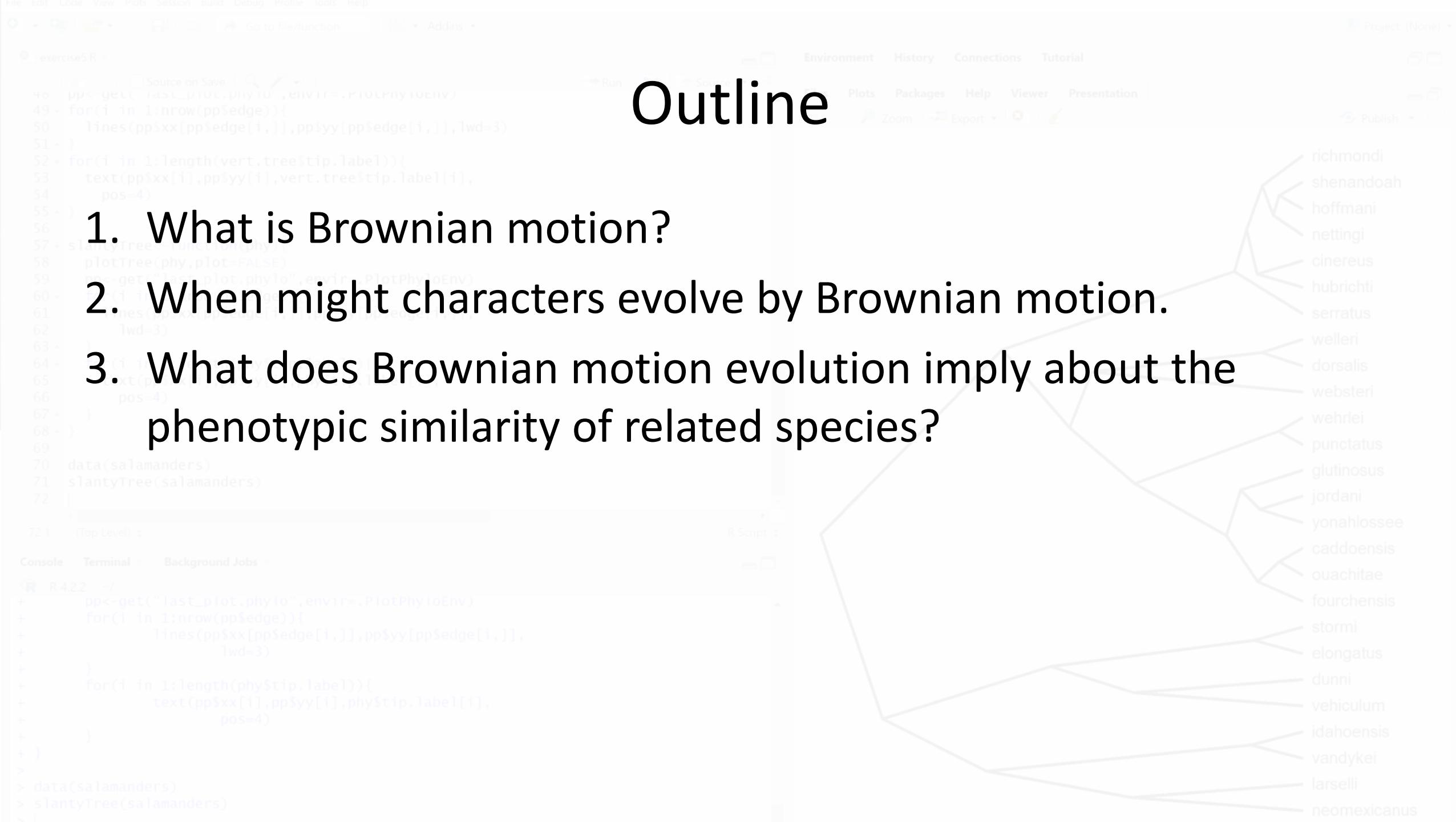
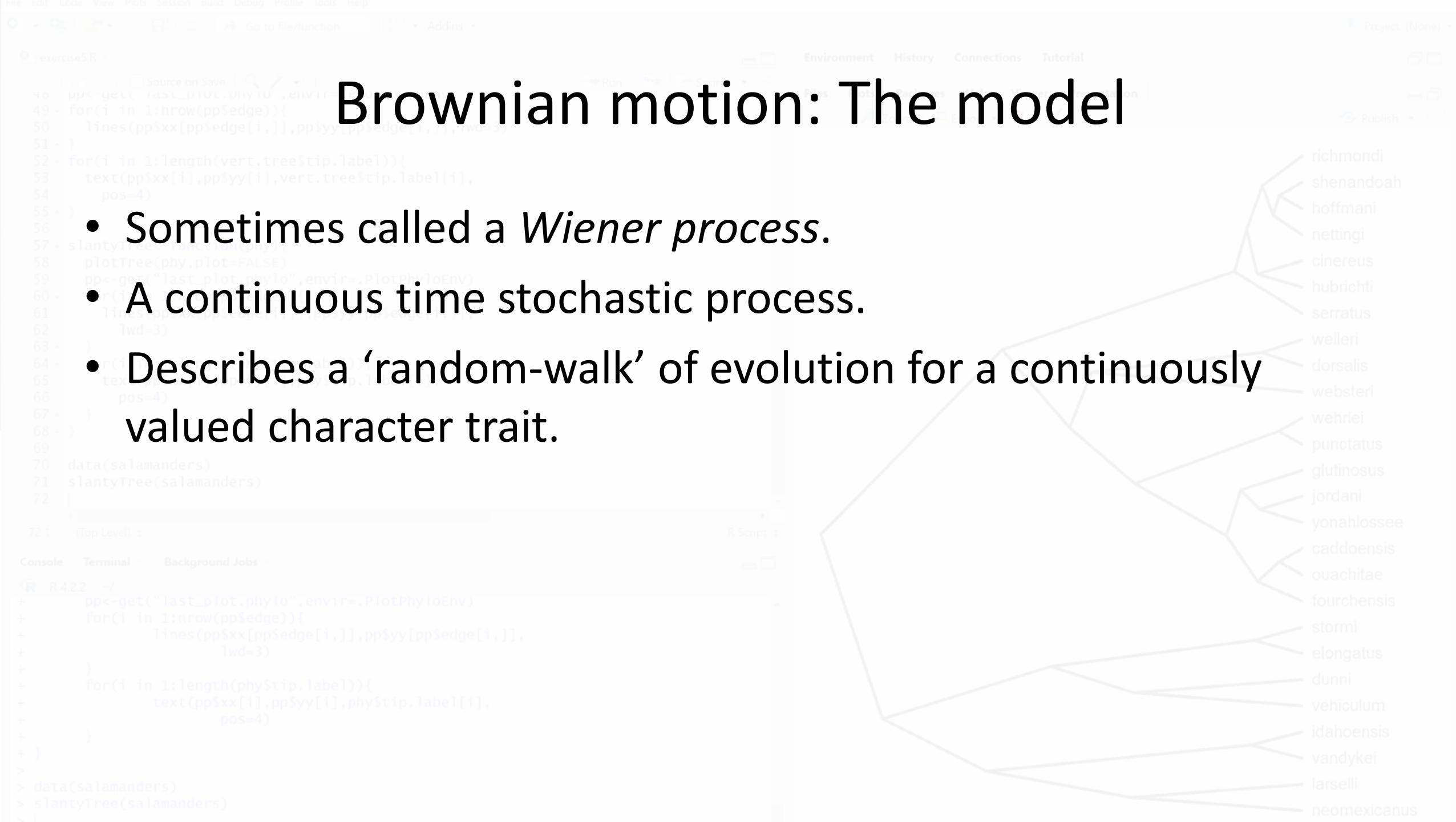


Brownian motion

- A stochastic model originally developed to describe the movement of particles in a fluid.
- A model for the evolution of continuous traits.
- Traits change continuously through time.
- After some time the trait distribution follows a normal distribution





Brownian motion: The model

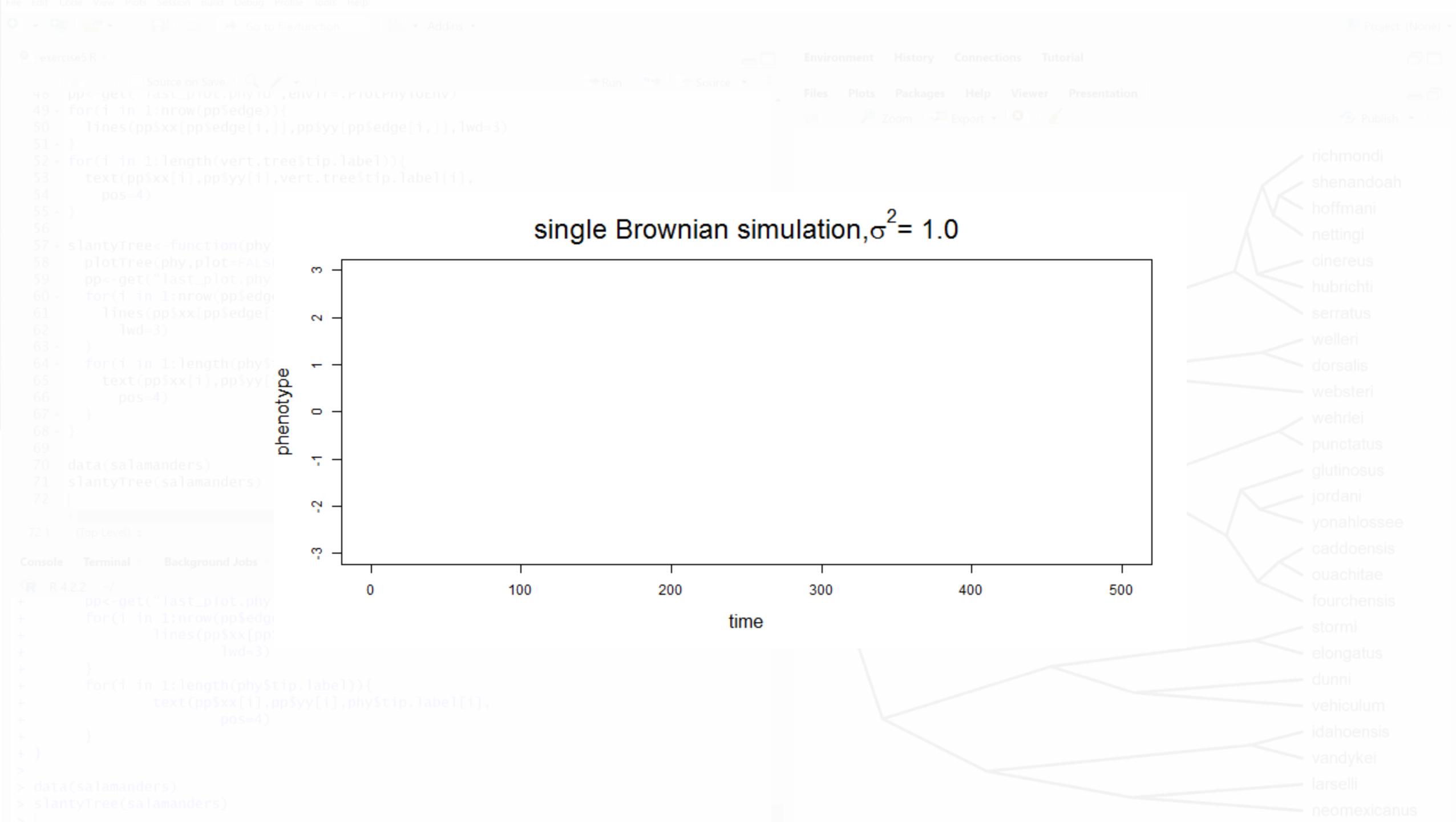
- Sometimes called a *Wiener process*.
- A continuous time stochastic process.
- Describes a ‘random-walk’ of evolution for a continuously valued character trait.

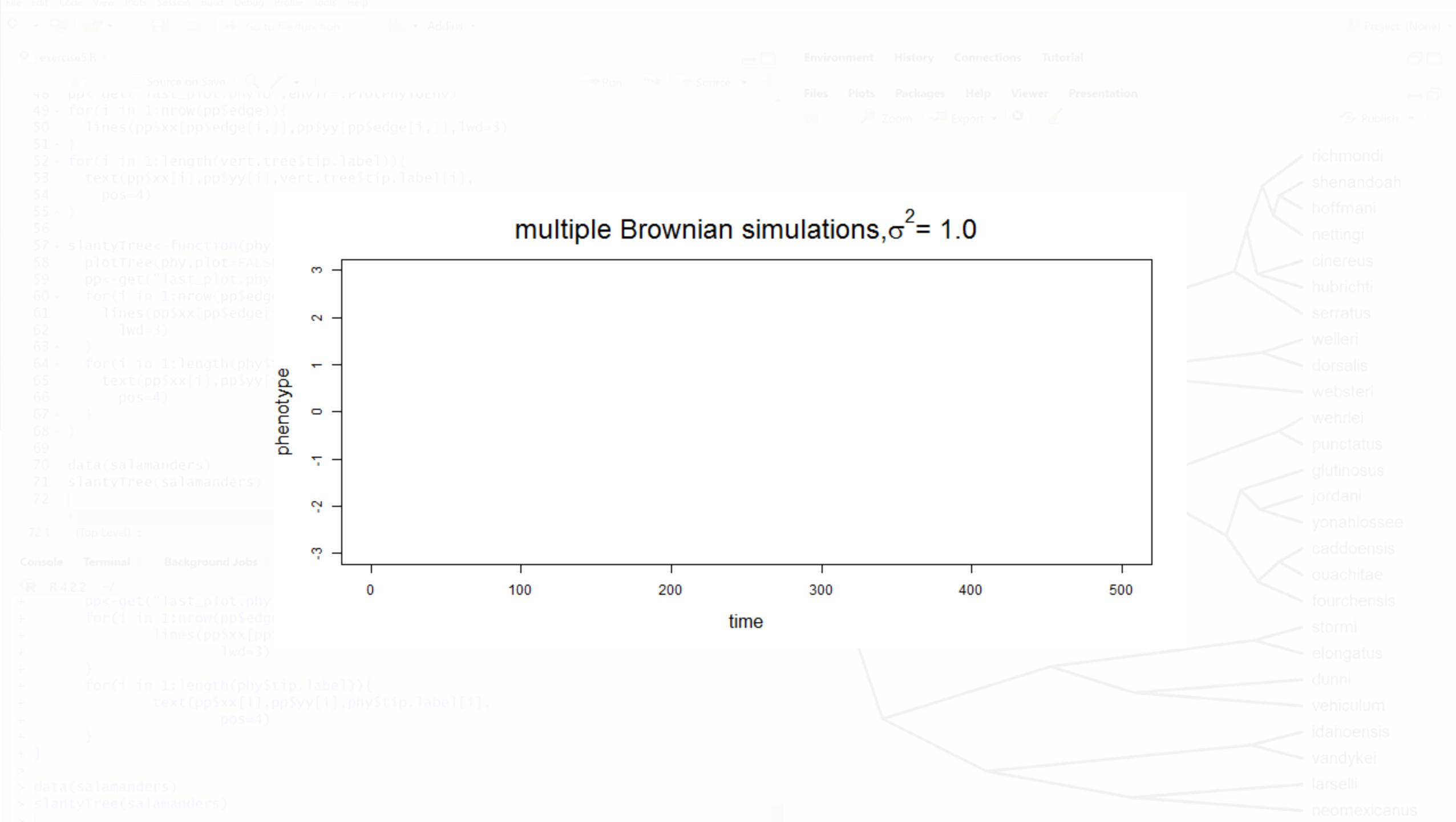
Three facts describe Brownian motion

- Let $W(t)$ be the value of the character at time t .
 1. $E[W(t)] = W(0)$
 - No trend.
 2. Successive changes are independent.
 3. $W(t) \sim N(W(0), \sigma^2 t)$
 - Expected values follow a normal distribution where variance depends on rate & time.

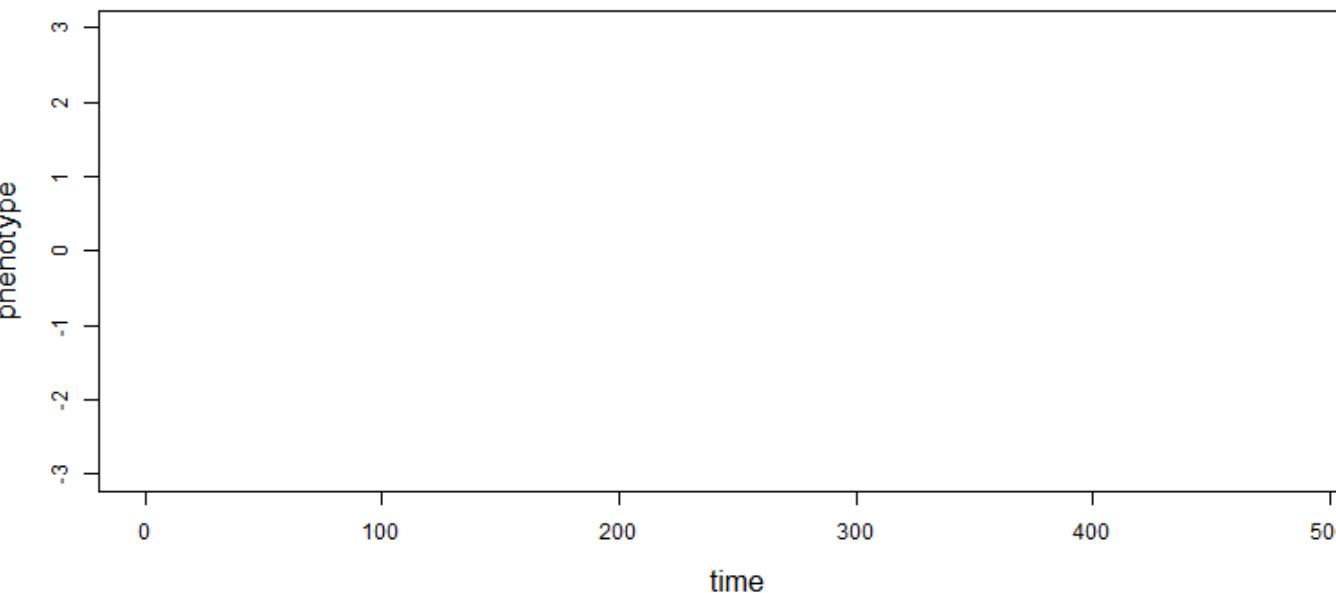
Parameters of the Brownian model

- The Brownian motion model has only two parameters:
 1. Θ , the starting value; $W(0) = \Theta$.
 2. σ^2 , the rate of accumulation of variance through time.

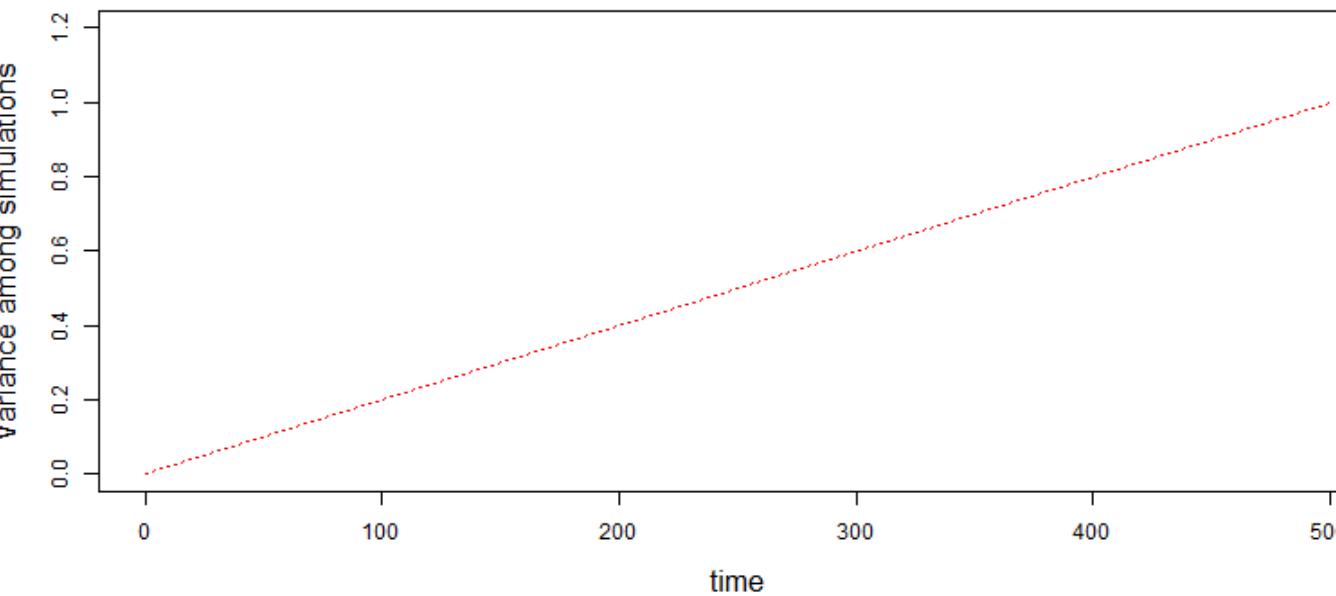




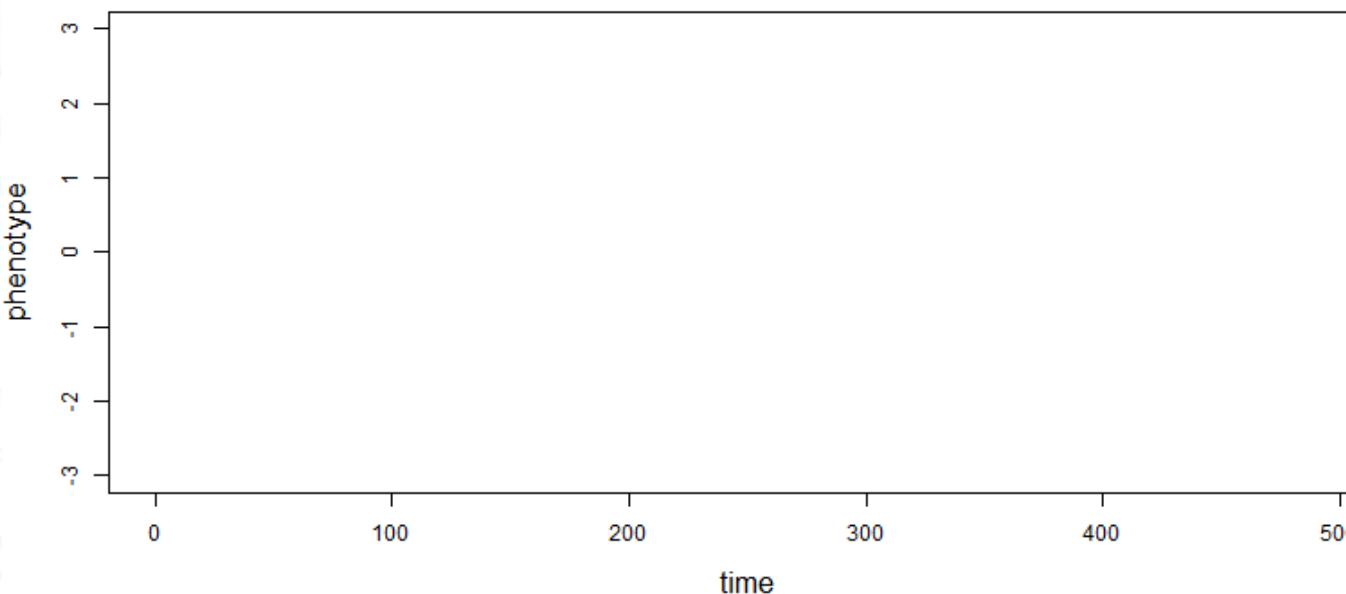
a) multiple Brownian simulations, $\sigma^2 = 1.0$



