

# Estimating asymmetry of dispersal and intensity of migration in time within a Bayesian framework

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## INTRODUCTION

### Dispersal patterns in space and time

Long-time changes in intensity and direction of migration often follow certain patterns rather than exhibit a random distribution. Identification of these patterns is important as it allows to test variety of hypotheses on significance of migration tracks and on ecological and geographical barriers. We propose simple methods of measuring dispersal asymmetry and of identifying temporal dispersal windows and we provide their implementation using R statistical environment (R Development Core Team, 2010) with COT package. The package is available from the Google Code project website (<http://code.google.com/p/cot-mr/>).

## THE APPROACH

### Input data

The input data comprises a set of ultrametric (calibrated) phylogenies annotated with Bayesian reconstructions of ancestral areas. Each taxon is restricted to a single area (widespread ranges are not allowed). Trees are sampled from the stationary distribution of Markov chain, for instance resulting from Bayesian analyzes using discrete phylogeographical model as implemented in BEAST (Lemey *et al.*, 2009).

### Intensity of migration in time

We assume that dispersals occur at stem nodes of respective branches (i.e. they are associated with allopatric speciation). The input trees are divided into equal time intervals beginning from the tips. Then, for each tree and each time interval, the number of stem nodes and the number of dispersals are scored (Fig. 1). The intensity of migration is estimated as the number of dispersals divided by the number of stem nodes. The values are summarized over all trees for given time intervals, migration tracks and directions of dispersal (Fig. 2).

### Asymmetry of migration

The asymmetry of migration for a given track and tree is evaluated using Dispersal Asymmetry Index (DAI) defined as follows:

$$DAI = 2[d_1/(d_1 + d_2) - 0.5]$$

where  $d_1$  is the number of dispersals in the dominant direction and  $d_2$  is the number of dispersals in the opposite direction along the analysed track. The DAI may vary between 1 (all dispersals inferred for a given tree are in the dominant direction) and -1 (all dispersals for a given tree are in the opposite direction), whereas its mean for the whole set of trees varies between 0 (symmetric bidirectional dispersal) and 1 (unidirectional dispersal). The distribution of DAI for a given track over all trees allows to test the statistical significance of asymmetry while mean value of DAI is an indicator of the strength of asymmetry (Fig. 3).

