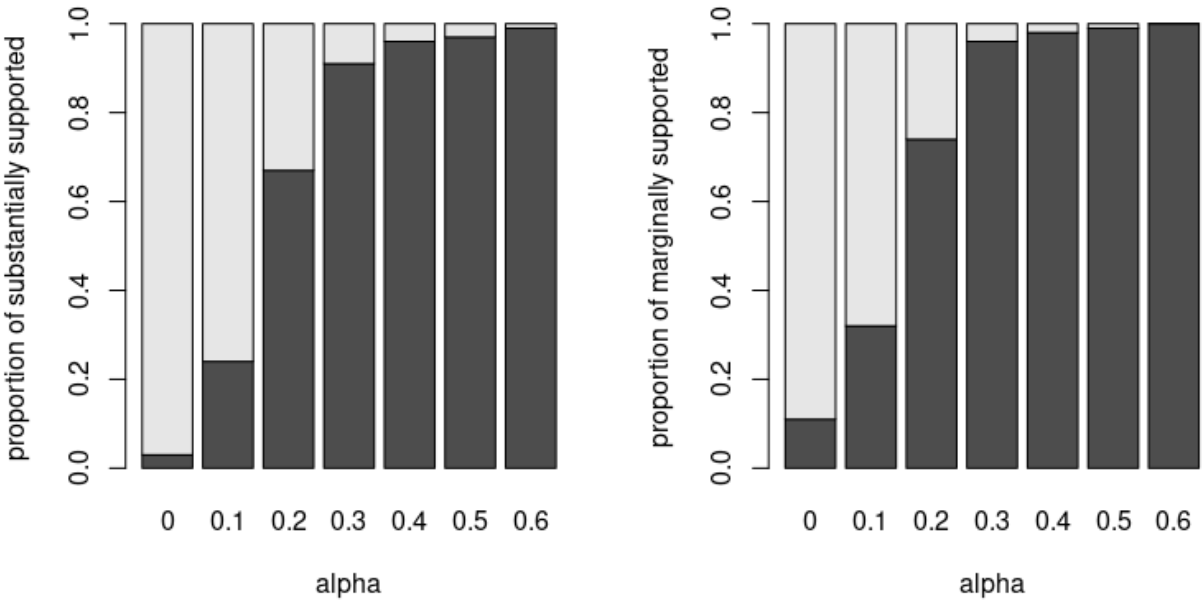


Fig. SM3.2 Sensitivity of multi-clade temperature-dependent models: The left panel shows proportion of phylogenies substantially supported as temperature-dependent (AICdiff>2), and the right panel shows the proportion of phylogenies marginally temperature-dependent (AICdiff>0), for different values of temperature-dependence parameter *alpha*.

Supplementary methods SM4 – Multi-clade state-dependent diversification model R vignette

Introduction

This vignette demonstrates functioning of multi-clade state-dependent speciation-extinction (SSE) model used throughout the paper. The main idea behind this method is that the analyzed phylogenies with attributed tip states are *n* observations of the shared diversification and state evolution process and a likelihood of observing them together is thus a product of individual likelihood functions.

$$L_{altogether}(x) = \prod_{i=1}^{n} L_i(x)$$

This product likelihood function can be maximized to estimate the set of optimal diversification parameters shared by all the phylogenies. This approach was used previously[25,26] and is implemented via the procedure *combine* in the *diversitree* R package[27]. However, the proper functioning and sensitivity of this approach was not demonstrated in previous works. Here, we use phylogenies simulated from SSE processes with parameters detected in our dataset for evolutionary assembly across elevation belts and bedrocks to show that the parameter estimates of both single lineage and shared diversification models match the parameters of the generating process. We also demonstrate here that AICs are useful for assessing whether the shared model fits better the data than the single lineage models.

Elevation model

We first generate a set of 6 phylogenetic trees using a ClaSSE model with diversification and migration rates reflecting maximum likelihood estimates detected across elevational belts (lambda111=0.2972257, lambda222=0.3919789, mu=0.4725019, q13=0.2191140 and q23=1.1092566) containing 30 species.

```
library(diversitree)
## Loading required package: ape
library(gplots)
##
## Attaching package: 'gplots'
## The following object is masked from 'package:stats':
##
##     lowess
lambda111el=0.2972257 #speciation in mid elevation
lambda222el=0.3919789 #speciation in high elevation
muel=0.4725019 #extinction in both elevations
q13el=0.2191140 #migration from mid to high
q23el=1.1092566 #migration from high to mid

reltreesim=function(lambda111el,lambda222el,muel, q13el, q23el){
  repeat{
    t=tree.classe(c(lambda111el, 0, 0, 0, 0, 0, 0, 0, 0,
                lambda222el, 0, 0, 0, 0,
                lambda111el, 0, lambda222el, 0,
                muel, muel, 0, 0,
                q13el, 0, q23el,
                muel, muel),
              max.taxa=30, max.t=Inf, include.extinct=F,x0=NA)
    if (inherits(t, "phylo"))
                break
  }
  t
  }
tellist=mapply(reltreesim,
               rep(lambda111el,6),
               rep(lambda222el,6),
               rep(muel,6),
               rep(q13el,6),
               rep(q23el,6),
               SIMPLIFY = F)
```