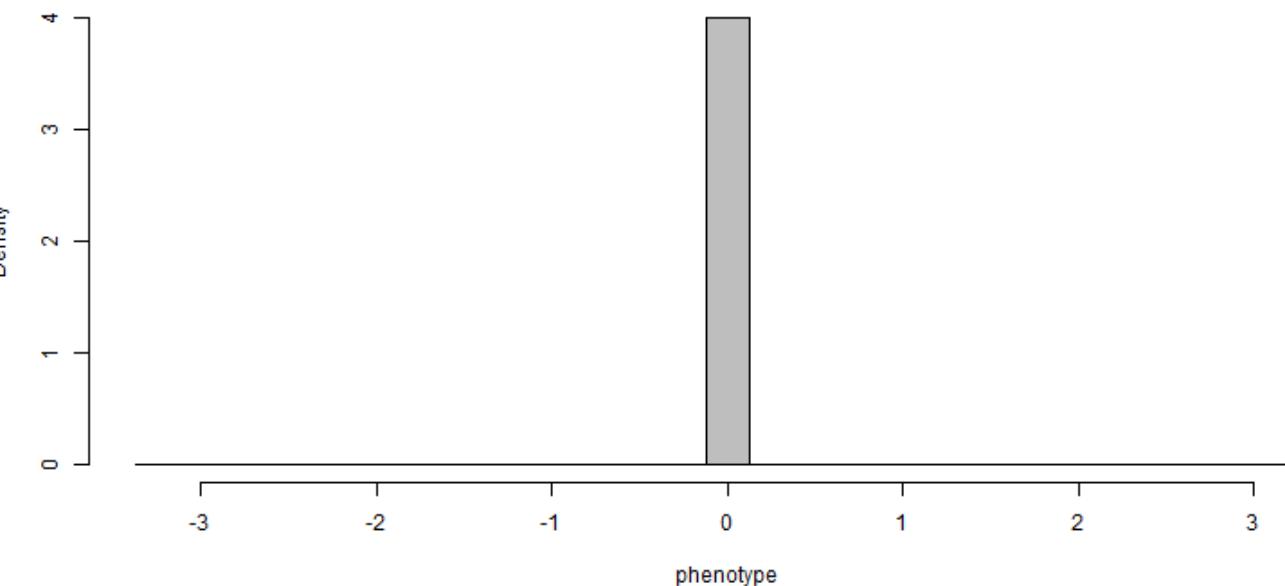
b) variance among simulations (compared to expected)

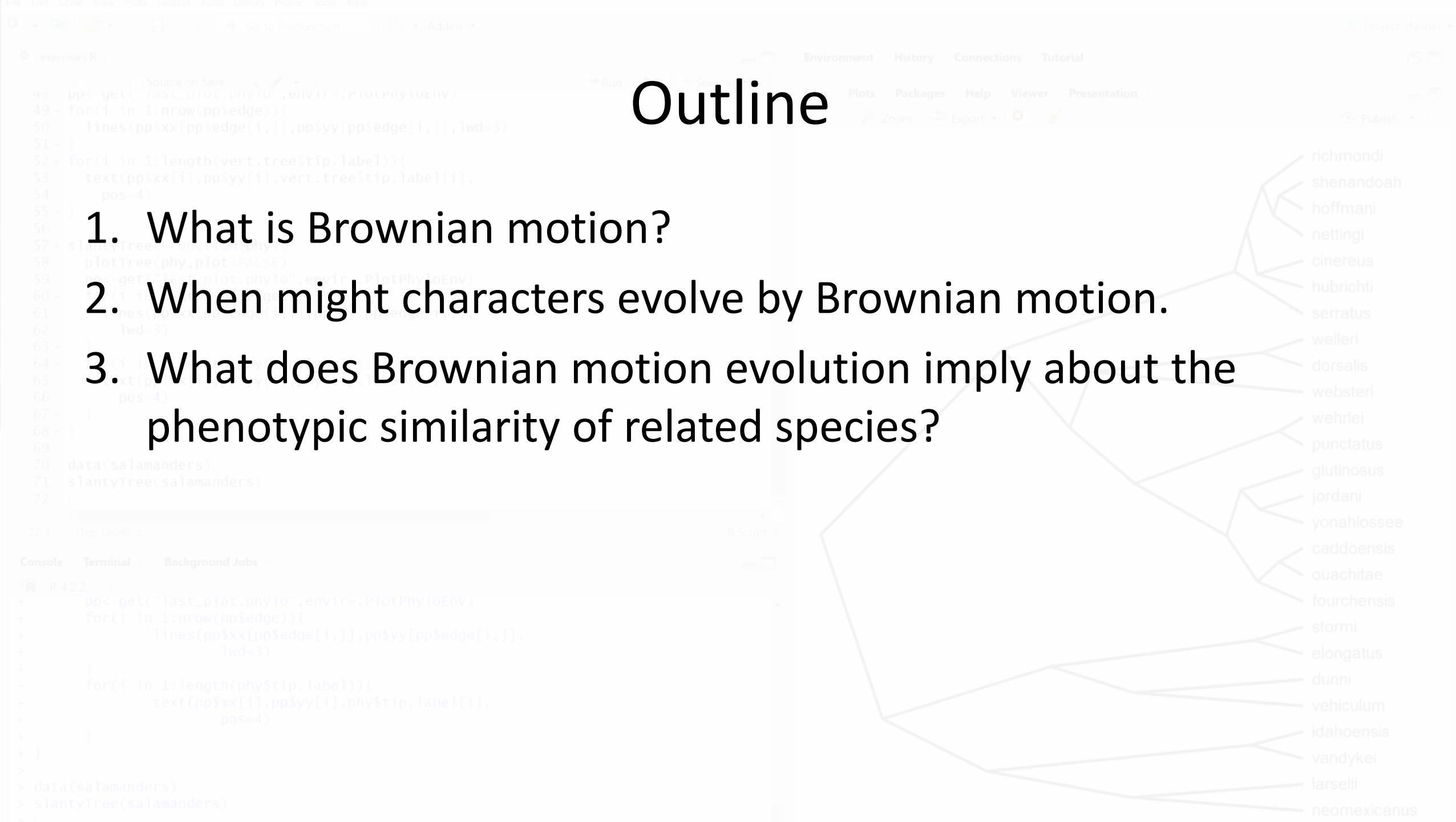


a) multiple Brownian simulations, $\sigma^2 = 1.0$



b) distribution among simulations





A physical model for Brownian motion



```
Source on Save Addins
```

Environment History Connections Tutorial

Why normal?

- BM can be used to describe motion that results from the combination of a large number of independent weak forces
- Adding many small independent variables result in normal distributions, no matter the original distribution (*Central limit theorem*)

richmondi
shenandoah
hoffmani
nettingi
cinereus
hubrichti
serratus
welleri
dorsalis
websteri
lelei
punctatus
glutinosus
jordani
yonahlossee
caddoensis
ouachitae
fourchensis
stormi
elongatus
dunni
vehiculum
idahoensis
vandykei
larselli
neomexicanus

```
Source on Save Addins
```

Environment History Connections Tutorial

```
46 pp<-get("last_plot.phylo",envir=.PlotPhyloEnv)
47 for(i in 1:nrow(pp$edge)){
48   lines(pp$xx[pp$edge[i,]],pp$yy[pp$edge[i,]],lwd=3)
49 }
50 for(i in 1:length(vert.tree$tip.label)){
51   text(pp$xx[i],pp$yy[i],vert.tree$tip.label[i],
52     pos=4)
53 }
54
55 i
56 slantyTree(salamanders)
57 plotTree(phy,pp)
58 pp<-get("last_plot.phylo",envir=.PlotPhyloEnv)
59 for(i in 1:nrow(pp$edge)){
60   lines(pp$xx[pp$edge[i,]],pp$yy[pp$edge[i,]],lwd=3)
61 }
62 for(i in 1:length(phy$tip.label)){
63   text(pp$xx[i],pp$yy[i],phy$tip.label[i],
64     pos=4)
65 }
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67 i
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69 data(salamanders)
70 slantyTree(salamanders)
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Normal

Uniform

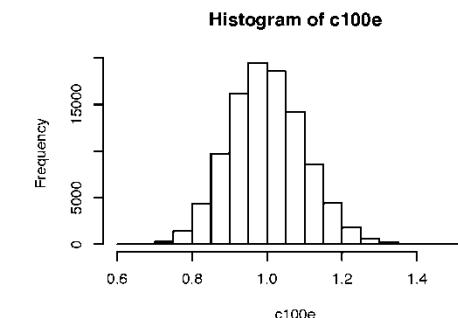
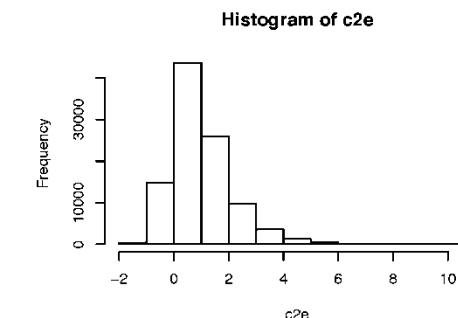
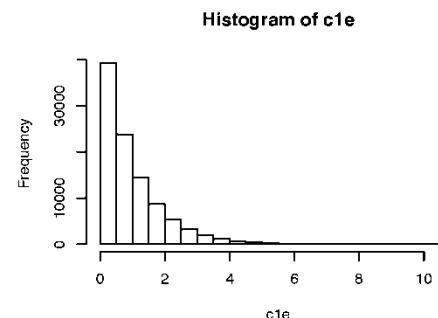
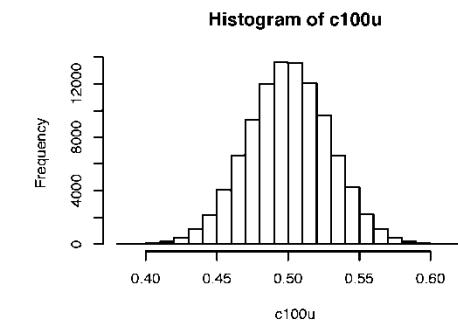
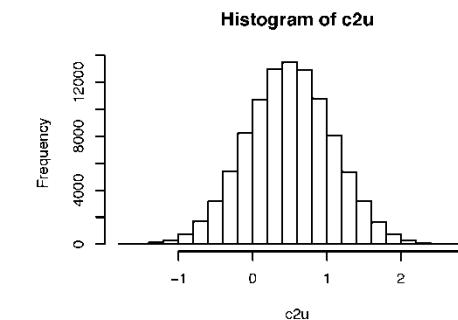
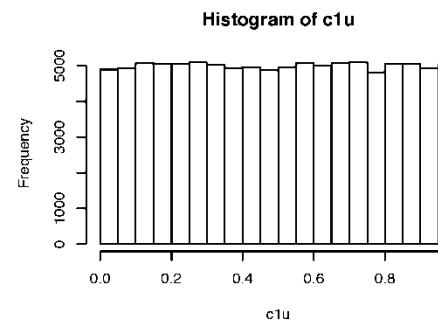
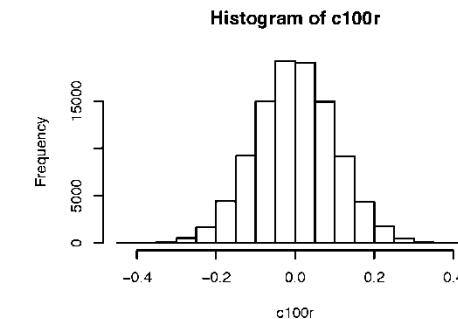
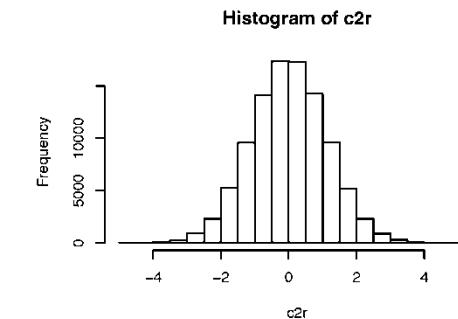
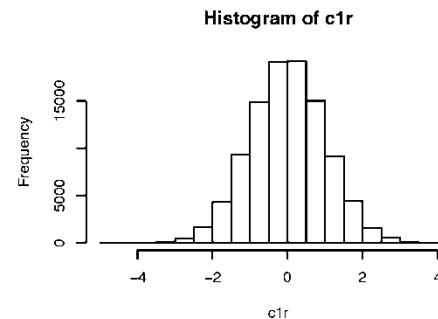
Exponential

Mean of

n=1

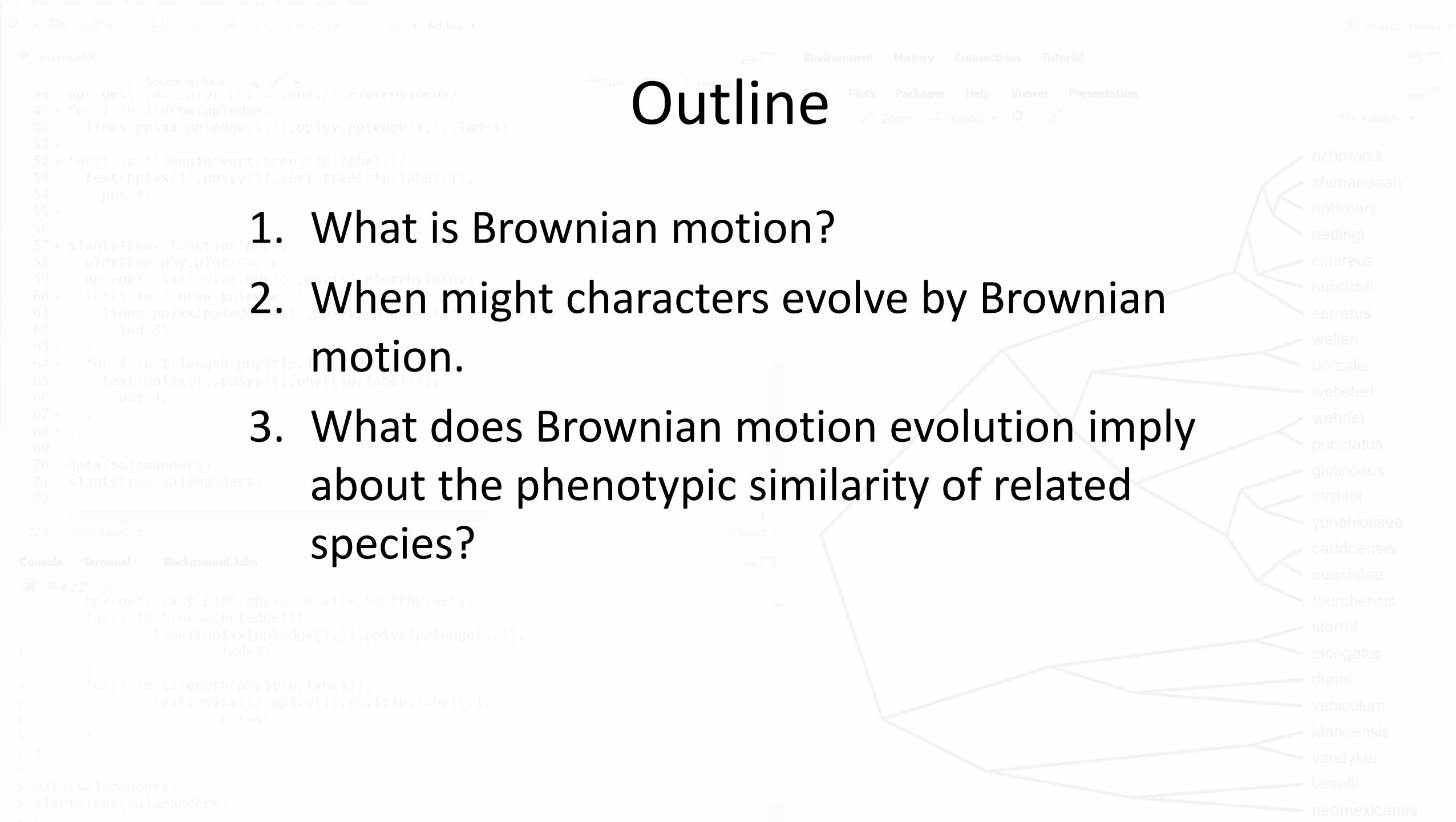
n=2

n=100



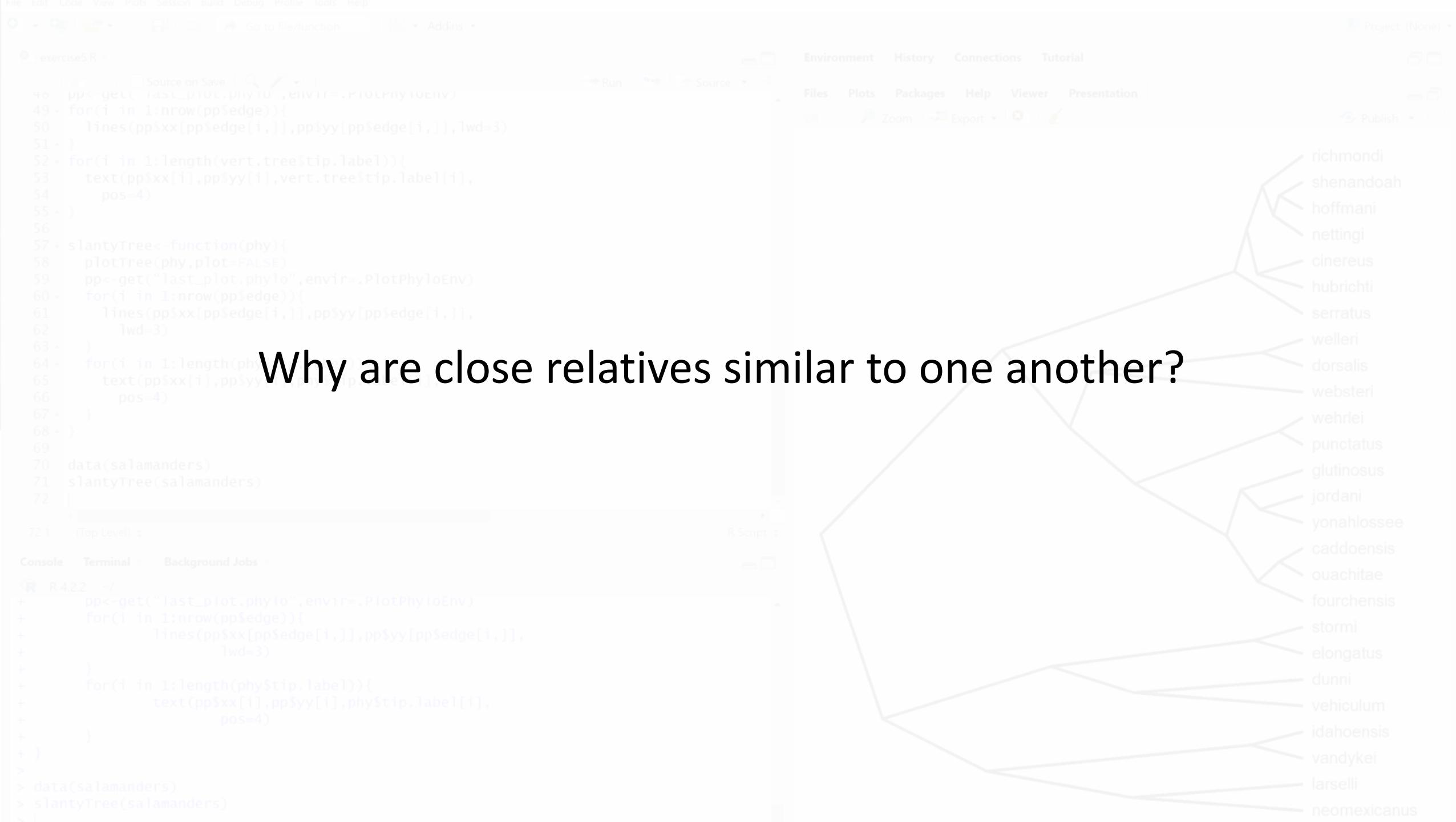
Evolution might approximate BM...

- Genetic drift
- Random punctuated change
- Selection that is weak relative to the time interval that is being considered
- Selection that changes randomly through time



Outline

1. What is Brownian motion?
2. When might characters evolve by Brownian motion.
3. What does Brownian motion evolution imply about the phenotypic similarity of related species?



File Edit Code View Plots Session

Project: (None)

```
Source exercise5.R
```

```
46 pp<-get("las")
47 for(i in 1:nrc)
48   lines(pp$xx)
49 }
50 for(i in 1:ler)
51   text(pp$xx[i]
52     pos=4)
53 }
54 pos=4)
55 }
56
57 slantyTree<-fi
58 plotTree(phy
59 pp<-get("las
60 for(i in 1:r
61   lines(pp$)
62   lwd=3)
63 )
64 for(i in 1:l
65   text(pp$xx)
66   pos=4)
67 )
68 )
69
70 data(salamande
71 slantyTree(sal
72 )
73 (Top Level) z
```

Console Terminal Back

```
R R 4.2.2 ->
+ pp<-get("las
+ for(i in 1:r
+   line
+
+   }
+   for(i in 1:l
+     text
+
+   }
+
+   }
> data(salamanders)
> slantyTree(salamar
>
```

```
graph TD; Root --- sp1[sp1]; Root --- sp2[sp2]; sp1 --- richmondi[richmondi]; sp1 --- shenandoah[shenandoah]; sp1 --- hoffmani[hoffmani]; sp1 --- nettingi[nettingi]; sp1 --- cinereus[cinereus]; sp1 --- hubrichti[hubrichti]; sp1 --- serratus[serratus]; sp1 --- welleri[welleri]; sp1 --- dorsalis[dorsalis]; sp1 --- websteri[websteri]; sp1 --- wehrlei[wehrlei]; sp1 --- punctatus[punctatus]; sp1 --- glutinosus[glutinosus]; sp1 --- jordani[jordani]; sp1 --- yonahlossee[yonahlossee]; sp1 --- caddoensis[caddoensis]; sp1 --- ouachitae[ouachitae]; sp1 --- fourchensis[fourchensis]; sp1 --- stormi[stormi]; sp1 --- elongatus[elongatus]; sp1 --- dunni[dunni]; sp1 --- vehiculum[vehiculum]; sp1 --- idahoensis[idahoensis]; sp1 --- vandykei[vandykei]; sp1 --- larselli[larselli]; sp1 --- neomexicanus[neomexicanus]
```

File Edit Code View Plots Session

Project: (None)