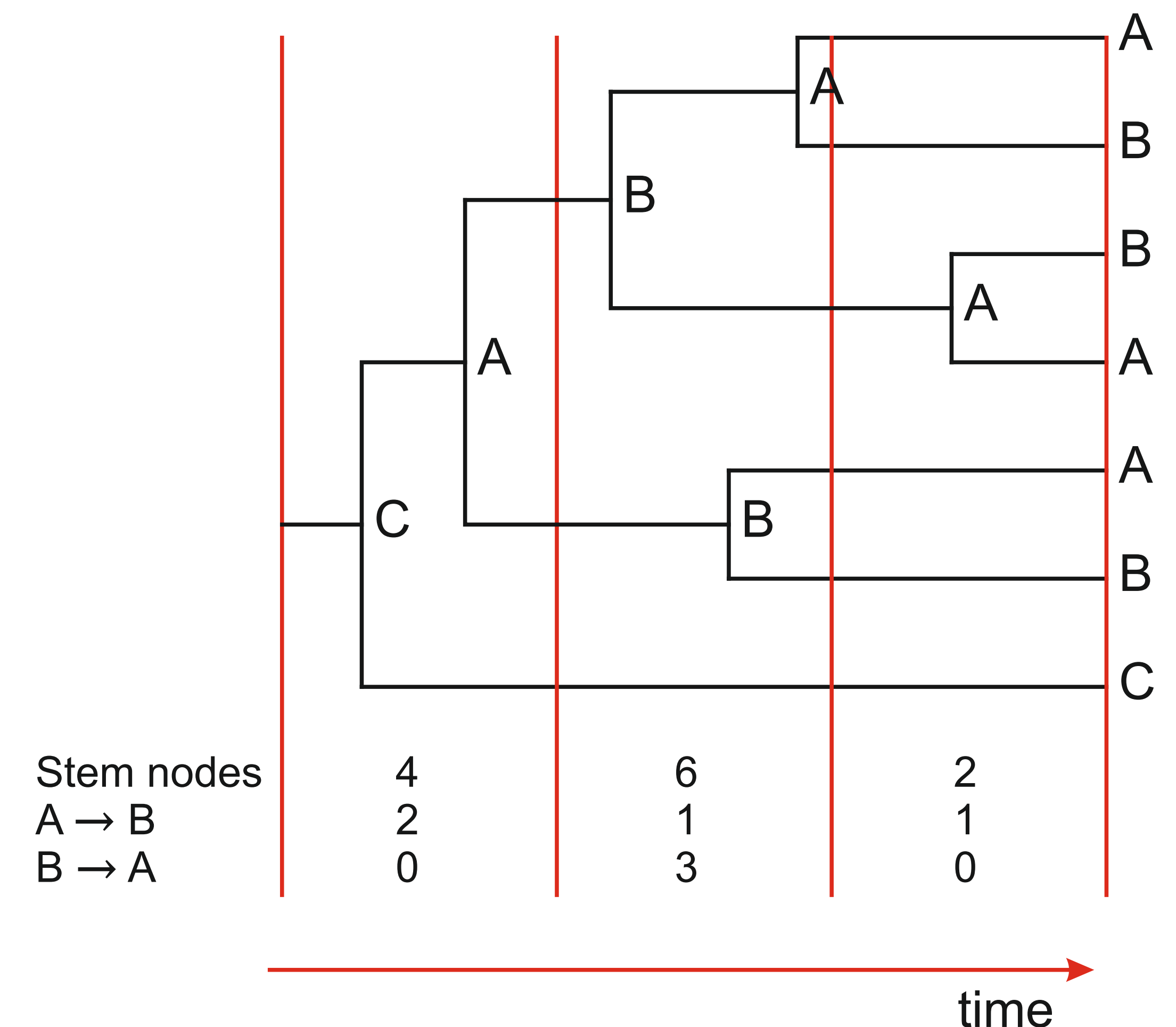
## CASE STUDY

### Discovering dispersal patterns in umbellifers

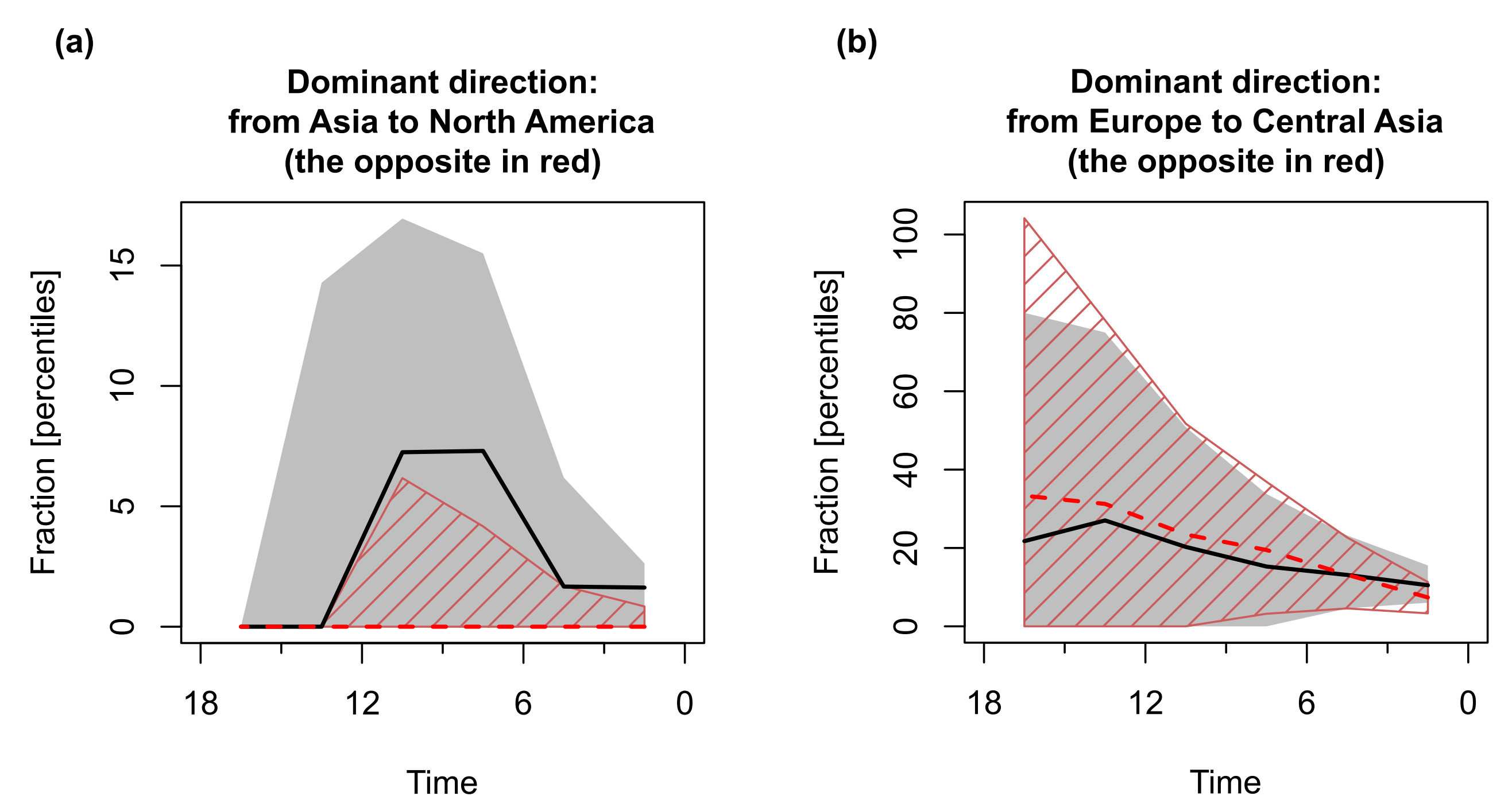
We applied the aforementioned approach for the biogeographical analysis of 1194 representatives of umbellifers (angiosperm family Apiaceae; Banasiak *et al.*, 2013). Using Bayesian biogeographical analyses, we identified 334 dispersal events (95% HPD: 309-358) and 17 statistically significant migration routes. Significant asymmetry of dispersal was found for five of them. The observed dispersal pattern – intense and symmetrical within the same climatic zone versus scarce and often unidirectional between climatic zones or along long-distance transoceanic tracks – suggested that both the availability of suitable habitats and geographical barriers have played crucial roles in determining the present distribution of umbellifers.