Then we define a function turning ClaSSE into multivariate generalization of GeoSSE[25].

```
#################################################################
#function for restricting ClaSSE parameter space to be geographically
meaningful
formula_builder=function(set){
  ########################
  #a small function for sticking set elements into formula system
  ########################
  if (length(set)>1) {paste(set[2:length(set)], set[1],sep="~")}
}


zero_builder=function(set){
  ########################
  #a small function for sticking set elements into 0
  ########################
  if (length(set)>=1) {paste(set,"0",sep="~")}
}


restrict_classe2geosse=function(table, forbidden=NULL,
                                single.sympatry=F, no.sympatry=F,
                                single.vicariance=F, no.vicariance=F,
                                pooled.founder=F, single.founder=F,no.founder=F,
                                single.extinction=F, no.extinction=F,
                                pooled.migration=F, single.migration=F,
no.migration=F){

  ########################
  #input - states table
  #output - list of formulas to be used as constrain(lik,formulae=formulas)
  ########################

  #libraries
  library(diversitree)
  library(rje)

  #table into set representation
  tableset=list()
  for (i in 1:length(table[,1])) {tableset[[i]]=names(table)
[as.logical(table[i,])]}
  #get parameter names
  phy <- rcoal(100)
  names=names(starting.point.classe(phy, k=length(table[,1])))
  names=setdiff(names,forbidden)

  #parameter states from strings
  ##############################
  #branching for k>10 DODELAT k>100
  if (length(table[,1])>10) {zp=1} else {zp=0}

  #lambdas
  lambdas=names[grep("lambda",names)]

  fromlambdas=as.numeric(substr(lambdas, 7, 7+zp*1))
  tolambdas1=as.numeric(substr(lambdas, 8+zp*1, 8+zp*2))
  tolambdas2=as.numeric(substr(lambdas, 9+zp*2, 9+zp*3))

  #mus
```

```
  mus=names[grep("mu",names)]
  frommus=as.numeric(substr(mus, 3, 3+zp*1))

  #qs
  qs=names[grep("q",names)]
  fromqs=as.numeric(substr(qs, 2, 2+zp*1))
  toqs=as.numeric(substr(qs, 3+zp*1, 3+zp*2))

  #biogeographic processes definition
  ############################
  #sympatry
  sympatry_logical_list=list()
  sympatry_list=list()

  for (j in 1:length(names(table))){

    sympatry_logical_list[[j]]=rep(F,length(lambdas))

    for (i in 1:length(lambdas)){
      sympatry_logical_list[[j]]
[i]=(setequal(tableset[[fromlambdas[i]]],tableset[[tolambdas1[i]]]) &&
is.subset(tableset[[tolambdas2[i]]],tableset[[fromlambdas[i]]]) &&
setequal(tableset[[tolambdas2[i]]], names(table)[j])) | #2 is the offspring
species
        (setequal(tableset[[fromlambdas[i]]],tableset[[tolambdas2[i]]]) &&
is.subset(tableset[[tolambdas1[i]]],tableset[[fromlambdas[i]]]) &&
setequal(tableset[[tolambdas1[i]]], names(table)[j]))   #1 is the offspring
species
    }

    sympatry_list[[j]]=lambdas[sympatry_logical_list[[j]]]

  }

  #vicariance
  vicariance_logical=rep(F,length(lambdas))
  for (i in 1:length(lambdas)){

vicariance_logical[i]=(length(intersect(tableset[[tolambdas1[i]]],tableset[[tola
mbdas2[i]]]))==0 && #it is allopatry

setequal(tableset[[fromlambdas[i]]],union(tableset[[tolambdas1[i]]],tableset[[to
lambdas2[i]]]))) #union of offsprings is equal to ancestor
  }

  vicariance=lambdas[vicariance_logical]

  #founder (sensu bgb)
  founder_logical_list=list()
  founder_list=list()

  for (j in 1:length(names(table))){

    founder_logical_list[[j]]=rep(F,length(lambdas))

    for (i in 1:length(lambdas)){
      founder_logical_list[[j]]
[i]=(length(intersect(tableset[[tolambdas1[i]]],tableset[[tolambdas2[i]]]))==0
&& #it is allopatry
```

```
((setequal(tableset[[fromlambdas[i]]],tableset[[tolambdas1[i]]]) &&