```
Source exercise5.R
```

```
46 pp<-get("las")
47 for(i in 1:nrc)
48   lines(pp$xx)
49 }
50 for(i in 1:ler)
51   text(pp$xx[i]
52     pos=4)
53 }
54 pos=4)
55 }
56
57 slantyTree<-fi
58 plotTree(phy
59 pp<-get("las"
60 for(i in 1:r
61   lines(pp$>
62   lwd=3)
63 )
64 for(i in 1:l
65   text(pp$xx)
66   pos=4)
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68 )
69
70 data(salamande
71 slantyTree(sal
72 )
73
74 (Top Level) :
```

```
Console Terminal Basic
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```
R R 4.2.2 ->
+ pp<-get("las"
+ for(i in 1:r
+   line
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+   }
+   for(i in 1:l
+     text
+
+   }
+ }
> data(salamanders)
> slantyTree(salamard
>
```

```
graph LR
    Root --- sp1_sp2[sp1, sp2]
    sp1_sp2 --- sp1
    sp1_sp2 --- sp2_sp1[sp2, sp1]
```

- richmondi
- shenandoah
- hoffmani
- nettingi
- cinereus
- hubrichti
- serratus
- welleri
- dorsalis
- websteri
- wehrlei
- punctatus
- glutinosus
- jordani
- yonahlossee
- caddoensis
- ouachitae
- fourchensis
- stormi
- elongatus
- dunni
- vehiculum
- idahoensis
- vandykei
- larselli
- neomexicanus

File Edit Code View Plots Session

Project: (None)

```
Source exercise5.R
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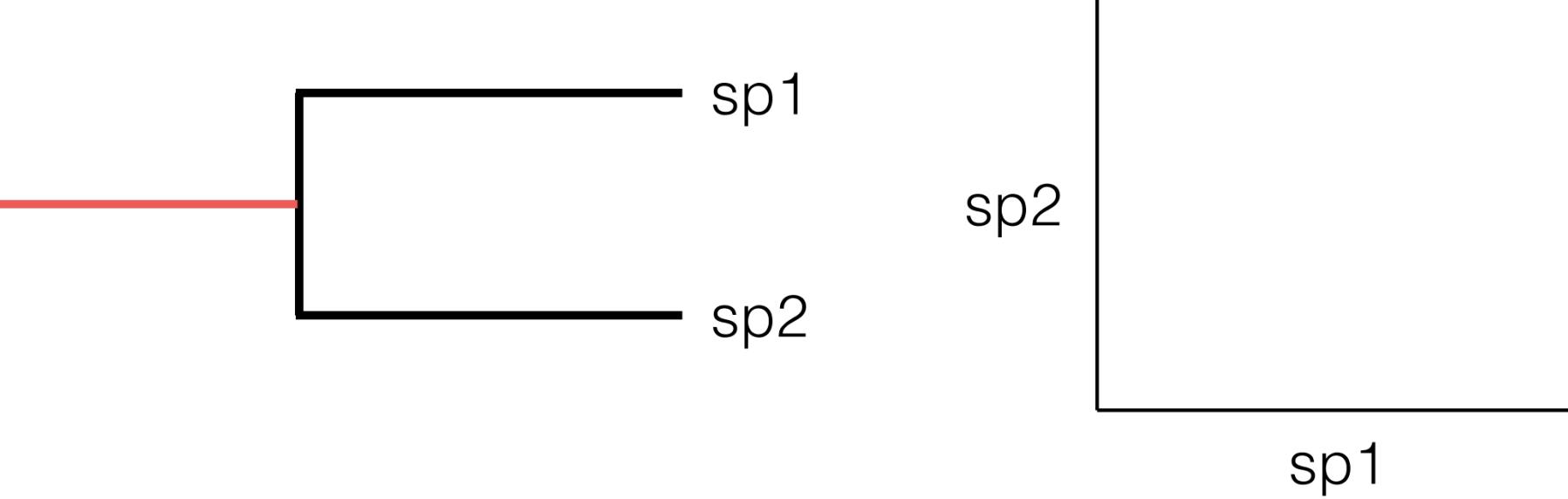
```
46 pp<-get("las")
47 for(i in 1:nrc)
48   lines(pp$xx)
49 }
50 for(i in 1:ler)
51   text(pp$xx[i]
52     pos=4)
53 }
54 pos=4)
55 }
56
57 slantyTree<-fi
58 plotTree(phy
59 pp<-get("las
60 for(i in 1:r
61   lines(pp$>
62   lwd=3)
63 }
64 for(i in 1:l
65   text(pp$xx>
66   pos=4)
67 }
68 }
69
70 data(salamande
71 slantyTree(sal
72 )
73
74 (Top Level) :
```

Console Terminal Back

```
R R 4.2.2 ->
+ pp<-get("las
+ for(i in 1:r
+   line
+
+   }
+   for(i in 1:l
+     text
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+   }
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+   }
+
> data(salamanders)
> slantyTree(salamar
>
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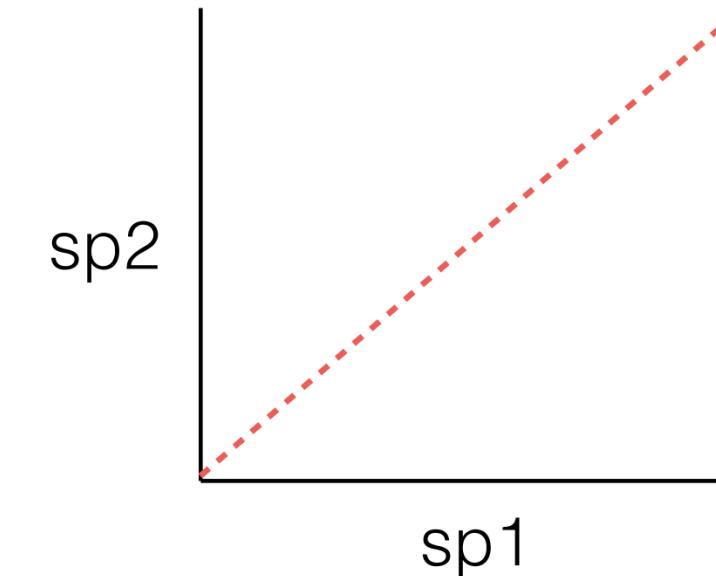
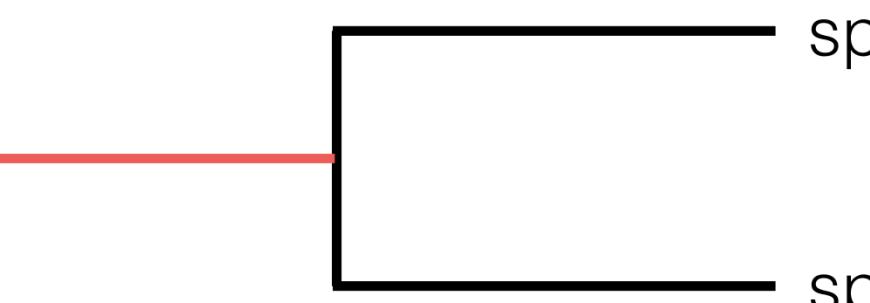
```
graph LR
    Root --- sp1_sp2[sp1, sp2]
    sp1_sp2 --- sp1
    sp1_sp2 --- sp2_sp1[sp2, sp1]
```

- richmondi
- shenandoah
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- nettingi
- cinereus
- hubrichti
- serratus
- welleri
- dorsalis
- websteri
- wehrlei
- punctatus
- glutinosus
- jordani
- yonahlossee
- caddoensis
- ouachitae
- fourchensis
- stormi
- elongatus
- dunni
- vehiculum
- idahoensis
- vandykei
- larselli
- neomexicanus

```
File Edit Code View Plots Session Project (None) Source exercise5.R  
46 pp<-get("las")  
47 for(i in 1:nrc  
48   lines(pp$xx)  
49 }  
50 for(i in 1:ler  
51   text(pp$xx[i  
52     pos=4)  
53 }  
54  
55 }  
56  
57 slantyTree<-f  
58 plotTree(phy  
59 pp<-get("la  
60 for(i in 1:r  
61   lines(pp$  
62     lwd=3)  
63 }  
64 for(i in 1:l  
65   text(pp$xx  
66     pos=4)  
67 }  
68 }  
69  
70 data(salamande  
71 slantyTree(sal  
72 )  
73 (Top Level) :  
74  
Console Terminal Basic  
R R 4.2.2 →  
+ pp<-get("la  
+ for(i in 1:r  
+   line  
+ }  
+ for(i in 1:l  
+   text  
+ }  
+ }  
> data(salamanders)  
> slantyTree(salamard  
>  


```
graph LR; Root --- sp1[sp1]; Root --- sp2[sp2]; sp1 --- clade1[]; sp2 --- clade1; clade1 --- punctatus[punctatus]; clade1 --- glutinosus[glutinosus]; clade1 --- jordani[jordani]; clade1 --- yonahlossee[yonahlossee]; clade1 --- caddoensis[caddoensis]; clade1 --- ouachitae[ouachitae]; clade1 --- fourchensis[fourchensis]; clade1 --- stormi[stormi]; clade1 --- elongatus[elongatus]; clade1 --- dunni[dunni]; clade1 --- vehiculum[vehiculum]; clade1 --- idahoensis[idahoensis]; clade1 --- vandykei[vandykei]; clade1 --- larselli[larselli]; clade1 --- neomexicanus[neomexicanus];
```


```

```
File Edit Code View Plots Session Project (None) Source exercise5.R  
46 pp<-get("las")  
47 for(i in 1:nrc)  
48 lines(pp$xx)  
49 }  
50 for(i in 1:ler)  
51 text(pp$xx[i]  
52 pos=4)  
53 }  
54 lwd=3)  
55 }  
56  
57 slantyTree<-fi  
58 plotTree(phy  
59 pp<-get("las")  
60 for(i in 1:r  
61 lines(pp$  
62 lwd=3)  
63 }  
64 for(i in 1:l  
65 text(pp$xx)  
66 pos=4)  
67 }  
68 }  
69  
70 data(salamande  
71 slantyTree(sal  
72 )  
73 (Top Level) :  
Console Terminal Back  
R R 4.2.2 →  
+ pp<-get("las")  
+ for(i in 1:r  
+ lines(pp$xx)  
+ }  
+ for(i in 1:l  
+ text(pp$xx)  
+ pos=4)  
+ }  
> data(salamanders)  
> slantyTree(salamar  
>  


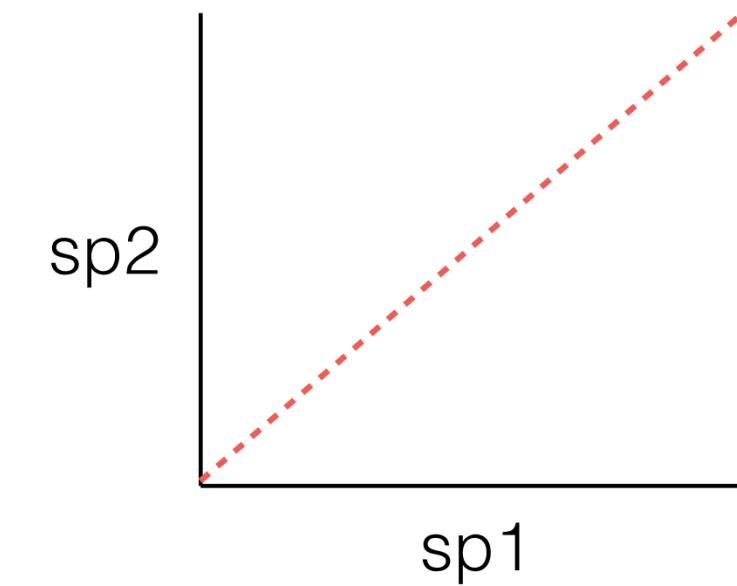
- richmondi
- shenandoah
- hoffmani
- nettingi
- cinereus
- hubrichti
- serratus
- welleri
- dorsalis
- websteri
- wehrlei
- punctatus
- glutinosus
- jordani
- yonahlossee
- caddoensis
- ouachitae
- fourchensis
- stormi
- elongatus
- dunni
- vehiculum
- idahoensis
- vandykei
- larselli
- neomexicanus

```

```
File Edit Code View Plots Session Project (None) 

```
Source
46 pp<-get("lasC"
47 for(i in 1:nrc
48 lines(pp$xx)
49 }
50 for(i in 1:ler
51 text(pp$xx[i
52 pos=4)
53 }
54)
55 }
56
57 slantyTree<-fi
58 plotTree(phy
59 pp<-get("las
60 for(i in 1:r
61 lines(pp$
62 lwd=3)
63 }
64 for(i in 1:l
65 text(pp$xx)
66 pos=4)
67 }
68 }
69
70 data(salamande
71 slantyTree(sal
72)
73 (Top Level) z
Console Terminal Back
R R 4.2.2 →
+ pp<-get("las
+ for(i in 1:r
+ lines(pp$
+ }
+ for(i in 1:l
+ text(pp$xx)
+ pos=4)
+ }
+ }
> data(salamanders)
> slantyTree(salamard
>
richmondi
shenandoah
hoffmani
nettingi
cinereus
hubrichti
serratus
welleri
dorsalis
websteri
wehrlei
punctatus
glutinosus
jordani
yonahlossee
caddoensis
ouachitae
fourchensis
stormi
elongatus
dunni
vehiculum
idahoensis
vandykei
larselli
neomexicanus
```


```



```
File Edit Code View Plots Session Project (None) 

```
Source
46 pp<-get("lasC"
47 for(i in 1:nrc
48 lines(pp$xx)
49 }
50 for(i in 1:ler
51 text(pp$xx[i
52 pos=4)
53 }
54
55 }
56
57 slantyTree<-f
58 plotTree(phy
59 pp<-get("las
60 for(i in 1:r
61 lines(pp$
62 lwd=3)
63 }
64 for(i in 1:l
65 text(pp$xx
66 pos=4)
67 }
68 }
69
70 data(salamande
71 slantyTree(sal
72)
73 (Top Level) z
Console Terminal Back
R R 4.2.2 →
+ pp<-get("las
+ for(i in 1:r
+ lines(pp$
+ }
+ for(i in 1:l
+ text(pp$xx
+ pos=4)
+ }
+ }
> data(salamanders)
> slantyTree(salamar
>
```



A phylogenetic tree diagram. A blue circle at the left tip represents a root node. A horizontal red line extends from this root to a black rectangular box. From the right side of this box, two horizontal black lines branch out: one pointing right labeled 'sp1' and one pointing down labeled 'sp2'.



A scatter plot with a dashed red regression line. The vertical axis is labeled 'sp2' and the horizontal axis is labeled 'sp1'. The plot shows a positive correlation between the two variables.

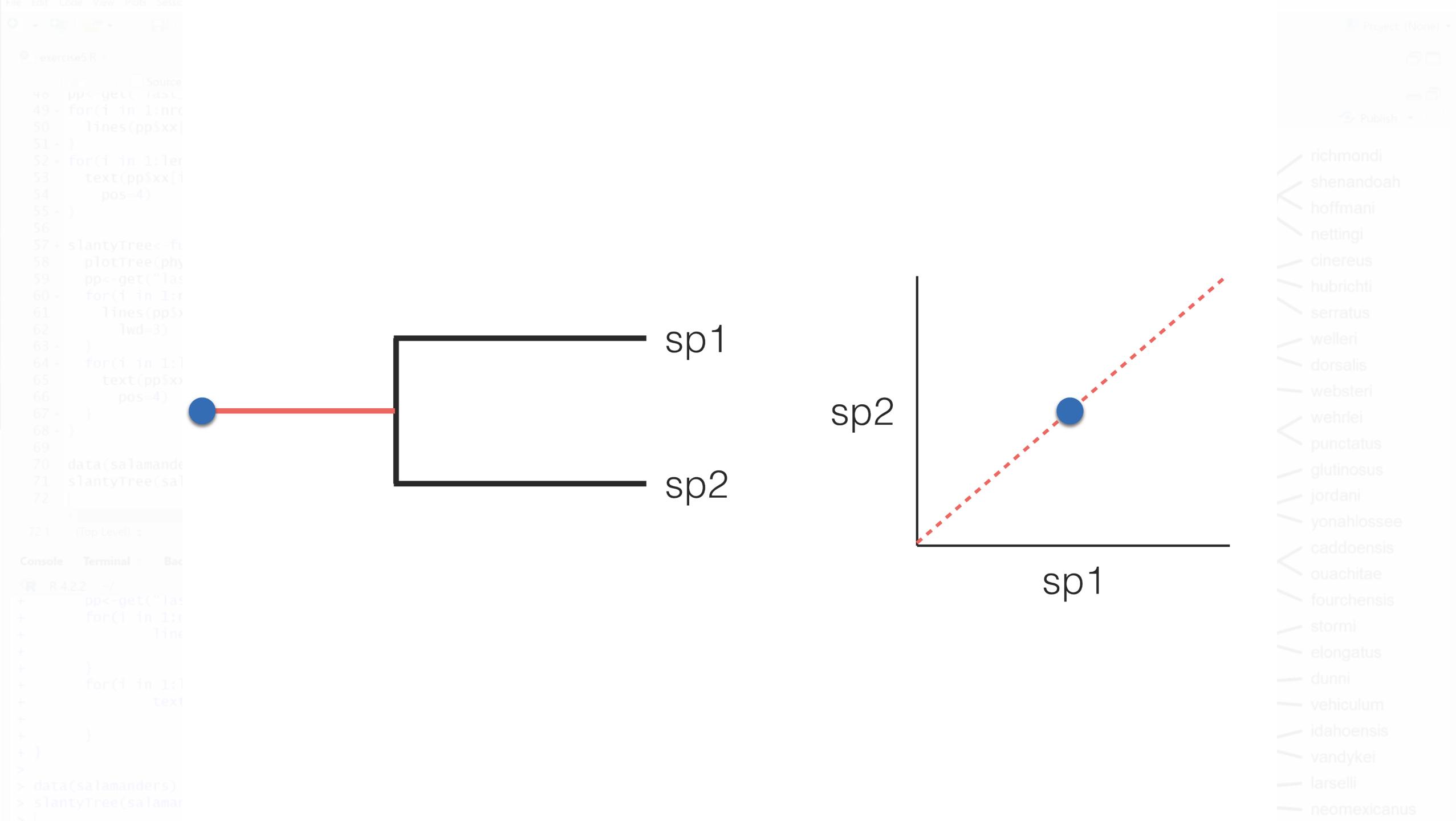


A sidebar showing a hierarchical file tree. The root folder 'salamanders' contains several subfolders and files, each represented by a yellow triangle icon:



- richmondi
- shenandoah
- hoffmani
- nettingi
- cinereus
- hubrichti
- serratus
- welleri
- dorsalis
- websteri
- wehrlei
- punctatus
- glutinosus
- jordani
- yonahlossee
- caddoensis
- ouachitae
- fourchensis
- stormi
- elongatus
- dunni
- vehiculum
- idahoensis
- vandykei
- larselli
- neomexicanus

```



```
File Edit Code View Plots Session Project (None) Source exercise5.R  
46 pp<-get("las")  
47 for(i in 1:nrc)  
48 lines(pp$xx)  
49 }  
50 for(i in 1:ler)  
51 text(pp$xx[i]  
52 pos=4)  
53 }  
54 lwd=3)  
55 }  
56  
57 slantyTree<-fi  
58 plotTree(phy  
59 pp<-get("las")  
60 for(i in 1:r  
61 lines(pp$  
62 lwd=3)  
63 }  
64 for(i in 1:l  
65 text(pp$xx)  
66 pos=4)  
67 }  
68 }  
69  
70 data(salamande  
71 slantyTree(sal  
72 |  
73 (Top Level) z  
Console Terminal Back  
R R 4.2.2 →  
+ pp<-get("las")  
+ for(i in 1:r  
+ lines(pp$xx)  
+ }  
+ for(i in 1:l  
+ text(pp$xx)  
+ pos=4)  
+ }  
> data(salamanders)  
> slantyTree(salamar  
>
```

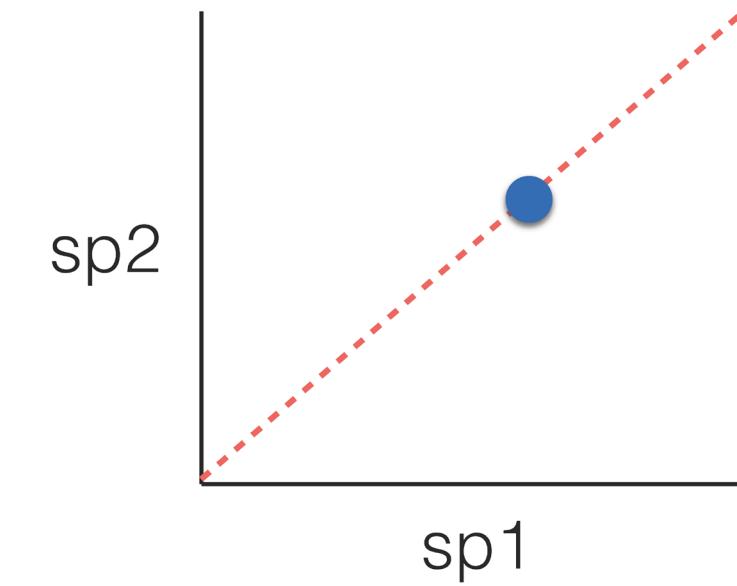
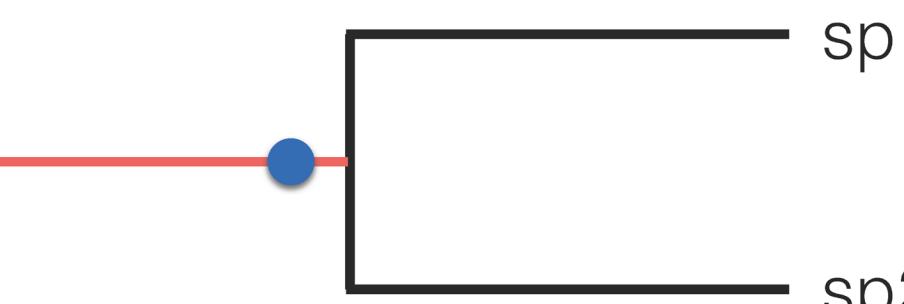
A phylogenetic tree diagram. The root node is marked with a blue dot. Two main clades are shown: 'sp1' and 'sp2'. 'sp1' is represented by a black rectangular box. 'sp2' is represented by a horizontal line segment. The labels 'sp1' and 'sp2' are placed to the right of their respective branches.

A scatter plot with 'sp2' on the vertical axis and 'sp1' on the horizontal axis. A single blue dot is plotted in the upper right quadrant. A dashed red line represents a linear regression fit through the data point.

- richmondi
- shenandoah
- hoffmani
- nettingi
- cinereus
- hubrichti
- serratus
- welleri
- dorsalis
- websteri
- wehrlei
- punctatus
- glutinosus
- jordani
- yonahlossee
- caddoensis
- ouachitae
- fourchensis
- stormi
- elongatus
- dunni
- vehiculum
- idahoensis
- vandykei
- larselli
- neomexicanus