#### References

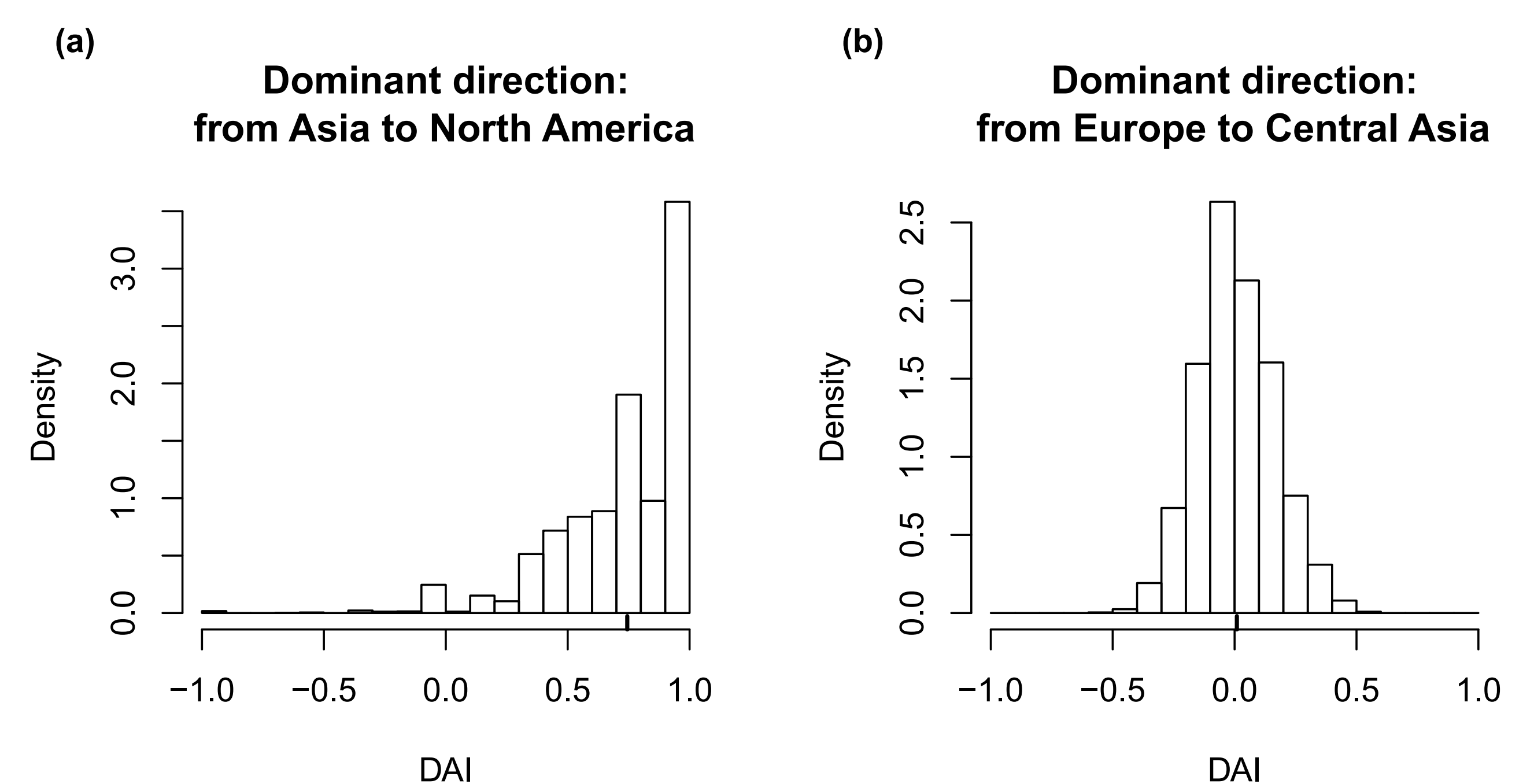
• Banasiak Ł. *et al.* (2013) Dispersal patterns in space and time: a case study of Apiaceae subfamily Apiaceae. *Journal of Biogeography*, in press • Lemey P. *et al.* (2009) Bayesian phylogeography finds its roots. *PLoS Computational Biology*, 5, e1000520 • R Development Core Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria



**Fig. 1. Counting dispersals between A and B based on calibrated phylogeny with Bayesian reconstruction of ancestral areas.** Letters indicate areas occupied by extant taxa (tips) and reconstructed ranges of the ancestors (internal nodes). The branch lengths are proportional to time. For each time interval (red vertical lines), the number of stem nodes and the numbers of dispersals between A and B are scored (dispersals are assumed to take place at stem nodes). The data are summarized over all trees to generate the plots of intensity of migration in time (see Fig. 2) and for the analysis of the asymmetry of dispersal.



**Fig. 2. Plots of changing intensity of migration in time.** Data for all trees are summarized with percentile median values (lines) and 95% HPD ranges (polygons) for 3 My intervals. The prevailing direction of dispersal is marked with a black line and grey shade while the opposite is indicated with a red dashed line and shade. (a) Connection between North America and Asia through Beringia with distinct peak of dispersal around 9 My. (b) Exchange between Europe and Central Asia showing almost uniformly distributed migrations in time. Examples are taken from a biogeographic analysis of 1194 representatives of Apiaceae subfamily Apiaceae (Banasiak *et al.*, 2013).



**Fig. 3. Histograms of dispersal asymmetry indices (DAI) over a set of Bayesian trees.** (a) Skewed distribution with mean (marked with a rug on abscissa axis) in the far right and more than 97% of DAIs greater than zero show significant and strong asymmetry of exchange with prevailing direction of dispersals from Asia to North America. (b) Normal distribution of DAI with mean close to zero indicates symmetrical exchange between Europe and Central Asia. Examples are taken from the study of Banasiak *et al.* (2013).

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