setequal(tableset[[tolambdas2[i]]], names(table)[j])) | #2 is offspring species

(setequal(tableset[[fromlambdas[i]]],tableset[[tolambdas2[i]]]) &&
setequal(tableset[[tolambdas1[i]]], names(table)[j]))) #1 is offspring species
    }

    founder_list[[j]]=lambdas[founder_logical_list[[j]]]

  }

  #extinction
  extinction_q_logical_list=list()
  extinction_mu_logical_list=list()
  extinction_list=list()

  for (j in 1:length(names(table))){

    #local extinction
    extinction_q_logical_list[[j]]=rep(F,length(qs))

    for (i in 1:length(qs)){
      extinction_q_logical_list[[j]]
[i]=is.subset(tableset[[toqs[i]]],tableset[[fromqs[i]]]) && #offspring is
subset of ancestor
        setequal(setdiff(tableset[[fromqs[i]]],tableset[[toqs[i]]]),names(table)
[j]) #their difference is focal area
    }

    #global extinction
    extinction_mu_logical_list[[j]]=rep(F,length(mus))

    for (i in 1:length(mus)){
      extinction_mu_logical_list[[j]]
[i]=setequal(tableset[[frommus[i]]],names(table)[j]) #it is extinction in focal
area
    }


extinction_list[[j]]=c(qs[extinction_q_logical_list[[j]]],mus[extinction_mu_logi
cal_list[[j]]])

  }



  #migration
  migration_logical_list=list()
  migration_list=list()

  for (j in 1:length(names(table))){

    migration_logical_list[[j]]=rep(F,length(qs))

    for (i in 1:length(qs)){
      migration_logical_list[[j]]
[i]=is.subset(tableset[[fromqs[i]]],tableset[[toqs[i]]]) && #ancestor is a
subset of offspring
        setequal(setdiff(tableset[[toqs[i]]],tableset[[fromqs[i]]]),
names(table)[j]) #their difference is focal area
```

```
    }

    migration_list[[j]]=qs[migration_logical_list[[j]]]

  }

  #everything else and the forbidden parameters is a zero combination
  zerocombinations=c(setdiff(names, c(unlist(sympatry_list), vicariance,
unlist(founder_list), unlist(extinction_list),
unlist(migration_list))),forbidden)


  #build formulas
  ###############################

  #sympatry
  if (no.sympatry) {
    sympatry_formulas=zero_builder(unlist(sympatry_list))
  } else if (single.sympatry) {
    sympatry_formulas=formula_builder(unlist(sympatry_list))
  } else {
    sympatry_formulas=unlist(lapply(sympatry_list, formula_builder))
  }

  #vicariance
  if (no.vicariance) {
    vicariance_formulas=zero_builder(vicariance)
  } else if (single.vicariance) {
    vicariance_formulas=formula_builder(vicariance)
  } else {
    vicariance_formulas=NULL
  }

  #founder
  if (no.founder) {
    founder_formulas=zero_builder(unlist(founder_list))
  } else if (single.founder) {
    founder_formulas=formula_builder(unlist(founder_list))
  } else if (pooled.founder){
    founder_formulas=unlist(lapply(founder_list, formula_builder))
  } else {
    founder_formulas=NULL
  }

  #extinction
  if (no.extinction) {
    extinction_formulas=zero_builder(unlist(extinction_list))
  } else if (single.extinction) {
    extinction_formulas=formula_builder(unlist(extinction_list))
  } else {
    extinction_formulas=unlist(lapply(extinction_list, formula_builder))
  }

  #migration
  if (no.migration) {
    migration_formulas=zero_builder(unlist(migration_list))
  } else if (single.migration) {
    migration_formulas=formula_builder(unlist(migration_list))
  } else if (pooled.migration) {
    migration_formulas=unlist(lapply(migration_list, formula_builder))
```

```
  } else {
    migration_formulas=NULL
  }

  #not meaningful parameters
  zerocombinations_formulas=zero_builder(zerocombinations)

  #stick them in one list
  ##############################
  formulas=as.list(c( sympatry_formulas,
                      vicariance_formulas,
                      founder_formulas,
                      extinction_formulas,
                      migration_formulas,
                      zerocombinations_formulas))
  return(formulas)
}
```