```
Source  
46 pp<-get("lasC"  
47 for(i in 1:nrc  
48 lines(pp$xx)  
49 )  
50 for(i in 1:ler  
51 text(pp$xx[i  
52 pos=4)  
53 )  
54 )  
55 )  
56  
57 slantyTree<-f  
58 plotTree(phy  
59 pp<-get("las  
60 for(i in 1:r  
61 lines(pp$  
62 lwd=3)  
63 )  
64 for(i in 1:l  
65 text(pp$xx)  
66 pos=4)  
67 )  
68 )  
69  
70 data(salamande  
71 slantyTree(sal  
72 )  
72.1 (Top Level) z
```

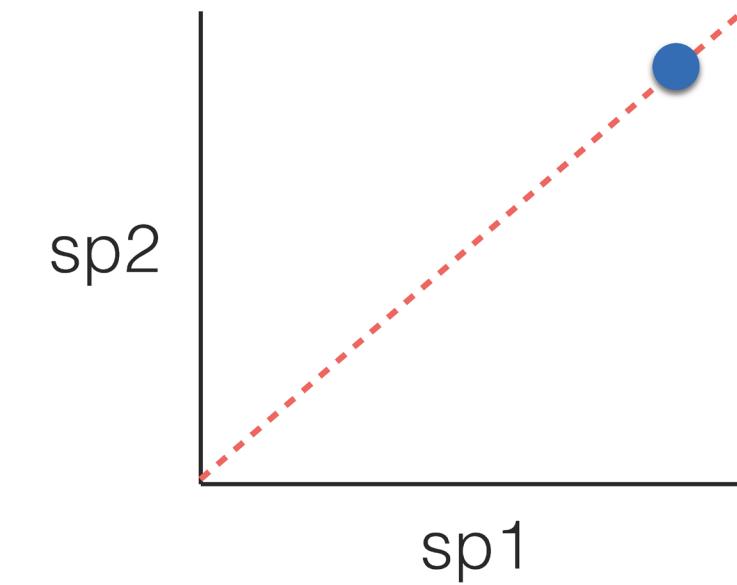
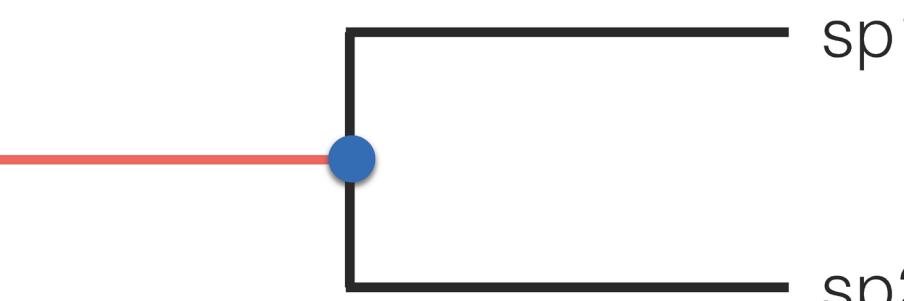
```
Console Terminal Back  
R R 4.2.2 ~>  
+ pp<-get("las  
+ for(i in 1:r  
+ lines  
+ )  
+ for(i in 1:l  
+ text  
+ )  
+ )  
> data(salamanders)  
> slantyTree(salamard  
>
```



richmondi
shenandoah
hoffmani
nettingi
cinereus
hubrichti
serratus
welleri
dorsalis
websteri
wehrlei
punctatus
glutinosus
jordani
yonahlossee
caddoensis
ouachitae
fourchensis
stormi
elongatus
dunni
vehiculum
idahoensis
vandykei
larselli
neomexicanus

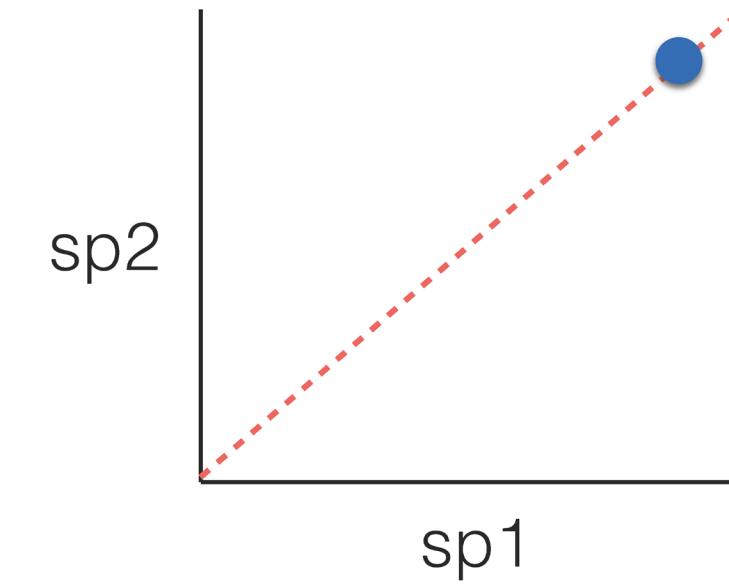
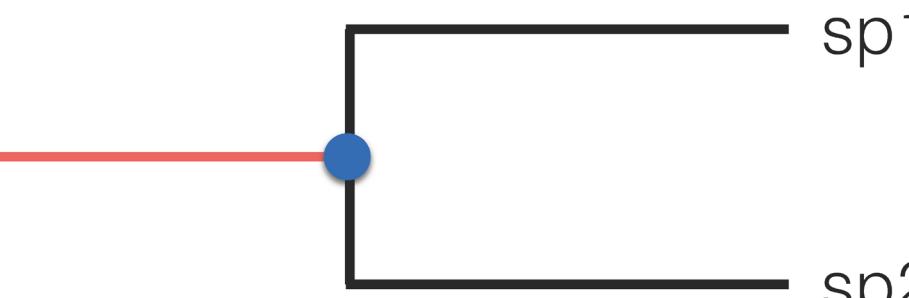
```
Source  
46 pp<-get("lasC"  
47 for(i in 1:nrc  
48 lines(pp$xx)  
49 )  
50 for(i in 1:ler  
51 text(pp$xx[i  
52 pos=4)  
53 )  
54 )  
55 )  
56  
57 slantyTree<-f  
58 plotTree(phy  
59 pp<-get("las  
60 for(i in 1:r  
61 lines(pp$  
62 lwd=3)  
63 )  
64 for(i in 1:l  
65 text(pp$xx)  
66 pos=4)  
67 )  
68 )  
69  
70 data(salamande  
71 slantyTree(sal  
72 )  
72:1 (Top Level) z
```

```
Console Terminal Back  
R R 4.2.2 ~>  
+ pp<-get("las  
+ for(i in 1:r  
+ lines  
+ )  
+ for(i in 1:l  
+ text  
+ )  
+ )  
> data(salamanders)  
> slantyTree(salamard  
>
```



richmondi
shenandoah
hoffmani
nettingi
cinereus
hubrichti
serratus
welleri
dorsalis
websteri
wehrlei
punctatus
glutinosus
jordani
yonahlossee
caddoensis
ouachitae
fourchensis
stormi
elongatus
dunni
vehiculum
idahoensis
vandykei
larselli
neomexicanus

```
File Edit Code View Plots Session  
Project (None)  
exercise5.R  
Source  
46 pp<-get("lasC"  
47 for(i in 1:nrc  
48 lines(pp$xx)  
49 }  
50 for(i in 1:ler  
51 text(pp$xx[i  
52 pos=4)  
53 }  
54 )  
55 }  
56  
57 slantyTree<-f  
58 plotTree(phy  
59 pp<-get("las  
60 for(i in 1:r  
61 lines(pp$  
62 lwd=3)  
63 }  
64 for(i in 1:l  
65 text(pp$xx  
66 pos=4)  
67 }  
68 }  
69  
70 data(salamande  
71 slantyTree(sal  
72 )  
73  
74 (Top Level) :  
Console Terminal Back  
R R 4.2.2 →  
+ pp<-get("las  
+ for(i in 1:r  
+ lines(pp$  
+ }  
+ for(i in 1:l  
+ text(pp$xx  
+ pos=4)  
+ )  
>  
> data(salamanders)  
> slantyTree(salamard  
>
```



richmondi
shenandoah
hoffmani
nettingi
cinereus
hubrichti
serratus
welleri
dorsalis
websteri
wehrlei
punctatus
glutinosus
jordani
yonahlossee
caddoensis
ouachitae
fourchensis
stormi
elongatus
dunni
vehiculum
idahoensis
vandykei
larselli
neomexicanus

```
File Edit Code View Plots Session Project (None) 

```
Source
46 pp<-get("lasC"
47 for(i in 1:nrc
48 lines(pp$xx)
49 }
50 for(i in 1:ler
51 text(pp$xx[i
52 pos=4)
53 }
54)
55 }
56
57 slantyTree<-f
58 plotTree(phy
59 pp<-get("las
60 for(i in 1:r
61 lines(pp$
62 lwd=3)
63)
64 for(i in 1:l
65 text(pp$xx)
66 pos=4)
67)
68 }
69
70 data(salamande
71 slantyTree(sal
72)
73 (Top Level) :
74
Console Terminal Back
R R 4.2.2 →
+ pp<-get("las
+ for(i in 1:r
+ lines(pp$
+)
+ for(i in 1:l
+ text(pp$xx)
+ pos=4)
+)
+)
> data(salamanders)
> slantyTree(salamar
>
```



A phylogenetic tree diagram showing two main lineages. A red horizontal bar at the base represents the root. From this root, a black branch splits into two lineages. The left lineage leads to a node labeled "sp1". From this node, a black branch leads to a node labeled "sp2".



A phylogenetic tree diagram showing a single node labeled "sp1". A red dashed line extends from this node upwards and to the right, ending at a blue circular marker.

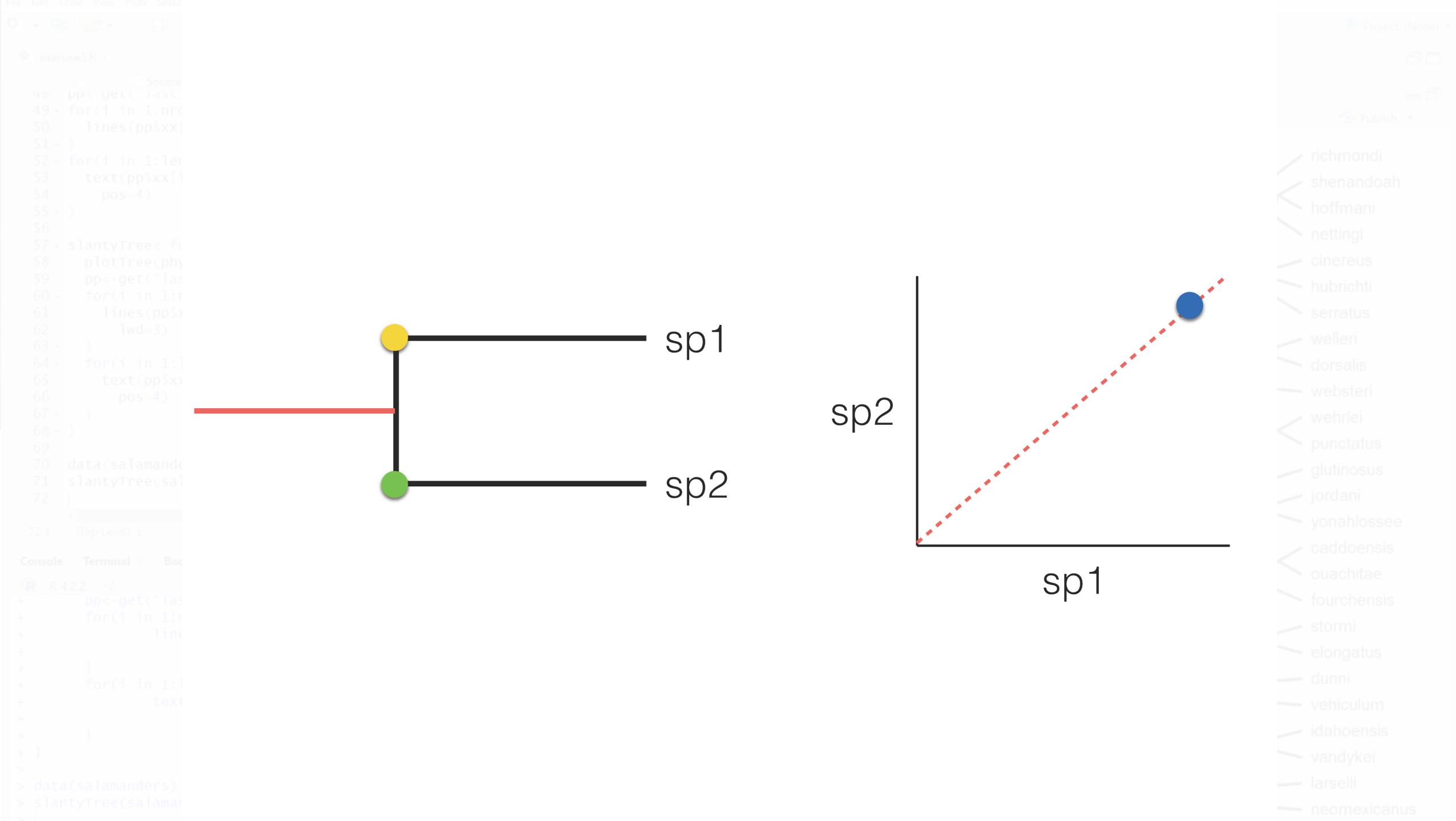


A phylogenetic tree diagram showing a single node labeled "sp2". A red dashed line extends from this node upwards and to the right, ending at a blue circular marker.



- richmondi
- shenandoah
- hoffmani
- nettingi
- cinereus
- hubrichti
- serratus
- welleri
- dorsalis
- websteri
- wehrlei
- punctatus
- glutinosus
- jordani
- yonahlossee
- caddoensis
- ouachitae
- fourchensis
- stormi
- elongatus
- dunni
- vehiculum
- idahoensis
- vandykei
- larselli
- neomexicanus

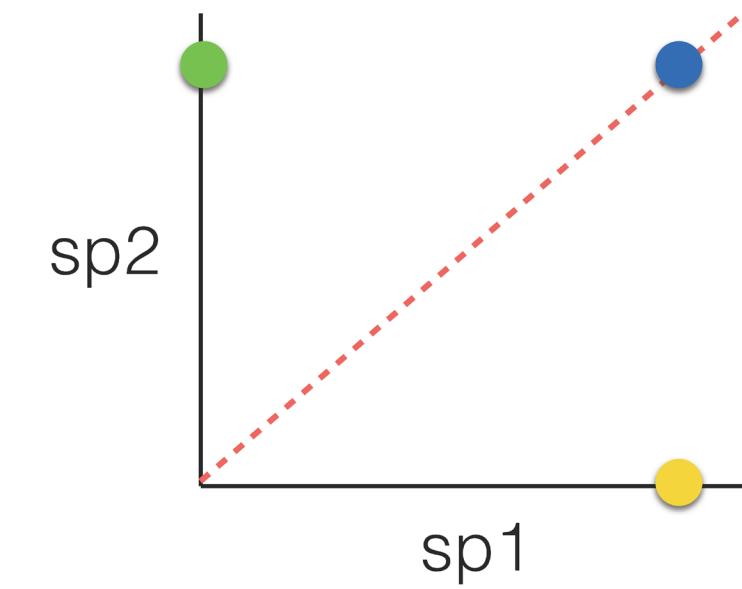
```



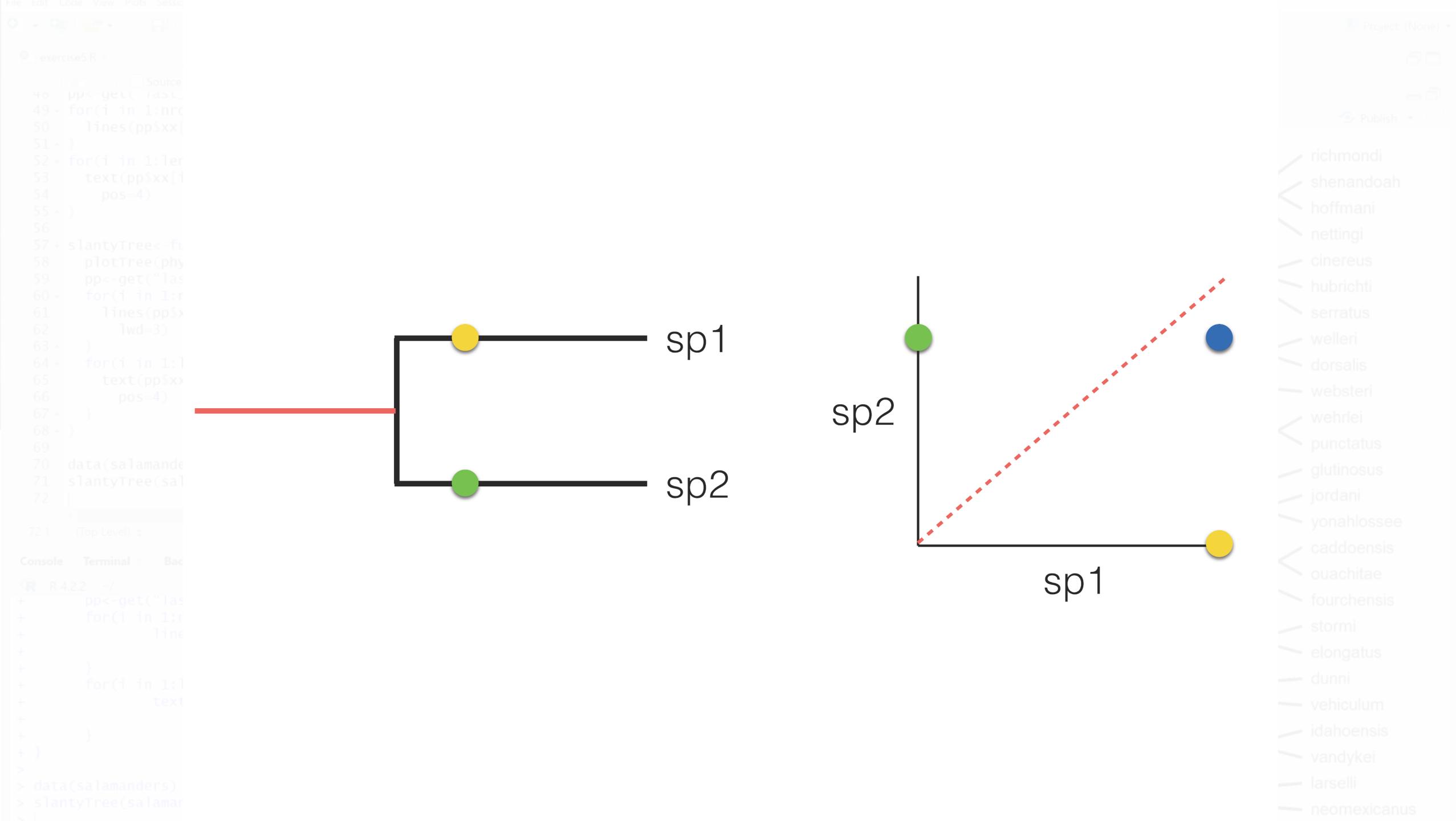
```
File Edit Code View Plots Session Project (None) 

```
exercise5.R
Source
46 pp<-get("lasC.
47 for(i in 1:nrc
48 lines(pp$xx)
49 }
50 for(i in 1:ler
51 text(pp$xx[i
52 pos=4)
53 }
54 }
55 }
56
57 slantyTree<-f
58 plotTree(phy
59 pp<-get("las
60 for(i in 1:r
61 lines(pp$
62 lwd=3)
63 }
64 for(i in 1:l
65 text(pp$xx)
66 pos=4)
67 }
68 }
69
70 data(salamande
71 slantyTree(sal
72)
73 (Top Level: z
Console Terminal Back
R R 4.2.2 →
+ pp<-get("las
+ for(i in 1:r
+ lines(pp$
+ }
+ for(i in 1:l
+ text(pp$xx)
+ pos=4)
+ }
+ }
> data(salamanders)
> slantyTree(salamard
>
```


```



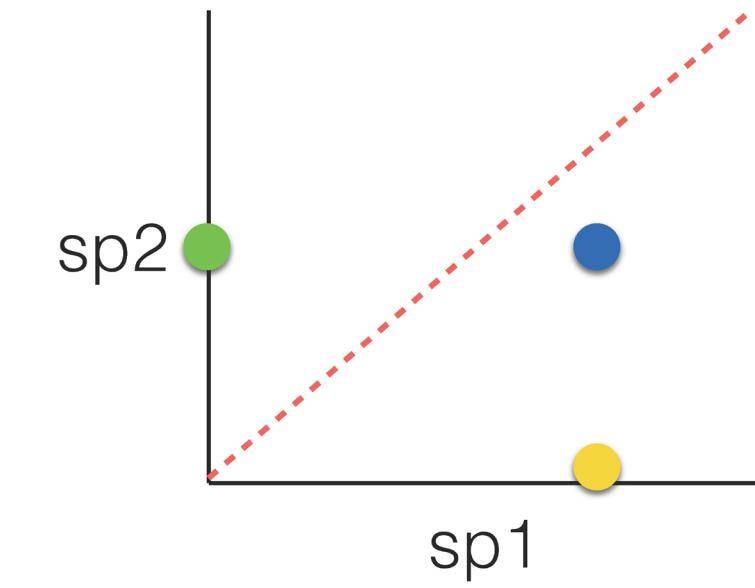
richmondi
shenandoah
hoffmani
nettingi
cinereus
hubrichti
serratus
welleri
dorsalis
websteri
wehrlei
punctatus
glutinosus
jordani
yonahlossee
caddoensis
ouachitae
fourchensis
stormi
elongatus
dunni
vehiculum
idahoensis
vandykei
larselli
neomexicanus



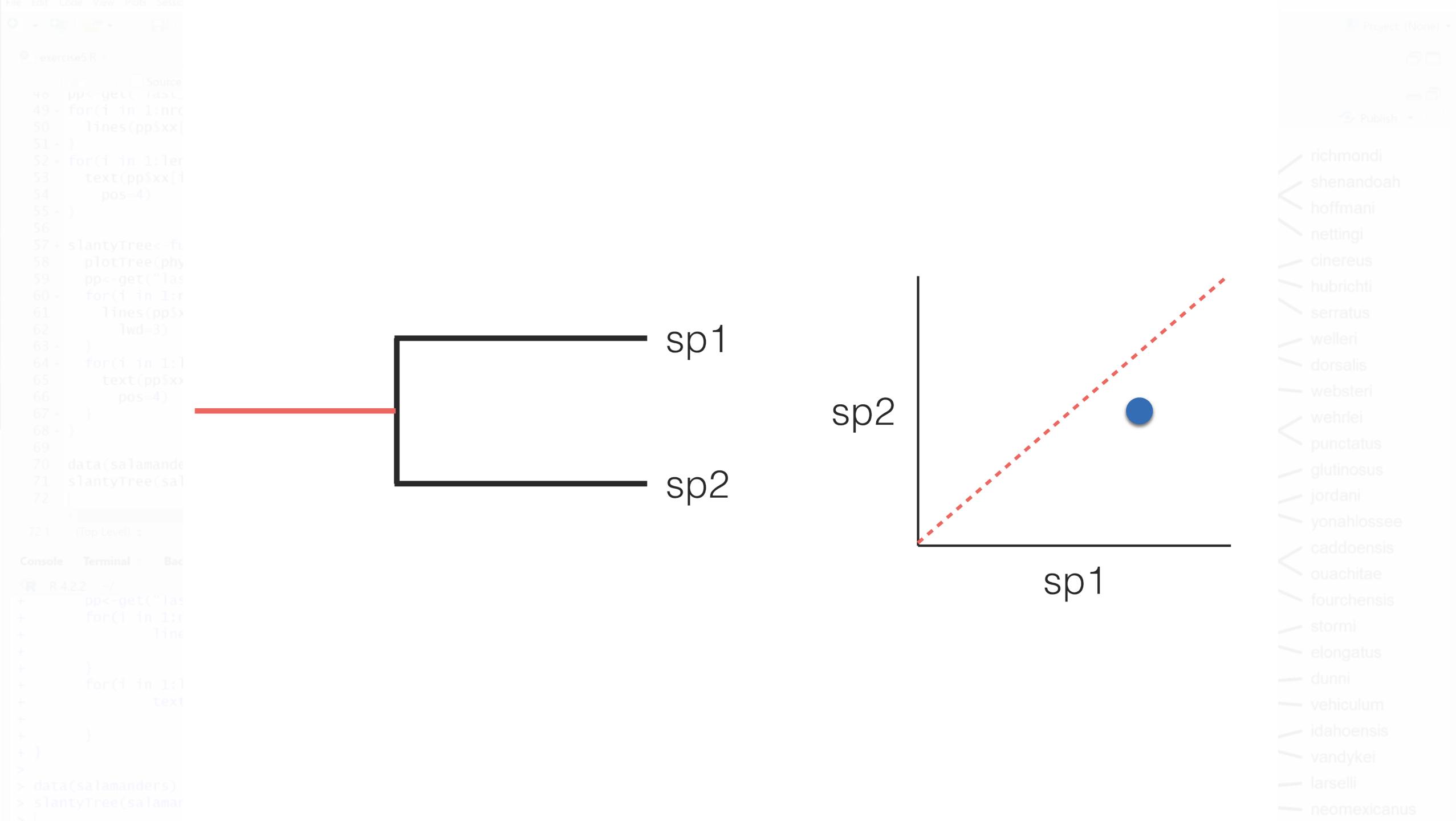
```
File Edit Code View Plots Session Project (None) 

```
exercise5.R
Source
46 pp<-get("las.
47 for(i in 1:nrc
48 lines(pp$xx)
49 }
50 for(i in 1:ler
51 text(pp$xx[i
52 pos=4)
53 }
54 }
55 }
56
57 slantyTree<-f
58 plotTree(phy
59 pp<-get("las
60 for(i in 1:r
61 lines(pp$
62 lwd=3)
63 }
64 for(i in 1:l
65 text(pp$xx)
66 pos=4)
67 }
68 }
69
70 data(salamande
71 slantyTree(sal
72)
73 (Top Level) :
Console Terminal Back
R R 4.2.2 →
+ pp<-get("las
+ for(i in 1:r
+ lines(pp$
+ }
+ for(i in 1:l
+ text(pp$xx)
+ }
+ }
> data(salamanders)
> slantyTree(salamard
>
```


```

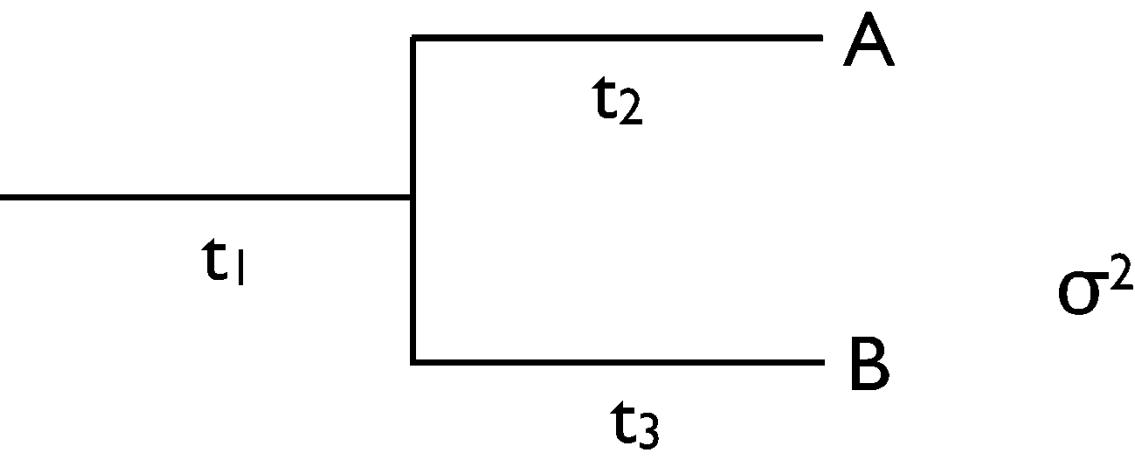


- richmondi
- shenandoah
- hoffmani
- nettingi
- cinereus
- hubrichti
- serratus
- welleri
- dorsalis
- websteri
- wehrlei
- punctatus
- glutinosus
- jordani
- yonahlossee
- caddoensis
- ouachitae
- fourchensis
- stormi
- elongatus
- dunni
- vehiculum
- idahoensis
- vandykei
- larselli
- neomexicanus





How do they covary?

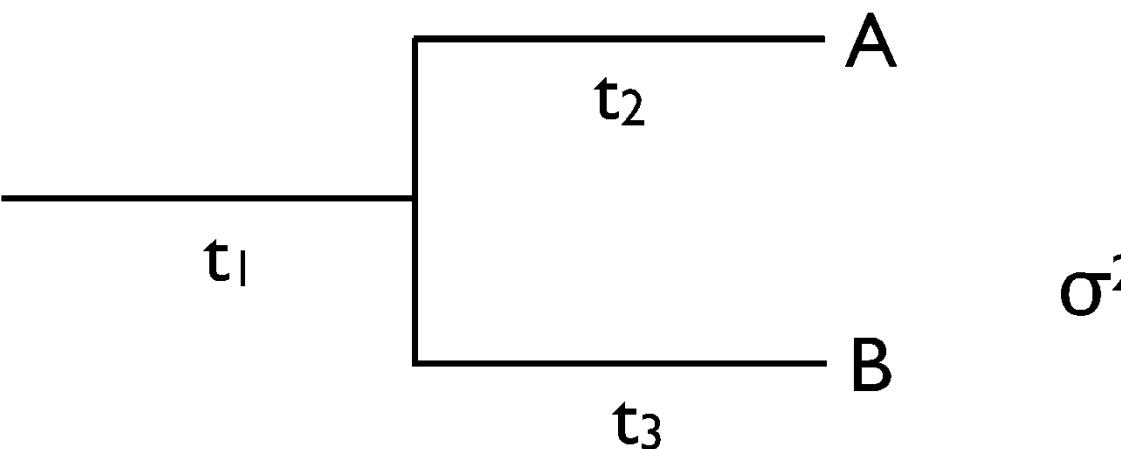