In the next step, we fit the model with shared parameters on the generated data.

```
#generate ClaSSE likelihoods of each tree
mcel=function(tree){
  make.classe(tree, tree$tip.state, k=3,strict = F)
}
fellist=lapply(tellist,mcel)

#create joint likelihood of multi-clade model
likel=combine(fellist)

#restrict ClaSSE parametrization to GeoSSE-like
table=data.frame(mid=c(1,0,1),high=c(0,1,1))
formulasel=restrict_classe2geosse(table,
                                  no.vicariance = T,

                                  single.extinction = T,
                                  no.founder = T)
likmultiel=constrain(likel, formulae=formulasel)

#fit the model
p=starting.point.classe(tellist[[1]], k=3)

fitmultiel=find.mle(likmultiel, p[argnames(likmultiel)])
```

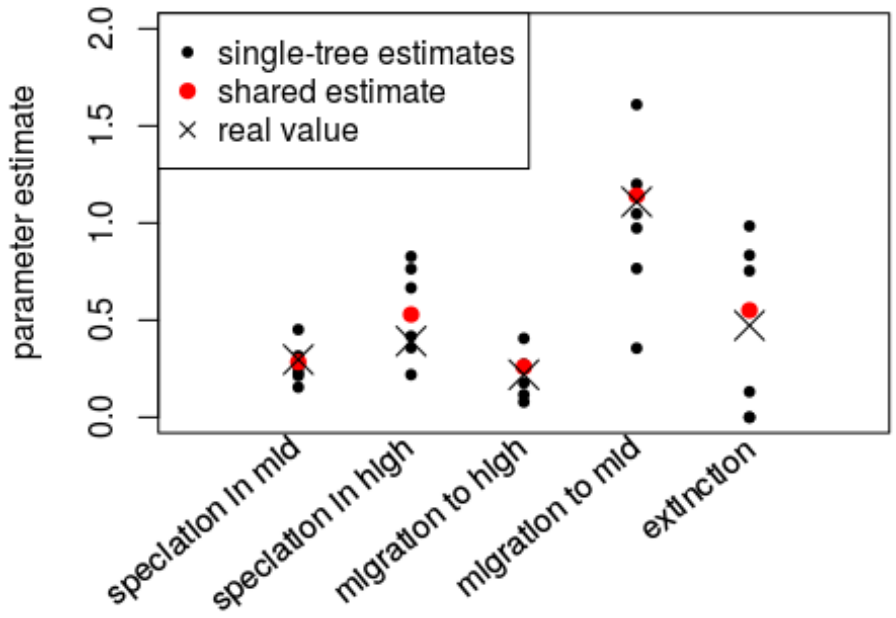
For comparison, we fit the diversification model on each tree separately.

```
#constrain likelihood function for each tree separately
scel=function(lik){
  constrain(lik, formulae=formulasel)
  }
slikellist=lapply(fellist,scel)

#fit each tree
fiel=function(lik){
  find.mle(lik, p[argnames(likmultiel)])
  }
sfitellist=lapply(slikellist,fiel)
```

The plot of the shared and single tree estimates shows that the shared estimates closely match the original value and that the single tree estimates are scattered around with larger variance. The aggregation of estimates around the original values suggests that the shared multi-clade model is correctly identifiable from the generated data. The single tree models are theoretically identifiable as well, but the large dispersion around the original values suggests that estimates of individual phylogenies may fairly deviate from the generating values for the considered size of phylogeny (30 species).

```
plot(NULL, xlim=c(0,6),ylim=c(0,2),xaxt="n", ylab="parameter estimate",xlab="")
for (i in 1:6){
  points(1:5,sfitellist[[i]]$par, pch=20)
}
points(1:5, fitmultiel$par, col="red", pch=19)
points(1:5, c(lambda111el,lambda222el, q13el, q23el,muel), pch=4,cex=2)
angleAxis(1,srt=40,at = 1:5,
          labels = c("speciation in mid", "speciation in high", "migration to
high", "migration to mid", "extinction"),
          offset=0.1)
legend(x='topleft',
       legend=c("single-tree estimates", "shared estimate", "real value"),
       col=c("black", "red", "black"), pch=c(20,19,4))
```



Then, we compare the AIC of the shared multi-clade model to the AIC of single-tree models to assess their relative goodness of fit. The AIC of single-tree models can be obtained based on the fact that optimizing multiple functions separately yields the same results as optimizing a sum of them, each having different parameters. Based on this, the AICs can be calculated from the sum of log-likelihoods and model parameter counts of the single-tree models. The resulting AIC of the shared multi-clade model is lower than the AIC of the set of single-tree models, reflecting that the dataset was indeed generated using one shared set of parameters.

```
aicmultiel=-2*(fitmultiel$lnLik-5)

slhel=rep(0,6)
for (i in 1:6){slhel[i]=sfitellist[[i]]$lnLik}
aicsingleel=-2*(sum(slhel)-5*6)

aicmultiel
## [1] 1046.624
aicsingleel
## [1] 1064.749
```

Bedrock model

In the second part, we generate a set of 6 phylogenetic trees using a ClaSSE model with diversification and migration rates reflecting maximum likelihood estimates detected across bedrock belts (lambda111=0.2051032, lambda222=0.4424083, lambda312=0.4527579, mu=0.4496823, q13=0.1406433 and q23=0.5780840) containing 30 species. It should be noted that, unlike for elevation, the bedrock model contains a state-change speciation term (lambda312).

```
lambda111be=0.2051032 #speciation on calcareous bedrock
lambda222be=0.4424083 #speciation on siliceous bedrock
lambda312be=0.4527579 #speciation with split to calcareous and species
mube=0.4496823 #extinction on both bedrocks
q13be=0.1406433 #migration from calcareous to siliceous
q23be=0.5780840 #migration from siliceous to calcareous

rbetreesim=function(lambda111be,lambda222be, lambda312be,mube, q13be, q23be){
  repeat{
    t=tree.classe(c(lambda111be, 0, 0, 0, 0, 0, 0, 0, 0,
                    lambda222be, 0, 0, 0,
                    lambda312be,
                    lambda111be, 0, lambda222be, 0,
                    mube, mube, 0, 0,
                    q13be, 0, q23be,
                    mube, mube),
                  max.taxa=30, max.t=Inf, include.extinct=F,x0=NA)
    if (inherits(t, "phylo"))
                    break
  }
  t
  }
tbelist=mapply(rbetreesim,
                rep(lambda111be,6),
                rep(lambda222be,6),
                rep(lambda312be,6),
                rep(mube,6),
                rep(q13be,6),
                rep(q23be,6),
                SIMPLIFY = F)
```

To fit the model with shared parameters, we use the same procedure as for elevational belts, that is, we use the function *combine* from *diversitree* to multiply the likelihood function.

```
#generate ClaSSE likelihoods of each tree
mcbe=function(tree){
  make.classe(tree, tree$tip.state, k=3,strict = F)
}
fbelist=lapply(tbelist,mcbe)

#create joint likelihood of multi-clade model
likbe=combine(fbelist)

#restrict ClaSSE parametrization to GeoSSE-like
table=data.frame(calc=c(1,0,1),cilic=c(0,1,1))
formulasbe=restrict_classe2geosse(table,
                                  single.extinction = T,
                                  no.founder = T)
likmultibe=constrain(likbe, formulae=formulasbe)

#fit the model
p=starting.point.classe(tbelist[[1]], k=3)

fitmultibe=find.mle(likmultibe, p[argnames(likmultibe)])
```

For comparison, we fit the model on each tree separately.

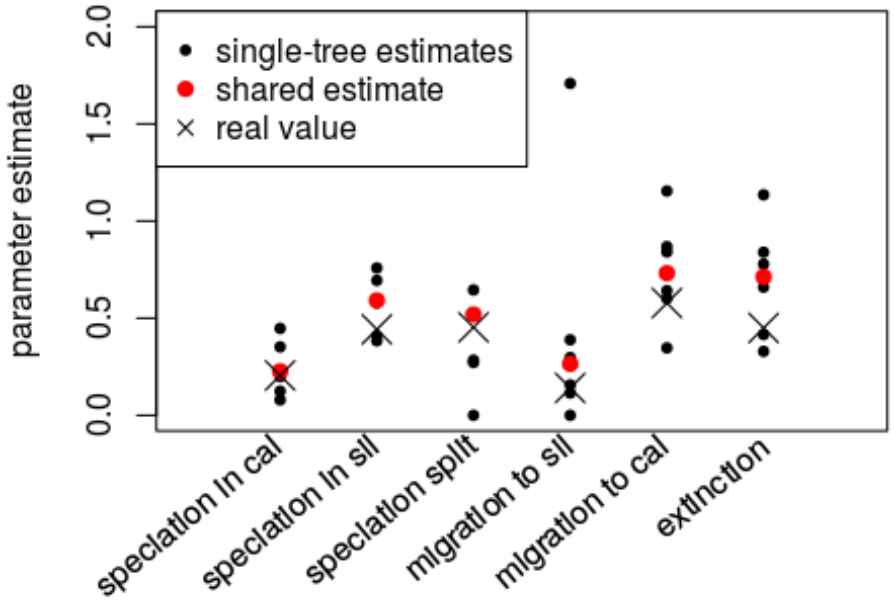
```
#constrain likelihood function for each tree separately
scbe=function(lik){
  constrain(lik, formulae=formulasbe)
  }
slikbelist=lapply(fbelist,scbe)

#fit each tree
fibe=function(lik){
  find.mle(lik, p[argnames(likmultibe)])
  }
sfitbelist=lapply(slikbelist,fibe)
```

The plot of the shared and single tree estimates shows that the shared estimates closely match the original value and the single tree estimates are scattered around with large variance, similarly as for the elevation SSE model. The shared multi-clade model of evolutionary assembly across bedrocks is thus correctly identifiable from the generated data, including the state-change speciation term. The same is true for single tree models, but in phylogenies of size ~30 species, there are considerable deviations of individual tree estimates from the generating values.

```
plot(NULL, xlim=c(0,7),ylim=c(0,2),xaxt="n", ylab="parameter estimate",xlab="")
for (i in 1:6){
  points(1:6,sfitbelist[[i]]$par, pch=20)
}
points(1:6, fitmultibe$par, col="red", pch=19)
points(1:6, c(lambda111be,lambda222be,lambda312be, q13be, q23be,mube),
pch=4,cex=2)

angleAxis(1,srt=40,at = 1:6,
          labels = c("speciation in cal", "speciation in sil","speciation
split", "migration to sil", "migration to cal", "extinction"),
          offset=0.1)
legend(x='topleft',
       legend=c("single-tree estimates", "shared estimate", "real value"),
       col=c("black", "red", "black"), pch=c(20,19,4))
```



Also here, we can also compare the AIC of the shared multi-clade model to the AIC of single-tree models to verify whether the model with a shared set of parameters fits better the data. The resulting AIC of the shared multi-clade model is lower than the AIC of the set of single-tree models, reflecting that the dataset was indeed generated using one shared set of parameters.

```
aicmultiel=-2*(fitmultiel$lnLik-5)

slhel=rep(0,6)
for (i in 1:6){slhel[i]=sfitellist[[i]]$lnLik}
aicsingleel=-2*(sum(slhel)-5*6)

aicmultiel
## [1] 1046.624
aicsingleel
## [1] 1064.749
```