```
var(A)
```

```
cov(A,B)
```

```
var(B)
```

How do they covary?



$$\text{var}(A) = \sigma^2(t_1 + t_2)$$

$$\text{cov}(A, B)$$

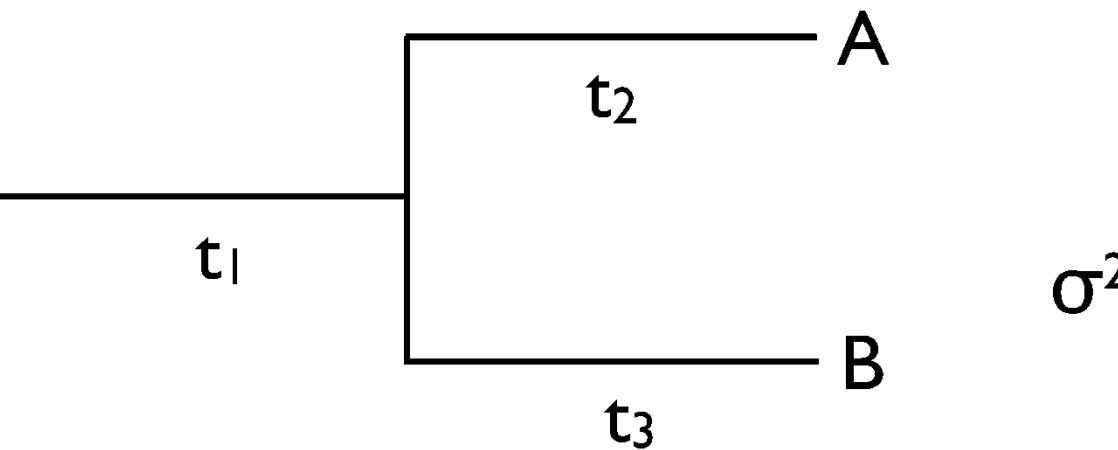
$$\text{var}(B)$$

```

richmondi
shenandoah
hoffmani
nettingi
cinereus
hubrichti
serratus
welleri
dorsalis
websteri
wehrlei
punctatus
glutinosus
jordani
yonahlossee
caddoensis
ouachitae
fourchensis
stormi
elongatus
dunni
vehiculum
idahoensis
vandykei
larselli
neomexicanus

```

How do they covary?

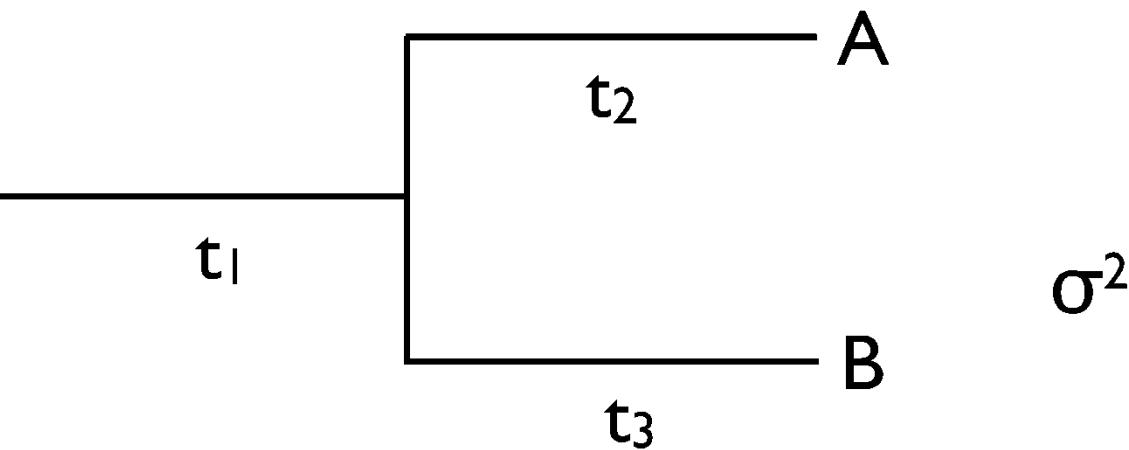


$$\text{var}(A) = \sigma^2(t_1 + t_2)$$

$$\text{cov}(A, B)$$

$$\text{var}(B) = \sigma^2(t_1 + t_3)$$

How do they covary?

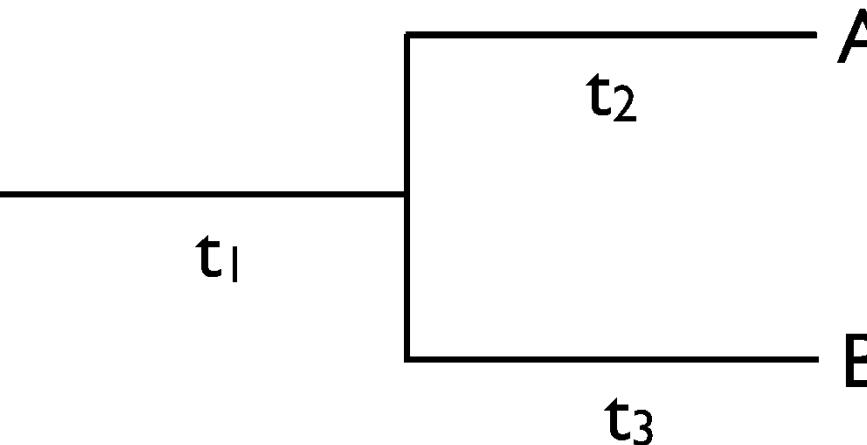


$$\text{var}(A) = \sigma^2(t_1 + t_2)$$

$$\text{cov}(A, B) = \sigma^2(t_1)$$

$$\text{var}(B) = \sigma^2(t_1 + t_3)$$

How do they covary?



**variance-covariance
matrix**

$$\sigma^2 \begin{bmatrix} t_1 + t_2 & t_1 \\ t_1 & t_1 + t_3 \end{bmatrix}$$

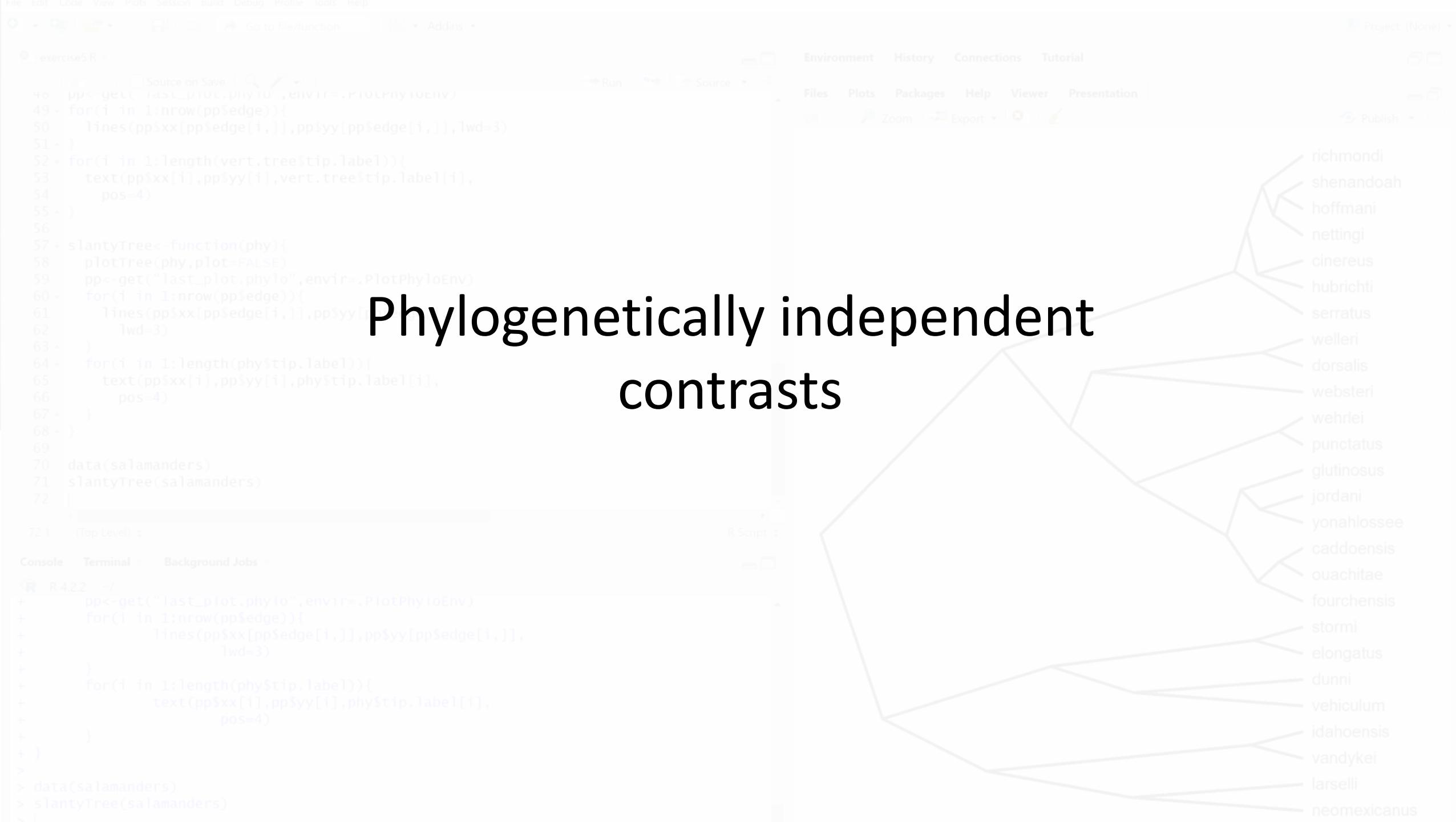
$$\text{var}(A) = \sigma^2(t_1 + t_2)$$

$$\text{cov}(A, B) = \sigma^2(t_1)$$

$$\text{var}(B) = \sigma^2(t_1 + t_3)$$

Brownian motion

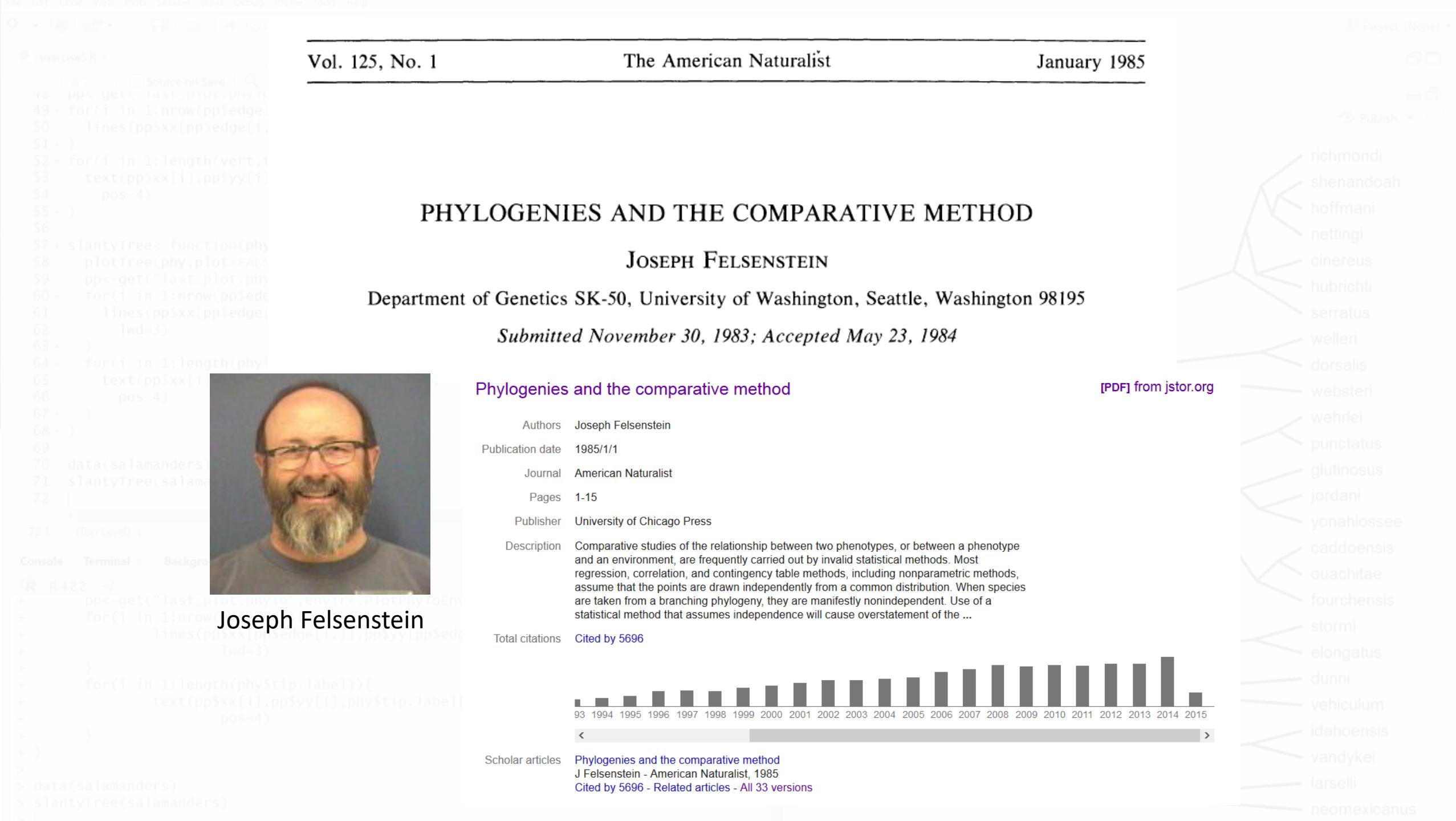
- Brownian motion has been & continues to be an important model for studying the evolution of quantitative traits.
- It provides the theoretical basis for other methods that we will learn (such as independent contrasts, phylogenetic regression, and ancestral state reconstruction).
- It also provides the foundation for more complex models of trait evolution on trees.



Phylogenetically independent contrasts

```
File Edit Code View Plots Session Build Debug Profile Tools Help
Go to file/function Addins Project (None)
exercise5.R
Source on Save Run Source Environment History Connections Tutorial
Files Plots Packages Help Viewer Presentation Publish
Zoom Export
richmondi
shenandoah
hoffmani
nettingi
cinereus
hubrichti
serratus
welleri
dorsalis
websteri
wehrlei
punctatus
glutinosus
jordani
yonahlossee
caddoensis
ouachitae
fourchensis
stormi
elongatus
dunni
vehiculum
idahoensis
vandykei
larselli
neomexicanus