Supplementary methods SM5 – Compilation of ecological and geographic information

Information about bedrock, elevational niche and geographical occurrences for each ingroup species was obtained from the following regional floristic literature: Flora Alpina[28] for the Alps, Flora Iberica[29] for species of Iberian peninsula, Flóra Slovenska[30] and Wildpflanzen Siebenbürgens[31] for Carpathians, and Flora Srbije[32] for the Balkans. Additional information about *Androsace*[33–35], *Phyteuma*[36] and *Saxifraga*[37] was obtained from published ecological and biogeographical studies focused on these lineages. The information about *Campanula* was in part compiled based on information available in herbarium specimens and local taxonomic literature. In several cases, we contacted local taxonomists and made categorization based on provided information. Where possible, the information from floristic literature was compared and supplemented with previously published[18] or publicly accessible (GBIF, https://www.gbif.org/) sources of point occurrence data.

The calcareous bedrock niche was defined by regular presence of species on calcareous, dolomitic or ultrabasic bedrocks, the siliceous bedrock niche was defined by regular presence of species on any bedrocks that do not fall in the calcareous category. For instance, in case of species covered by Flora Alpina [28], species is considered present to a calcareous niche if regular presence is indicated either from limestones (ca) or serpentinites (ser), and to siliceous niche if regular presence is indicated from silicates (si), intermediate substrates (ca/si) or volcanic rocks (bas).

The mid-elevation niche was defined by regular presence of species in habitats below timberline, i.e. up to subalpine elevational zone *sensu* Flora Alpina[28]. High elevation niche was defined by regular presence above timberline, i.e. in alpine and nival zone *sensu* Flora Alpina[28]. In the cases in which floristic information did not refer to elevational belts, specifically Flora Iberica[29], we marked species presence in mid-elevation niche if the species was inhabiting habitats lower that 200 m below regional timberline and in high elevation niche if the species was inhabiting habitats 200 m above regional timberline. No such treated species was restricted to the range +- 200 m around timberline.

As the small scale geographic regions, we used operative geographic units in Flora Alpina [28] for the Alps, and mountain regions based on Körner et al. 2017[38] for other European mountains, with subsequent modifications that better reflect structuring of biogeographic information in local floristic literature.
Specifically, we merged:

- Pennines and Cambrian Mountains to England
- MacGillycuddy's Reeks and Wicklow Mountains to Ireland
- Vosges, Black Forest and Jura Mountains to Rhine Valley
- Grampian Mountains, Northwestern Highlands and Southern Uplands to Scotland

We joined:

- Basque Mountains and Tras-os-montes to Cantabrian Mountains
- Korab, Sar Planina and Jablanica to Dinaric Alps
- Kontovounia, Tayetos Oros, Crete and Parnon Oros to Peloponnisos
- Gribe, Mali i Gjere, Mount Nemercke, Mount Olympus and Mount Othris to Pindos
- Osogovo, Maleshevo, Belasica, Voras Mountains, Rila, Pirin and Pangaion Hills to Rhodope mountains

We renamed:

- Balkan Mountains to Stara Planina

We divided:

- Carpathian Mountains to Western Carpathians and South Eastern Carpathians along the border between Slovakia and Ukraine

We newly defined:

- lower mountain ranges in Czechia not included into Western Carpathians as Sudetes

In addition to this, whole Africa, Middle East (including Caucasus) and Arctic (including Siberian mountains) were represented by one region each, accommodating species with ranges extending out of Europe. Species occurring in lowlands out of mountain regions were always attributed to geographically closest mountain region.

The 5 major geographic regions were defined as sets of small scale geographic regions, specifically:

- Alps: Alps, Massif central and Rhine valley
- Apeninnes: Apennines, Corsica, Sardinia and Sicily
- Balkans: Dinaric Alps, Rhodopes, Stara planina, Peloponnisos, Pindos and Middle East (the latter region was merged within the Balkans because no focal endemic species and strong floristic connections)
- Carpathians: Carpathians, Sudetes, all northern European regions and Arctic (the latter region was merged within the Carpathians because very few focal endemic species and strong floristic connections)
- Iberian mountains: all mountains on Iberian Peninsula, Mallorca, Madeira and northern Africa (the latter two regions were merged within Iberian mountains because of very few focal endemic species and strong floristic connections)

For table of ecological niches and regions for each species, see Supplementary dataset SD4.

Supplementary methods SM6 – Species sampling and taxonomic treatment

Our ingroup sampling included 38 samples of 26 species for *Androsace* sect. *Aretia* (which includes in total 29 species excluding subgenus *Douglasia*, see below), 80 samples of 45 species for *Campanula* sect. *Heterophylla* (in total 50 species), 31 samples of 28 species for *Gentiana* sections *Gentiana, Ciminalis and Calanthianae* (in total 35 species; all 3 sections considered together, see below), 33 samples of 27 species for *Phyteuma* (in total 27 species), 28 samples of 24 species for *Primula* sect. *Auriculata* (in total 24 species), 69 samples of 62 species for *Saxifraga* sect. *Saxifraga* (in total 86 species). Concerning outgroups, we included 49 outgroup samples of Campanulaceae, 14 outgroup samples of Gentianaceae, 95 outgroup samples of Primulaceae, and 49 and 6 outgroup samples of Saxifragaceae and Grossulariaceae, respectively. In total our dataset contains 492 samples. The large majority of dataset was collected in the field, but 10 samples come from herbarium specimens, and 22 samples come from individuals cultivated in botanical gardens from seeds collected in the field. Please see the accession tables in Supplementary dataset SD1 for details.