46 pp<-get("last_plot.phylo",envir=.PlotPhyloEnv)
47 for(i in 1:nrow(pp$edge)){
48   lines(pp$xx[pp$edge[i,]],pp$yy[pp$edge[i,]],lwd=3)
49 }
50 for(i in 1:length(vert.tree$tip.label)){
51   text(pp$xx[i],pp$yy[i],vert.tree$tip.label[i],
52     pos=4)
53 }
54
55 }
56
57 slantyTree<-function(phy){
58   plotTree(phy,plot=FALSE)
59   pp<-get("last_plot.phylo",envir=.PlotPhyloEnv)
60   for(i in 1:nrow(pp$edge)){
61     lines(pp$xx[pp$edge[i,]],pp$yy[pp$edge[i,]],
62       lwd=3)
63   }
64   for(i in 1:length(phy$tip.label)){
65     text(pp$xx[i],pp$yy[i],phy$tip.label[i],
66       pos=4)
67   }
68 }
69
70 data(salamanders)
71 slantyTree(salamanders)
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R 4.2.2 ->
+ pp<-get("last_plot.phylo",envir=.PlotPhyloEnv)
+ for(i in 1:nrow(pp$edge)){
+   lines(pp$xx[pp$edge[i,]],pp$yy[pp$edge[i,]],
+     lwd=3)
+ }
+ for(i in 1:length(phy$tip.label)){
+   text(pp$xx[i],pp$yy[i],phy$tip.label[i],
+     pos=4)
+ }
+ data(salamanders)
+ slantyTree(salamanders)
+ 
```



File Edit Code View Plots Session Build Debug Profile Tools Help

Go to file/function Addins

exercise5.R

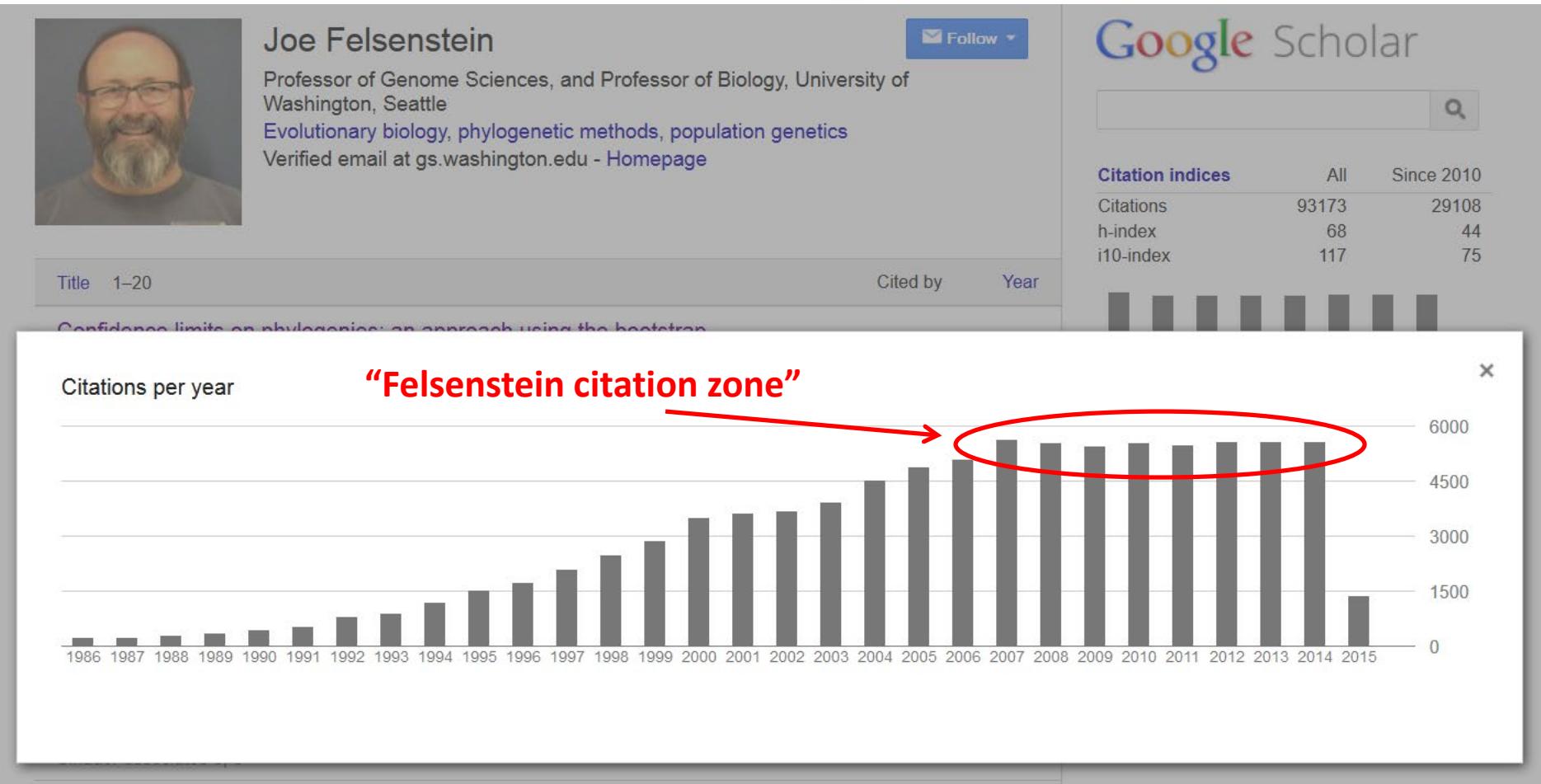
```
Source on Save Run Source Environment History Connections Tutorial
```

```
46 pp<-get("last_prun.phy", envir=.procEnv)
47 for(i in 1:nrow(pp$edge)){
48   lines(pp$xx(pp$edge[i,1],pp$yy(pp$edge[i,1],lwd=3))
49 }
50 for(i in 1:length(pp$xx)){
51   text(pp$xx[i], pos=4)
52 }
53 for(i in 1:length(pp$yy)){
54   text(pp$yy[i], pos=4)
55 }
56 slantyTree<-function(phy,
57   plotTree(phy,
58   pp<-get("last",
59   for(i in 1:nrow(pp$edge)){
60     lines(pp$xx(pp$edge[i,1],pp$yy(pp$edge[i,1],lwd=3))
61   }
62   for(i in 1:length(pp$xx)){
63     text(pp$xx[i], pos=4)
64   }
65   for(i in 1:length(pp$yy)){
66     text(pp$yy[i], pos=4)
67   }
68 }
69 data(salamander)
70 slantyTree(salamander)
71 for(i in 1:nrow(slantyTree(salamander)$edges)){
72   lines(slantyTree(salamander)$edges[i,1],slantyTree(salamander)$edges[i,2],lwd=3)
73 }
74 (Top Level) <--
```

Console Terminal Background R 4.2.2 ~/

```
pp<-get("last"
for(i in 1:nrow(pp$edge)){
  lines(pp$xx(pp$edge[i,1],pp$yy(pp$edge[i,1],lwd=3))
  text(pp$xx(pp$edge[i,1],pp$yy(pp$edge[i,1],lwd=3),label[i],pos=4)
}
for(i in 1:length(pp$xx)){
  text(pp$xx[i], pos=4)
}
for(i in 1:length(pp$yy)){
  text(pp$yy[i], pos=4)
}
}
```

> data(salamanders)
> slantyTree(salamanders)



Joe Felsenstein

Professor of Genome Sciences, and Professor of Biology, University of Washington, Seattle

Evolutionary biology, phylogenetic methods, population genetics

Verified email at gs.washington.edu - Homepage

Citation indices

	All	Since 2010
Citations	93173	29108
h-index	68	44
i10-index	117	75

Citations per year

"Felsenstein citation zone"

A red arrow points from the text "Felsenstein citation zone" to a red oval highlighting a cluster of bars in the bar chart for the years 2007-2014, which shows citation counts between 5000 and 6000.

richmondi
shenandoah
hoffmani
nettingi
cinereus
hubrichti
serratus
welleri
dorsalis
websteri
wehrlei
punctatus
glutinosus
jordani
yonahlossee
caddoensis
ouachitae
fourchensis
stormi
elongatus
dunni
vehiculum
idahoensis
vandykei
larselli
neomexicanus

```
File Edit Code View Plots Session Build Debug Profile Tools Help
Go to file/function Addins
exercise5.R Source on Save Environment History Connections Tutorial
46 pp<-get("last_plot.phylo",envir=.PlotPhyloEnv)
47 for(i in 1:nrow(pp$edge)){
48   lines(pp$xx[pp$edge[i,]],pp$yy[pp$edge[i,]],lwd=3)
49 }
50 for(i in 1:length(vert.tree$tip.label)){
51   text(pp$xx[i],pp$yy[i],vert.tree$tip.label[i],
52     pos=4)
53 }
54 }
55 }
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57 slantyTree<-function(phy){
58   plotTree(phy,plot=F)
59   pp<-get("last_plot.phylo",envir=.PlotPhyloEnv)
60   for(i in 1:nrow(pp$edge)){
61     lines(pp$xx[pp$edge[i,]],pp$yy[pp$edge[i,]],lwd=3)
62   }
63   for(i in 1:length(phy$tip.label)){
64     text(pp$xx[i],pp$yy[i],phy$tip.label[i],
65       pos=4)
66   }
67 }
68
69
70 data(salamanders)
71 slantyTree(salamanders)
72
73
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72:1 (Top Level) z
R Script R 4.2.2 ~
+ pp<-get("last_plot.phylo",envir=.PlotPhyloEnv)
+ for(i in 1:nrow(pp$edge)){
+   lines(pp$xx[pp$edge[i,]],pp$yy[pp$edge[i,]],
+         lwd=3)
+ }
+ for(i in 1:length(phy$tip.label)){
+   text(pp$xx[i],pp$yy[i],phy$tip.label[i],
+        pos=4)
+ }
+ }
> data(salamanders)
> slantyTree(salamanders)
>
richmondi
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caddoensis
ouachitae
fourchensis
stormi
elongatus
dunni
vehiculum
idahoensis
vandykei
larselli
neomexicanus
```

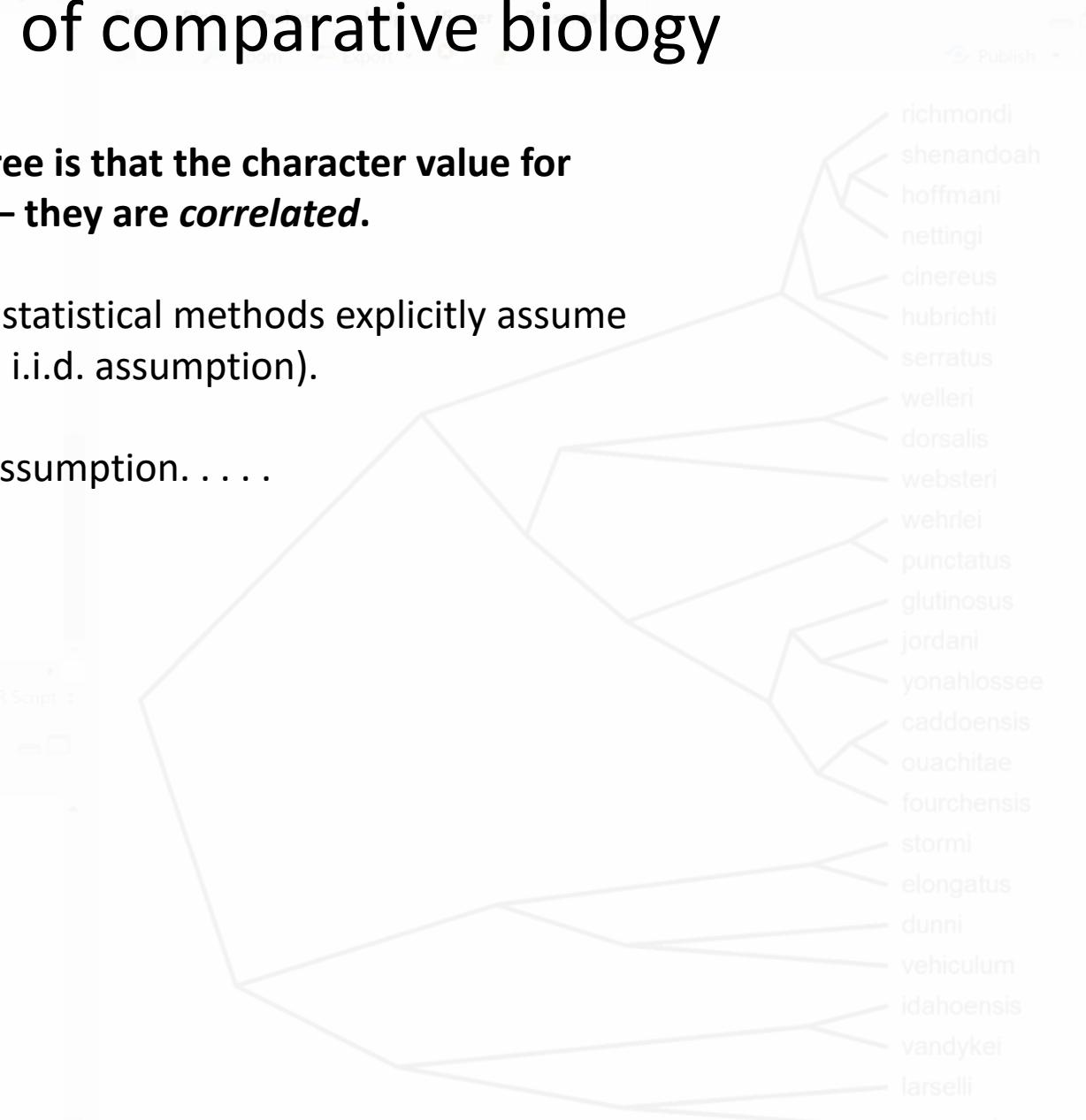
The statistical paradigm of comparative biology

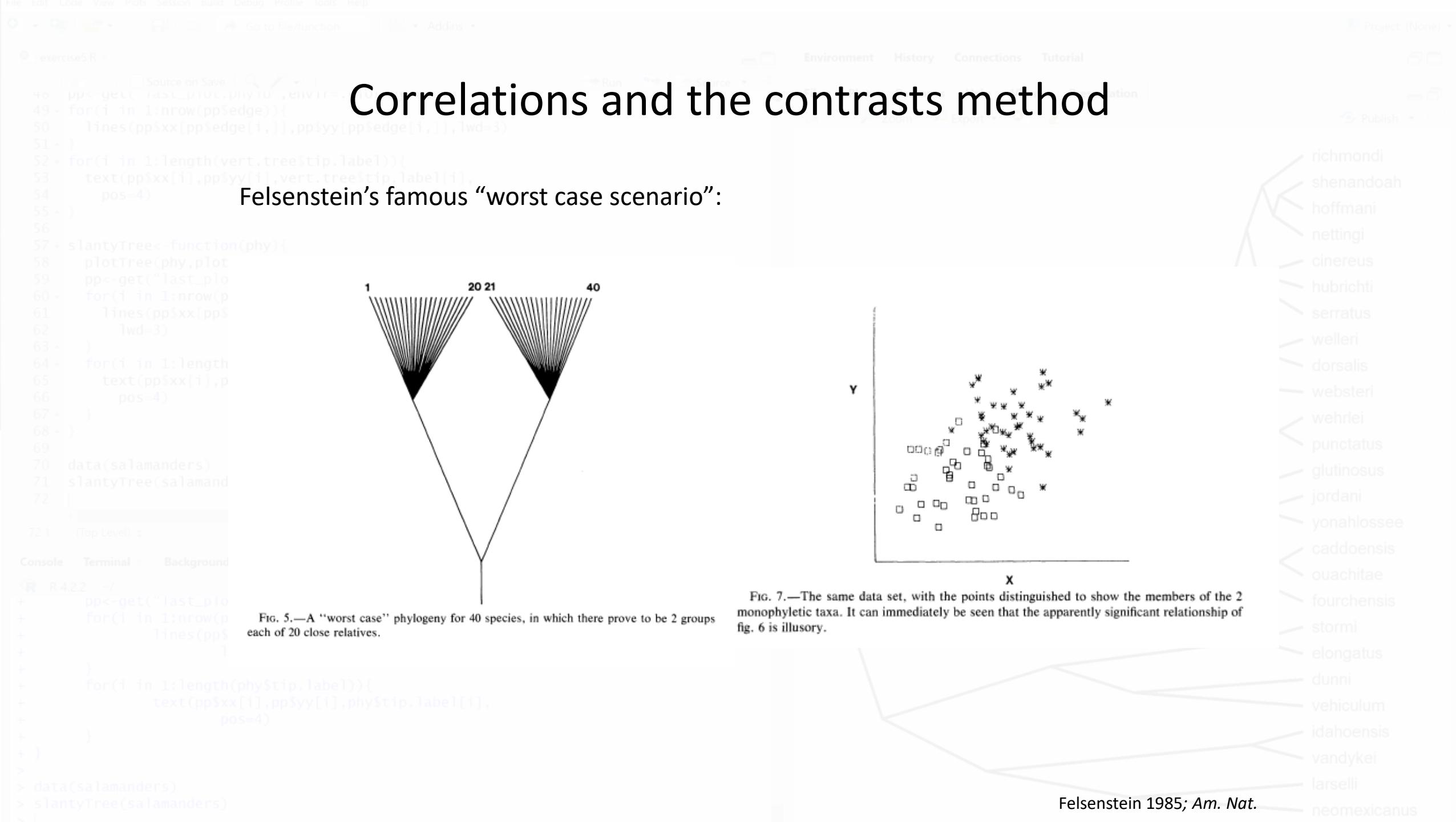
A consequence of evolution on the tree is that the character value for related species are not independent – they are *correlated*.

Most parametric and non-parametric statistical methods explicitly assume independence of the data values (i.e., i.i.d. assumption).

Species data will tend to violate this assumption. . . .

. . . so what?





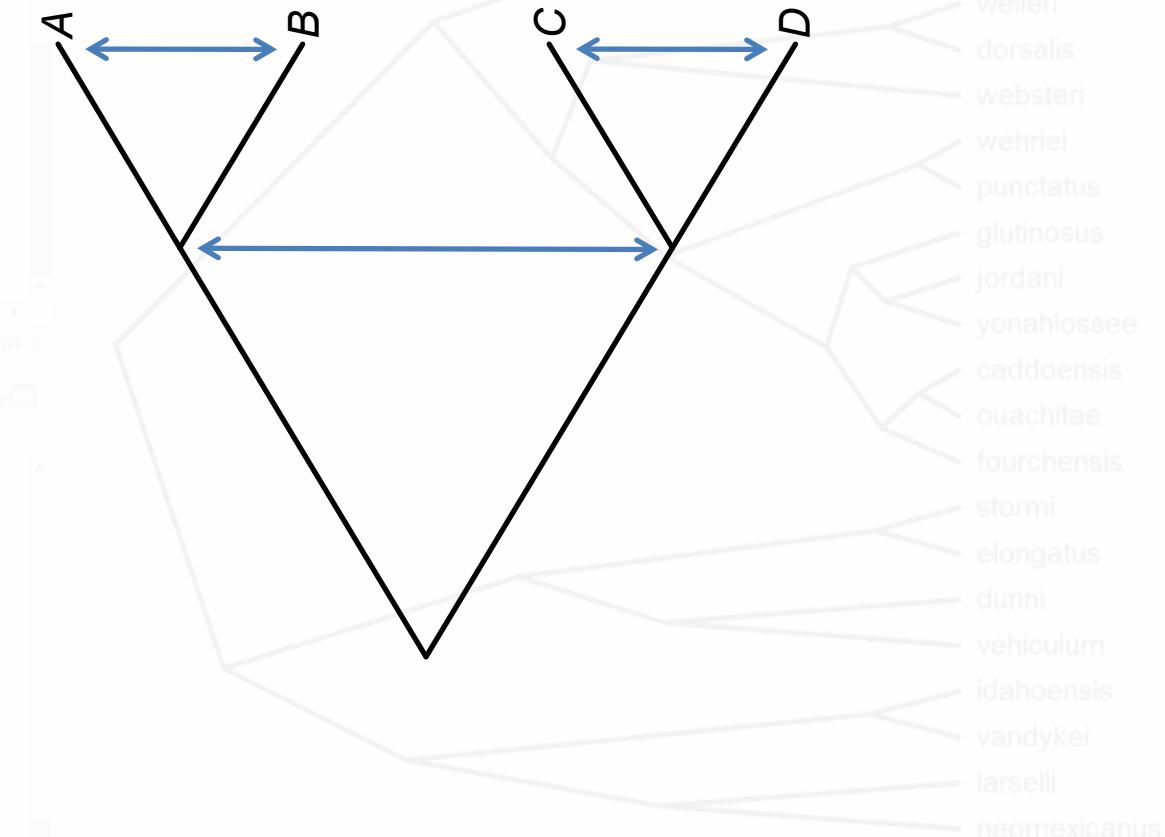
Correlations and the contrasts method

Felsenstein's key insight was that although the data for species are not independent *the differences between species** are.
(*and nodes)

That is to say: although the species values for A, B, C, and D are non-independent...

...the differences are independent.

Felsenstein's method of *independent contrasts* computes the *standardized** differences between sister species and nodes; which then have the property of independence under a BM assumption, and can be used in standard regression and correlation analyses.



Phylogenetic Independent Contrasts

- PICs are a way to analyze data that comes from phylogenetic trees
- Test for *evolutionary correlations* among characters
- We can think of PICs as a statistical transformation that creates independent data points

Standard correlation

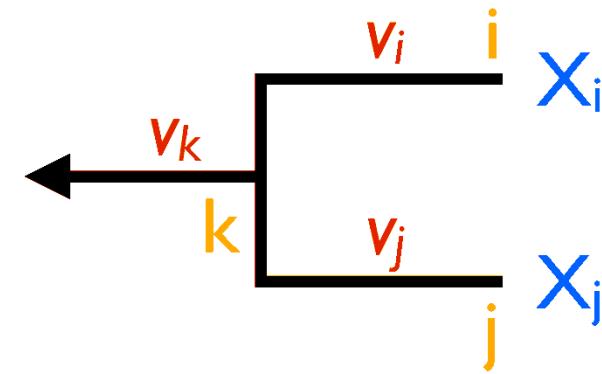
- Can we predict Y from X?
- We might be able to do this for two reasons: species are related, or X and Y tend to evolve together

Evolutionary correlation

- X and Y evolve in a correlated fashion
- When X changes, Y tends to change in a predictable way

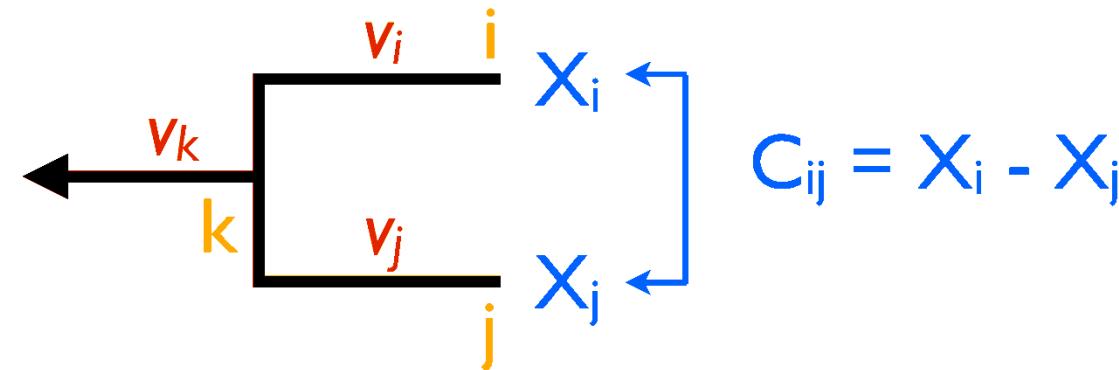
Calculating Contrasts*

1. Find two tips on the phylogeny that are adjacent (say nodes i and j) and have a common ancestor, say node k
2. Compute the contrast $X_i - X_j$. This has expectation zero and variance proportional to $v_i + v_j$



Calculating Contrasts*

1. Find two tips on the phylogeny that are adjacent (say nodes i and j) and have a common ancestor, say node k
2. Compute the contrast $X_i - X_j$. This has expectation zero and variance proportional to $v_i + v_j$

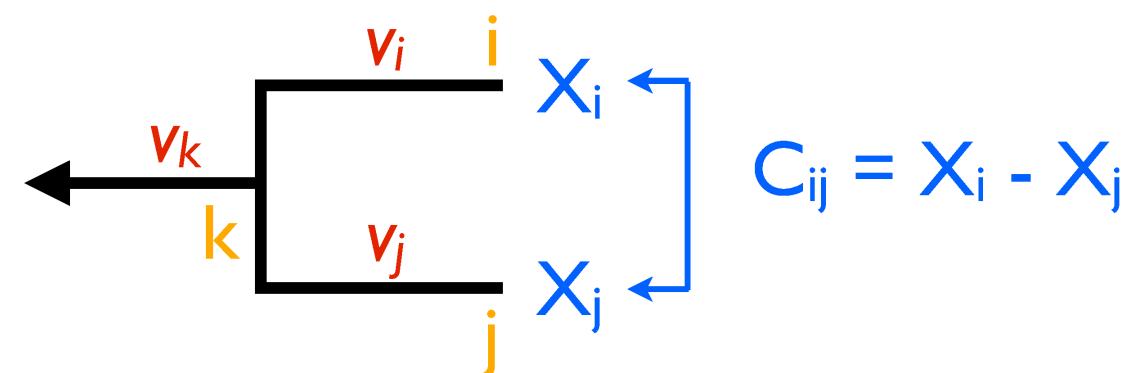


Calculating Contrasts*

3. Remove the two tips from the tree, leaving behind only the ancestor k, which now becomes a tip. Assign it the character value:

$$X_k = \frac{(1/v_i) X_i + (1/v_j) X_j}{1/v_i + 1/v_j}$$

This is a weighted average of X_i and X_j , but not an ancestral state reconstruction.

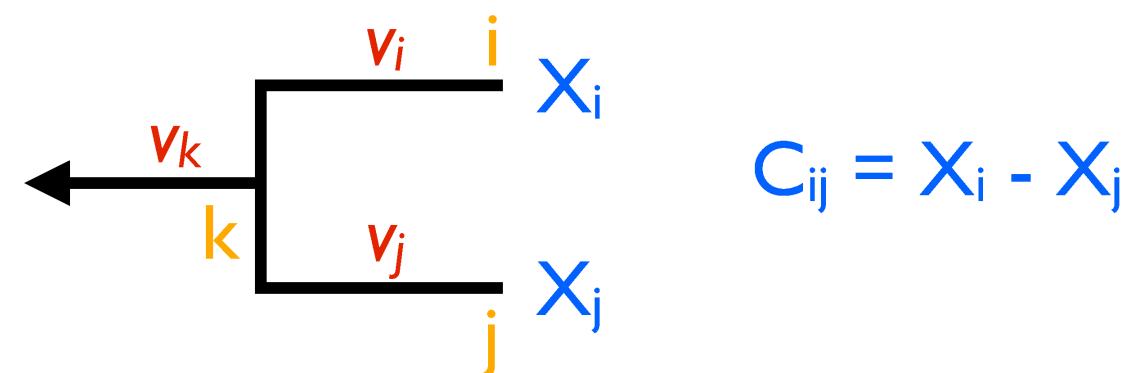


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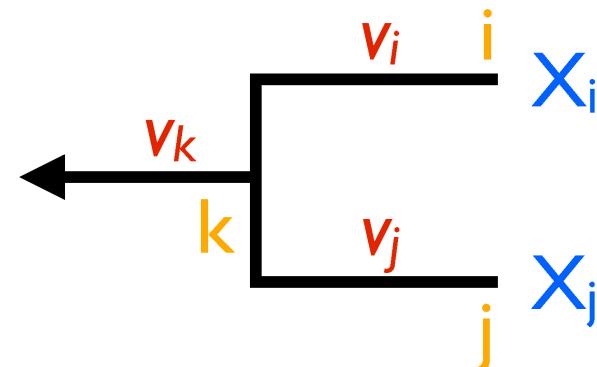
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$$C_{ij} = X_i - X_j$$



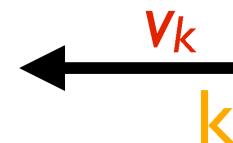
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```
File Edit Code View Plots Session
Source
46 pp<-get("las")
47 for(i in 1:nrc)
48   lines(pp$xx)
49 }
50 for(i in 1:ler)
51   text(pp$xx[i]
52     pos=4)
53 }
54
55
56
57 slantyTree<-f
58 plotTree(phy
59 pp<-get("las
60 for(i in 1:r
61   lines(pp$>
62   lwd=3)
63 )
64 for(i in 1:l
65   text(pp$xx
66     pos=4)
67 )
68 )
69
70 data(salamande
71 slantyTree(sal
72 )
73
74
75 (Top Level: z
76
Console Terminal Backup
R R 4.2.2 ->
+ pp<-get("las
+ for(i in 1:r
+   line
+
+   }
+   for(i in 1:l
+     text
+
+   )
+
+   }
+
> data(salamanders)
> slantyTree(salamar
>
```



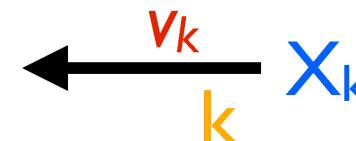
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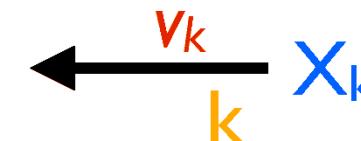
$$C_{ij} = X_i - X_j$$



Calculating Contrasts*

4. Lengthen the branch below node k by increasing its length from v_k to $v_k + v_i v_j / (v_i + v_j)$. This accounts for the error in assigning a value to X_k .

$$C_{ij} = X_i - X_j$$



Calculating Contrasts*

4. Lengthen the branch below node k by increasing its length from v_k to $v_k + v_i v_j / (v_i + v_j)$. This accounts for the error in assigning a value to X_k .

$$C_{ij} = X_i - X_j$$



Calculating Contrasts*

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Calculating Contrasts*

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$$C_{ij} = X_i - X_j$$



Calculating Contrasts*

5. Calculate the standardized contrast by dividing the raw contrast by its variance

$$C_{ij} = X_i - X_j$$



Calculating Contrasts*

5. Calculate the standardized contrast by dividing the raw contrast by its variance

$$C_{ij} = X_i - X_j$$

$$S_{ij} = \frac{X_i - X_j}{v_i + v_j}$$



```
exercise5.R
Source
46 pp<-get("las")
47 for(i in 1:nrc)
48   lines(pp$xx)
49 }
50 for(i in 1:ler)
51   text(pp$xx[i]
52     pos=4)
53 }
54 }
55 }
56
57 slantyTree<-fi
58 plotTree(phy)
59 pp<-get("las")
60 for(i in 1:r)
61   lines(pp$)
62   lwd=3)
63 }
64 for(i in 1:l)
65   text(pp$)
66     pos=4)
67 }
68 }
69
70 data(salamander)
71 slantyTree(sal)
72 |
73 [REDACTED]
72.1 (Top Level) z
Console Terminal Back
R R 4.2.2 ~
+ pp<-get("las")
+ for(i in 1:r)
+   line
+
+ }
+ for(i in 1:l)
+   text
+
+ }
> data(salamanders)
> slantyTree(salamard
>
```

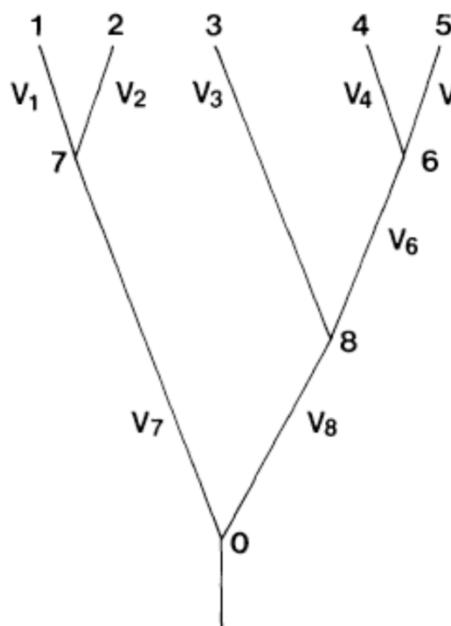


TABLE 1

THE FOUR CONTRASTS EXTRACTED FROM THE PHYLOGENY
SHOWN IN FIGURE 9, EACH WITH ITS VARIANCE, ALL
COMPUTED USING STEPS 1–4 IN THE TEXT

CONTRAST	VARIANCE
$X_1 - X_2$	$v_1 + v_2$
$X_4 - X_5$	$v_4 + v_5$
$X_3 - X_6$	$v_3 + v'_6$
$X_7 - X_8$	$v'_7 + v'_8$

where

$$X_6 = \frac{v_4 X_5 + v_5 X_4}{v_4 + v_5}$$

$$v'_6 = v_6 + v_4 v_5 / (v_4 + v_5)$$

$$X_7 = \frac{v_2 X_1 + v_1 X_2}{v_1 + v_2}$$

$$v'_7 = v_7 + v_1 v_2 / (v_1 + v_2)$$

$$X_8 = \frac{v'_6 X_3 + v_3 X_6}{v_3 + v_6}$$

$$v'_8 = v'_7 + v_3 v'_6 / (v_3 + v'_6)$$

(Felsenstein 1981)

- richmondi
- shenandoah
- hoffmani
- nettingi
- cinereus
- hubrichti
- serratus
- welleri
- dorsalis
- websteri
- wehrlei
- punctatus
- glutinosus
- jordani
- yonahlossee
- caddoensis
- ouachitae
- fourchensis
- stormi
- elongatus
- dunni
- vehiculum
- idahoensis
- vandykei
- larselli
- neomexicanus

What are contrasts?

- Each standardized contrast is telling us something about the RATE of evolution

What are contrasts?

- Each standardized contrast is telling us something about the RATE of evolution

$$S_{ij} = \frac{X_i - X_j}{v_i + v_j}$$

What are contrasts?

- Each standardized contrast is telling us something about the RATE of evolution

$$S_{ij} = \frac{X_i - X_j}{v_i + v_j}$$

“amount of change”

What are contrasts?

- Each standardized contrast is telling us something about the RATE of evolution

$$S_{ij} = \frac{X_i - X_j}{v_i + v_j}$$

“amount of change”
“time”

What are contrasts?

- The contrasts have a close relationship with σ^2 , the rate parameter from BM
- The sum of the squared contrasts divided by n gives the ML estimate of σ^2

Using and Interpreting Contrasts

- Independent contrasts should be thought of as vectors
- They summarize information about the amount and direction of evolution at each node in the tree
- Standardized contrasts provide information about the rate of evolution

Using and Interpreting Contrasts

$$\hat{\sigma}^2 = \frac{\sum S_i}{n - 1}$$

- This provides an unbiased estimate of evolutionary rate
- The expected value of this estimate is equal to the actual rate parameter
- The maximum likelihood estimate of the rate parameter is biased

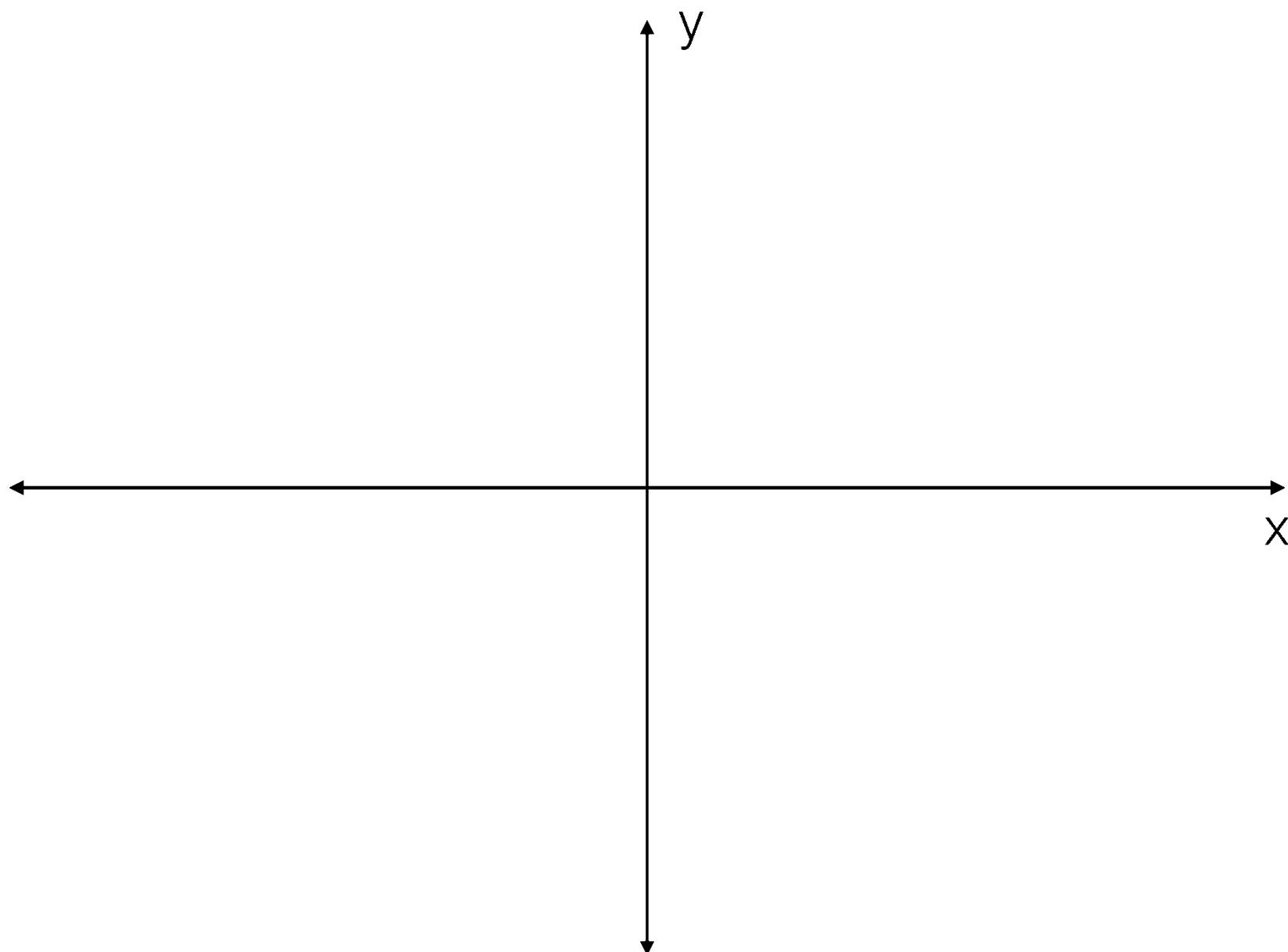
Character correlations

- Most common use for ICs: testing for character correlations
- Are two characters evolving in a correlated fashion?

Character correlations

- Calculate independent contrasts for two characters, x and y
- Carry out a regression analysis of y on x with **no intercept** (force regression line through the origin)
- $P < 0.05$, then reject the null hypothesis of no evolutionary correlation

```
Source  
46 pp<-get("lasC.  
47 for(i in 1:nrc  
48 lines(pp$xx)  
49 }  
50 for(i in 1:ler  
51 text(pp$xx[i  
52 pos=4)  
53 }  
54 }  
55 }  
56 }  
57 slantyTree<-fi  
58 plotTree(phy  
59 pp<-get("las  
60 for(i in 1:r  
61 lines(pp$  
62 lwd=3)  
63 }  
64 for(i in 1:l  
65 text(pp$xx  
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67 }  
68 }  
69 }  
70 data(salamande  
71 slantyTree(sal  
72 |  
72.1 (Top Level) z
```

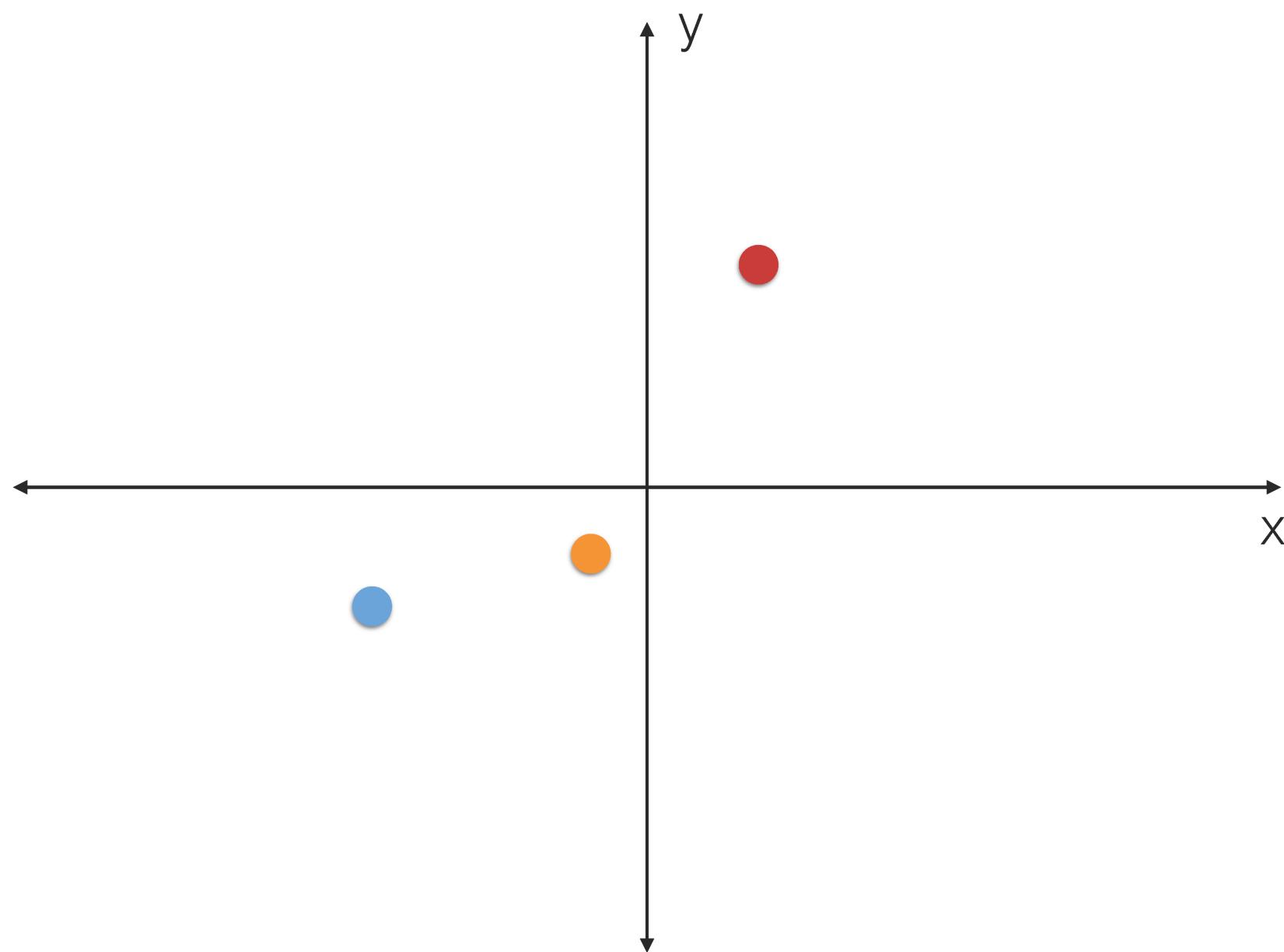


```
Console Terminal Back  
R R 4.2.2 >  
+ pp<-get("las  
+ for(i in 1:r  
+ lines(pp$  
+ }  
+ for(i in 1:l  
+ text(pp$xx  
+ pos=4)  
+ }  
> data(salamanders)  
> slantyTree(salamar  
>
```

- richmondi
- shenandoah
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- nettingi
- cinereus
- hubrichti
- serratus
- welleri
- dorsalis
- websteri
- wehrlei
- punctatus
- glutinosus
- jordani
- yonahlossee
- caddoensis
- ouachitae
- fourchensis
- stormi
- elongatus
- dunni
- vehiculum
- idahoensis
- vandykei
- larselli
- neomexicanus

```
exercise5.R  
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55 }  
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59 pp<-get("las  
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62 lwd=3)  
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64 for(i in 1:l  
65 text(pp$xx  
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72.1 (Top Level) z
```

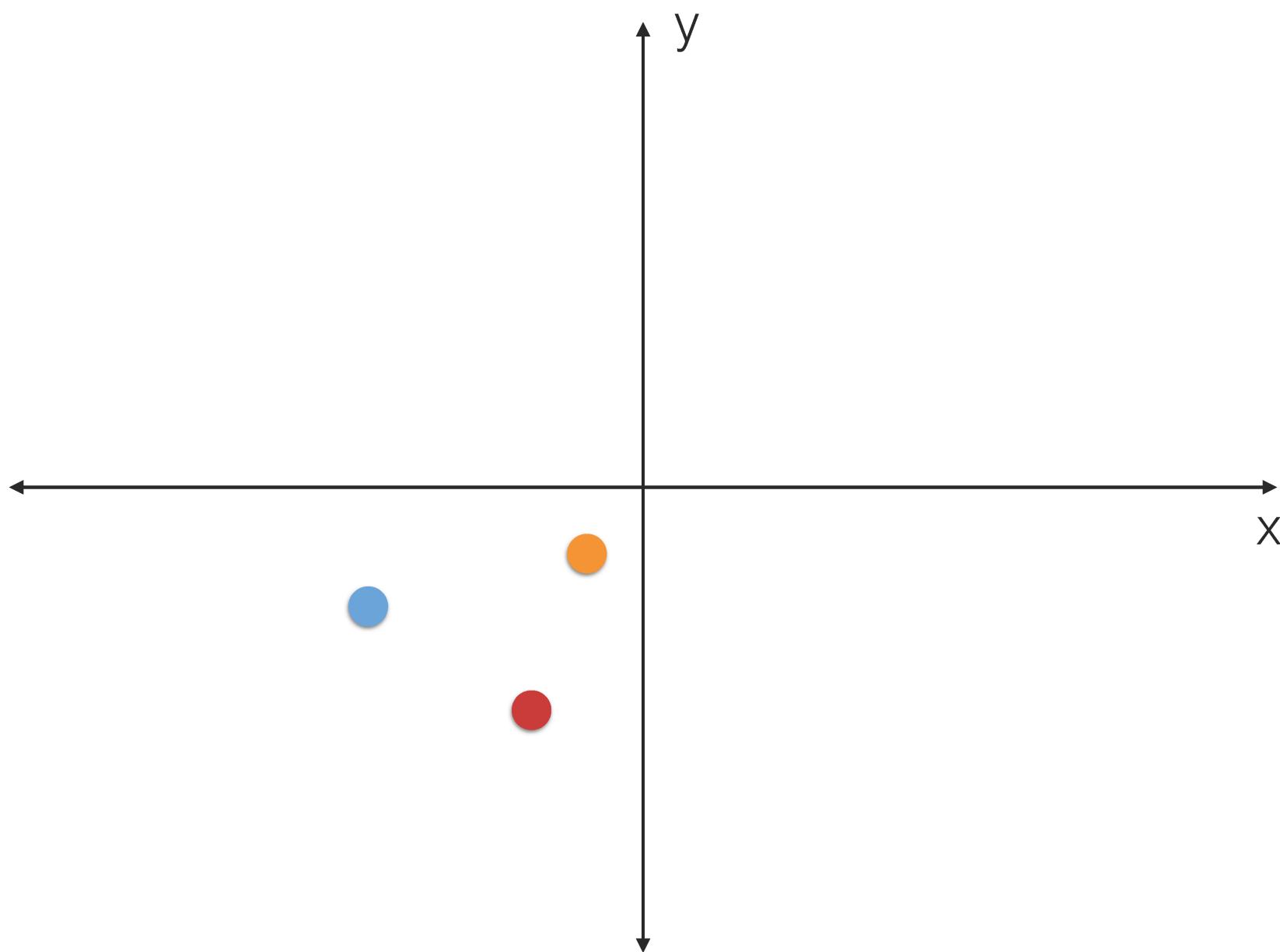
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Console Terminal Back  
R R 4.2.2 -->  
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+ for(i in 1:l  
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+ pos=4)  
+ }  
> data(salamanders)  
> slantyTree(salamander)
```