We detail below the taxonomic literature and molecular phylogenetic studies that we took in account to generate the list of ingroup species and subspecies with unambiguously attributable morphological description, ecology and geographic range. For all the lineages, we took in account information from regional floristic literature: Flora Alpina[28], Flora Iberica[29], Flóra Slovenska[30], Wildpflanzen Siebenbürgens[31] and Flora Srbije[32]. In addition to this, we took in account specific taxonomic literature for each of the lineages, specifically:
- For *Androsace* sect. *Aretia* we used Schneeweiss et al. 2004[39], Schonswetter et al. 2009[33], Boucher et al. 2012[40], Schonswetter et al. 2015[34] and Boucher et al. 2015[18].
-For *Campanula* sect. *Heterophylla* we used Mansion et al. 2012[3], Kovačić 2004[41] and Fenaroli et al. 2013[42]. As this lineage is the most complex one of those included in this study from the taxonomic point of view, we established a specific collaboration with Kristýna Šemberová (co-author of this study) because she is currently conducting a detailed taxonomic revision of the species of this group. For controverted species, we included several individuals to check for species monophyly. In addition, a specific study integrating molecular and morphological data of Pyrenean species has been conducted for the taxonomic revision and species delimitation of controverted species endemic to this area[43].
- For *Gentiana* we used Favre 2015[4], and specifically for section *Gentiana* we used Rossi 2011[44] and for section *Calathianae* we used Hämmerli 2007[45].
-For *Phyteuma we used* Schneeweiss et al. 2013[36].
- For *Primula* sect. *Auriculata* we used Zhang and Kadereit 2004[46] and Boucher et al. 2015[18].
- For *Saxifraga* sect. *Saxifraga* we used Vargas 2000[47], Webb and Gornall 1989[37] and Tkach et al. 2015[48].

Where available and specifically for controverted taxa, we used more than one sample per species for constructing phylogenies. To turn the sample topologies into species trees, we applied several specific treatments:
- We selected the tips of paraphyletic species to conserve most recent splitting node: 4 species in our phylogenies (*Gentiana lutea* ssp. *lutea*, *Androsace halleri* ssp. *halleri*, *Androsace cylindrica* ssp. *hirtella*, *Saxifraga glabella*) proved to be paraphyletic, i.e. with another species arising from within subtree of their samples. This phenomenon may be caused by incomplete lineage sorting, but may also reflect evolutionary reality of budding speciation within these lineages. In order to keep the most realistic splitting date between such hierarchically organized species, we selected the samples of paraphyletic species in order to conserve the most recent splitting node.
- We pruned the sample of *Campanula witasekiana* from Eastern Alps: *Campanula witasekiana* was a seemingly polyphyletic species in our dataset, with one sample from Dinaric mountains in Bosnia and another from Austrian Alps, lying in different parts of *Campanula* sect. *Heterophylla* phylogeny. Given the inconsistency between species descriptions by botanical communities in the Balkans and in Austria, and the fact that the type locality of species is in Bosnia, we assumed that the description *C. witasekiana* from Eastern Alps is erroneous and decided to keep the sample of *C. witasekiana* from Bosnia in our species tree.
- We pruned those samples determined in the field that could not be later verified without doubt from herbarium sheets. In other words, those samples identified in the field as belonging to the species complexes of *Campanula rotundifolia*, *C. scheuchzerii*, *Gentiana verna* or *Primula auricul*a that could not be without

doubts attributed to the taxon identified in the field were not considered when constructing the species trees. These *sensu lato* samples are marked with the text “sl” following scientific name in the accession tables.

In addition to this, we took two specific taxonomic treatments:
- We considered *Gentiana* sect. *Gentiana*, *Ciminalis* and *Calathianae* as a single lineage. Monophyly of these lineages was previously suggested[4]. We found that these three European sections of *Gentiana* form a monophyletic clade with a posterior probability of 1, so we treat them as a single lineage.
- We pruned the subgenus *Douglasia* from the *Androsace* sect. *Aretia* phylogeny: The subgenus *Douglasia* is monophyletic and endemic to north America. It thus represents, at most, a single speciation event in relation to the European mountain system, while the diversification of this subgenus took place in North America, which is out of the geographic scope of our study.