```
richmondi  
shenandoah  
hoffmani  
nettingi  
cinereus  
hubrichti  
serratus  
welleri  
dorsalis  
websteri  
wehrlei  
punctatus  
glutinosus  
jordani  
yonahlossee  
caddoensis  
ouachitae  
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72 |  
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72.2
```

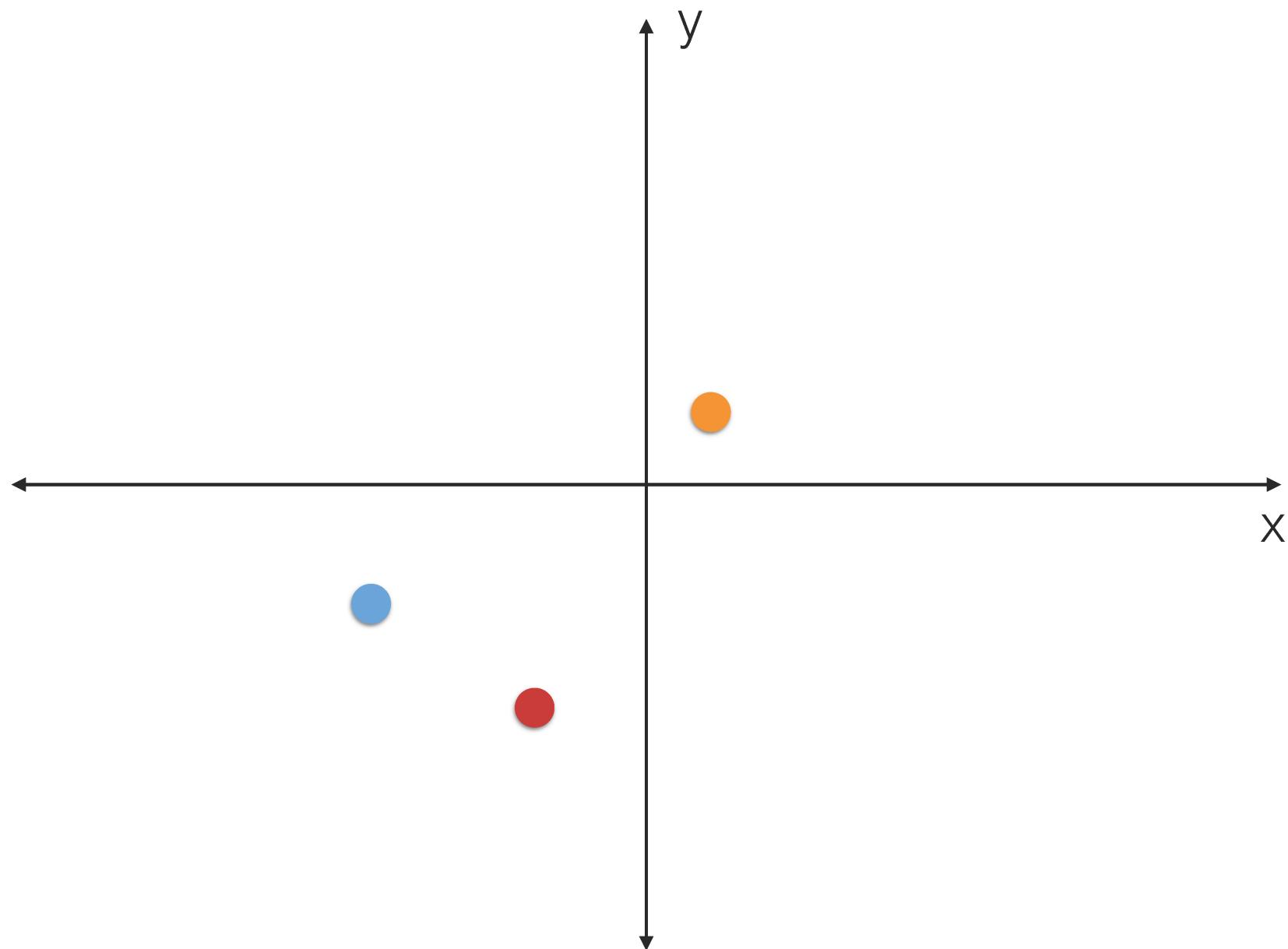
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```



```
richmondi  
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jordani  
yonahlossee  
caddoensis  
ouachitae  
fourchensis  
stormi  
elongatus  
dunni  
vehiculum  
idahoensis  
vandykei  
larselli  
neomexicanus
```

```
Source  
46 pp<-get("lasC"  
47 for(i in 1:nrc  
48 lines(pp$xx)  
49 }  
50 for(i in 1:ler  
51 text(pp$xx[i  
52 pos=4)  
53 })  
54 }  
55 }  
56  
57 slantyTree<-f  
58 plotTree(phy  
59 pp<-get("las  
60 for(i in 1:r  
61 lines(pp$  
62 lwd=3)  
63 }  
64 for(i in 1:l  
65 text(pp$xx  
66 pos=4)  
67 }  
68 }  
69  
70 data(salamande  
71 slantyTree(sal  
72 |  
72.1 (Top Level) z
```

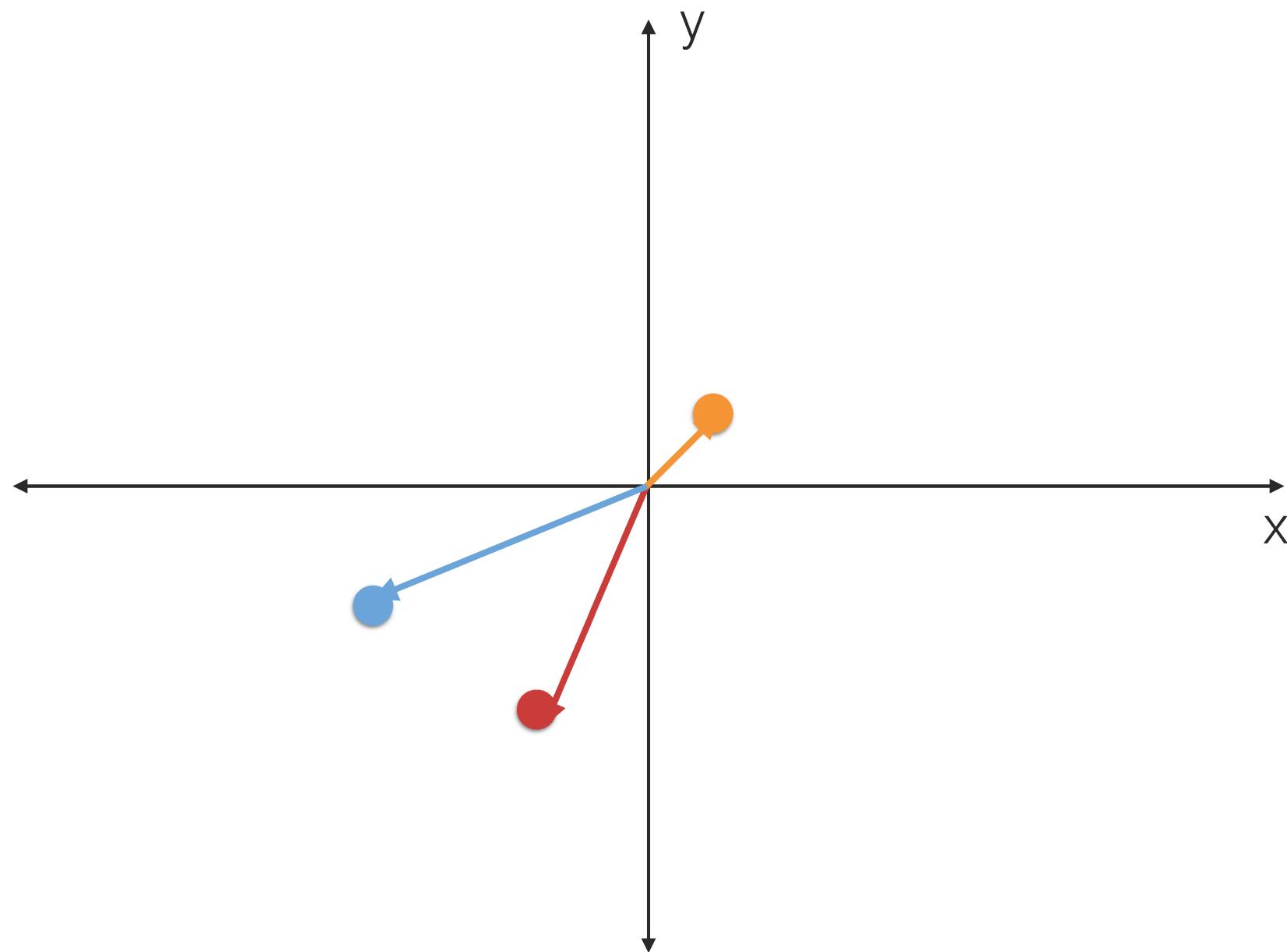
```
Console Terminal Back  
R R 4.2.2 ~>  
+ pp<-get("las  
+ for(i in 1:r  
+ lines  
+ }  
+ for(i in 1:l  
+ text  
+ }  
+ }  
> data(salamanders)  
> slantyTree(salamander)
```



```
richmondi  
shenandoah  
hoffmani  
nettingi  
cinereus  
hubrichti  
serratus  
welleri  
dorsalis  
websteri  
wehrlei  
punctatus  
glutinosus  
jordani  
yonahlossee  
caddoensis  
ouachitae  
fourchensis  
stormi  
elongatus  
dunni  
vehiculum  
idahoensis  
vandykei  
larselli  
neomexicanus
```

```
Source  
46 pp<-get("lasC"  
47 for(i in 1:nrc  
48 lines(pp$xx)  
49 }  
50 for(i in 1:ler  
51 text(pp$xx[i  
52 pos=4)  
53 }  
54 }  
55 }  
56 }  
57 slantyTree<-f  
58 plotTree(phy  
59 pp<-get("la  
60 for(i in 1:r  
61 lines(pp$  
62 lwd=3)  
63 }  
64 for(i in 1:l  
65 text(pp$xx  
66 pos=4)  
67 }  
68 }  
69 }  
70 data(salamande  
71 slantyTree(sal  
72 |  
72.1 (Top Level) z
```

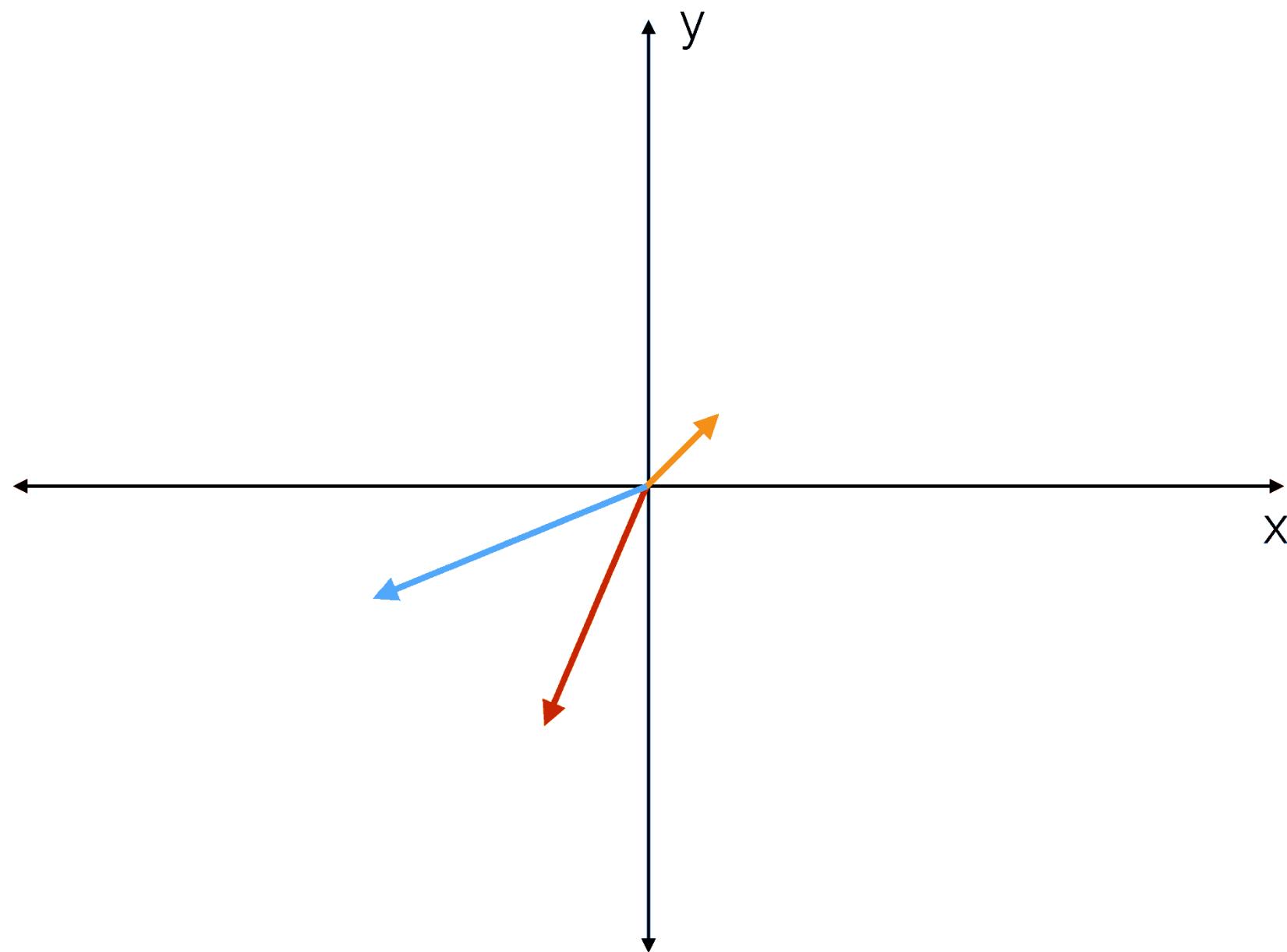
```
Console Terminal Back  
R R 4.2.2 ->  
+ pp<-get("la  
+ for(i in 1:r  
+ line  
+ }  
+ for(i in 1:l  
+ text  
+ }  
+ }  
> data(salamanders)  
> slantyTree(salamar  
>
```



```
richmondi  
shenandoah  
hoffmani  
nettingi  
cinereus  
hubrichti  
serratus  
welleri  
dorsalis  
websteri  
wehrlei  
punctatus  
glutinosus  
jordani  
yonahlossee  
caddoensis  
ouachitae  
fourchensis  
stormi  
elongatus  
dunni  
vehiculum  
idahoensis  
vandykei  
larselli  
neomexicanus
```

```
exercise5.R  
Source  
46 pp<-get("lasC"  
47 for(i in 1:nrc  
48 lines(pp$xx)  
49 }  
50 for(i in 1:ler  
51 text(pp$xx[i  
52 pos=4)  
53 }  
54 }  
55 }  
56 }  
57 slantyTree<-fli  
58 plotTree(phy  
59 pp<-get("las  
60 for(i in 1:r  
61 lines(pp$  
62 lwd=3)  
63 }  
64 for(i in 1:l  
65 text(pp$xx  
66 pos=4)  
67 }  
68 }  
69 }  
70 data(salamande  
71 slantyTree(sal  
72 |  
72.1 (Top Level) z
```

```
Console Terminal Back  
R R 4.2.2 ->  
+ pp<-get("las  
+ for(i in 1:r  
+ lines(pp$  
+ }  
+ for(i in 1:l  
+ text(pp$xx  
+ }  
+ }  
> data(salamanders)  
> slantyTree(salamander)
```

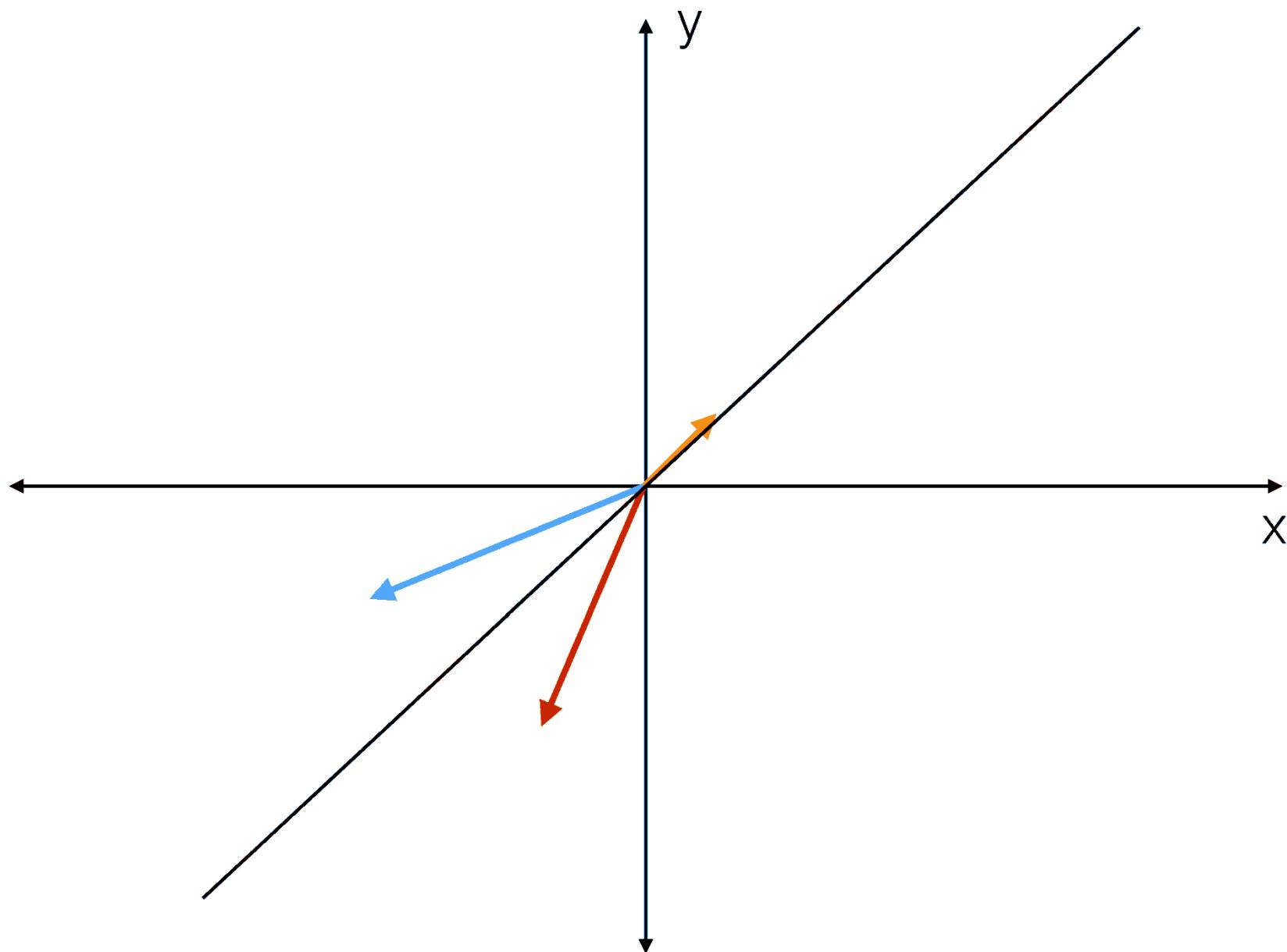


```
richmondi  
shenandoah  
hoffmani  
nettingi  
cinereus  
hubrichti  
serratus  
welleri  
dorsalis  
websteri  
wehrlei  
punctatus  
glutinosus  
jordani  
yonahlossee  
caddoensis  
ouachitae  
fourchensis  
stormi  
elongatus  
dunni  
vehiculum  
idahoensis  
vandykei  
larselli  
neomexicanus
```

```
File Edit Code View Plots Session Project (None) 

```
exercise5.R
Source
46 pp<-get("lasC"
47 for(i in 1:nrc
48 lines(pp$xx)
49)
50 for(i in 1:ler
51 text(pp$xx[i
52 pos=4)
53)
54)
55)
56
57 slantyTree<-f
58 plotTree(phy
59 pp<-get("las
60 for(i in 1:r
61 lines(pp$
62 lwd=3)
63)
64 for(i in 1:l
65 text(pp$xx
66 pos=4)
67)
68)
69
70 data(salamande
71 slantyTree(sal
72)
73 <-->
74 (Top Level)
Console Terminal Back
R R 4.2.2 ->
+ pp<-get("las
+ for(i in 1:r
+ line
+)
+ for(i in 1:l
+ text
+)
+)
> data(salamanders)
> slantyTree(salamar
>
```


```



- richmondi
- shenandoah
- hoffmani
- nettingi
- cinereus
- hubrichti
- serratus
- welleri
- dorsalis
- websteri
- wehrlei
- punctatus
- glutinosus
- jordani
- yonahlossee
- caddoensis
- ouachitae
- fourchensis
- stormi
- elongatus
- dunni
- vehiculum
- idahoensis
- vandykei
- larselli
- neomexicanus

Character correlations

- Why force contrasts through the origin?
- Because, for each contrast, the direction of subtraction is arbitrary; the signs of all the contrasts could be reversed
- Regression through the origin treats the contrasts as vectors