Supplementary methods SM7 – Shotgun sequencing

DNA was extracted from silicagel-conserved collections of leaf tissues gathered by the sampling project PhyloAlps (https://data.phyloalps.org/), using custom DNA extraction kits from Macherey-Nagel and Qiagen. The shotgun libraries were prepared and sequenced with methodology depending on the sequencing facility (see Supplementary dataset SD1 for sequencing facility used for each sample):

For the samples sequenced in Genoscope (Paris, France), the library preparation protocol applied before sequencing was chosen on the basis of the DNA extraction yield. When available, 250 ng of genomic DNA were sonicated using the E210 Covaris instrument (Covaris, Inc., USA) and the NEBNext DNA Modules Products (New England Biolabs, MA, USA) were used for end-repair, 3`-adenylation and ligation of NextFlex DNA barcodes (Bioo Scientific Corporation). After two consecutive 1x AMPure XP clean ups, the ligated products were amplified by 12 cycles PCR using Kapa Hifi Hotstart NGS library Amplification kit (Kapa Biosystems, Wilmington, MA), followed by 0.6x AMPure XP purification. When the extraction yielded low DNA quantities, 10 - 50 ng of genomic DNA were sonicated. Fragments were end-repaired, 3'-adenylated and NEXTflex DNA barcoded adapters were added by using NEBNext Ultra II DNA Library prep kit for Illumina (New England Biolabs). After two consecutive 1x AMPure clean ups, the ligated products were PCR-amplified with NEBNext® Ultra II Q5 Master Mix included in the kit, followed by 0.8x AMPure XP purification. All libraries were subjected to size profile analysis conducted by Agilent 2100 Bioanalyzer (Agilent Technologies, USA) and qPCR quantification (MxPro, Agilent Technologies, USA), then sequenced using 101 base-length read chemistry in a paired-end flow cell on the Illumina HiSeq2000 sequencer (Illumina, USA). On average, 5 billion useful paired-end reads were obtained. An Illumina filter was applied to remove the least reliable data from the analysis. The raw data were filtered to remove any clusters with too much intensity corresponding to bases other than the called base. Adapters and primers were removed on the whole read and low quality nucleotides were trimmed from both ends (while quality value is lower than 20). Sequences between the second unknown nucleotide (N) and the end of the read were also removed. Reads shorter than 30 nucleotides after trimming were discarded. Finally, the reads and their mates that mapped onto run quality control sequences (PhiX genome) were removed. These trimming steps were achieved using internal software based on the FastX package (http://hannonlab.cshl.edu/fastx_toolkit/index.html).

For the samples sequenced in Fasteris (Geneva, Switzerland), custom commercial protocol for preparation was applied. The prepared libraries were sequenced on Illumina HiSeq2000 sequencer (Illumina, USA), using 101 base-length read chemistry in a paired-end flow cell.

Supplementary methods SM8 – Gene regions selection and sequence processing

We aimed to work with all chloroplast coding regions that were present in our chloroplast genome assembled sequences. To do so, we detected all open reading frames in our reconstructions and automatically compared them with a curated database of annotated genes from GenBank, following the Org.Annot procedure implemented in the program Org.Asm (Coissac in prep., https://git.metabarcoding.org/org-asm/org-asm/wikis/home). The non-coding regions we used in our study were selected on the basis of their universal phylogenetic informativeness[49] or previous use in one of the focal lineages[3,4,36,44,45,48,50,51]. The non-coding regions were identified and extracted based on their positioning relative to the neighboring coding regions.

Coding and non-coding regions of ingroup and outgroup samples were further filtered in order to minimize missing data in our family-level alignment matrices. The filtering resulted in 72 coding regions, of which 40 are shared across all study families, and 17 non-coding regions of which 5 are shared across all the families, see Supplementary dataset SD2 for details. Samples with missing data for some of the regions were kept in specific cases: when they corresponded to the only representative of an ingroup species or to an outgroup species defining the dating node and at the same time had so large portion of missing data that excluding missing regions would severely limit the resolution of the whole family phylogeny. To make sure that inclusion/exclusion had no impact on resulting topology or dating (with exception of dating-node outgroups), we reran phylogenetic reconstruction analyses without these samples and compared the resulting trees with all-samples phylogenies. The samples with missing data are indicated as such in the accession tables in Supplementary dataset SD1.

For each of the four families, we aligned the coding regions gene-by-gene using MACSE[52] acknowledging the triplet structure of codon alignment. All the positions were quality filtered by Gblocks[53] (specifying that the data type corresponded to codon alignments), and concatenated together using FasConCat[54]. The noncoding regions were aligned by Mafft[55], quality filtered by Gblocks (specifying that the data corresponded to DNA alignments) and concatenated together.

Supplementary dataset SD1 Accession table. A csv table containing information about taxonomy, database identity, sampling information and species tree treatment of each sample. NOTE: NCBI accession codes are to be added.

Supplementary dataset SD2 Genomic regions. A csv table of coding and non-coding regions used for phylogenies of the four families.

Supplementary dataset SD3 Maximum credibility species trees. A list of maximum credibility species trees for each clade in Newick format.

Supplementary dataset SD4 Ecological and geographic information. A csv table of ecological (bedrock and elevation belt) and geographic (coarse and fine scale) information for each ingroup species.

Supplementary dataset SD5 Alternative maximum credibility species trees. A list of maximum credibility species trees in Newick format using alternative dating approaches and interpretation of fossil record.

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