Phylogenetic Structure Analysis Based on Blue Light Receptor Cryptochrome: Insights into How Light Shape the Vertical Structure of Forest Community

Qiming Mei[1, 2, 3, 4, *], Juyu Lian[1, 2, 3, 4, *], Yue Wang[1, 2, 3, 4], Meng Li[1, 2, 3, 4], Xujun Gui[1, 2, 3, 4], Zhengfeng Wang[1, 2, 3, 4], Hongling Cao[1, 2, 3, 4] and Wanhui Ye[1, 2, 3, 4, #]

[1] Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou, Guangdong 510650, China

[2] Center of Plant Ecology, Core Botanical Gardens, Chinese Academy of Sciences, Guangzhou, Guangdong 510650, China

[3] Southern Marine Science and Engineering Guangdong Laboratory (Guangzhou), Guangzhou 511458, China

[4] Guangdong Provincial Key Laboratory of Applied Botany, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China

* The authors contributed equally to the paper

[#] Correspondence to why@scib.ac.cn

Abstract

Light-regime variability is an important environmental factor which shapes a forest

community. So far, none focused on the phylogenetic pattern of plant light receptors, which reflects how genes' evolution influences the coexistence of species in a community. In this study, we analyzed community phylogenetic structure of the south subtropical forest by sequences of plant blue light receptor cryptochrome (CRY) and compared the results of DNA barcodes. Patterns of community assembly was estimated by net relatedness index (NRI) and nearest taxon index (NTI). We found that CRY showed quite different phylogenetic structure as compared to DNA barcoding results, all habitats displayed consistent phylogenetic structure patterns, suggesting a convergent evolution of light sensing system of plant in local adaptation. Also, both NRI and NTI values increased through the time, indicating that the phylogenetic structure of tree community became more overdispersion as succession proceeds; phylogenetic closely-related species tended to co-occur and environmental filtering played a more important role in the community assembly. Furthermore, phylogenetic patterns were more clustering in upper canopy layers, and NTI values of all canopy layers were above zero, suggesting that phylogenetically related species tended to coexist and adapted to similar light conditions.

Keywords

Community assembly, Phylogenetic structure, Cryptochrome, Vertical structure

Introduction

The integrating of evolutionary history of species into community ecology proved a new method to study community assembly and monitor diversity (Webb, Losos et al. 2006, Cavender-Bares, Kozak et al. 2009). Kress et al. (2009) originally developed an advanced method of constructing community phylogeny using DNA barcode sequence data which generates highly resolved phylogenies. In the last decade,

numerous researchers used DNA barcoding method in monitoring biodiversity of forest communities (Kress, Erickson et al. 2009, Pei, Lian et al. 2011, Shapcott, Forster et al. 2015, Heckenhauer, Abu Salim et al. 2017, Comita, Uriarte et al. 2018). DNA barcoding is proven to be a fast and reliable tool that generated fully resolved phylogeny thus improve the accuracy of assement (Heckenhauer, Abu Salim et al. 2017). However, the community phylogenetic analyses by DNA barcode sequences have its limitation. These DNA sequences (i.e., rbcL, matK and trnH-psbA) evolved under constant rate thus do not correspond to environmental changes. On the other hand, whether the phylogenetic pattern reflect the process of community assembly is still under debate (Gerhold, Cahill et al. 2015). Multiple processes involved in community assembly can lead to similar phylogenetic pattern. (Mayfield and Levine 2010, Vellend 2010). Thus, we tried to analyze community phylogenetic structure using blue light receptor gene cryptochrome (CRY).

Light-regime variability is one of the most important environmental factor which shapes a forest community (Sercu, Baeten et al. 2017, Tang and Dubayah 2017). Light is not only the energy resource of green plants, but also an important environmental signal, which regulates the growth of plants (Ruban 2009). The light sensing of plants is conducted by light receptor proteins including CRY (McClung 2006, Fortunato, Annunziata et al. 2015). Cryptochrome performs essential physiological functions of plants, such as photomorphogenesis, circadian rhythm and phototropism of plants (Somers, Devlin et al. 1998).

Light spectrum various in forest especially for blue light (390–500 nm); blue light is filtered by canopies and topographical variations thus blue-light-sensing for shaded trees is a great challenge (Thery 2001). CRY plays an important role in shade avoidance syndrome (SAS) of forest plants under low blue light (Fankhauser and Batschauer 2016). Therefore, we hypothesize evolution of cryptochrome may

influence the habitat selection and local adaptation of plant species in the forest community.

In this study, we reconstructed the phylogeny of 20-ha Dinghushan forest dynamics plot (DHS FDP) by using the sequences of plant blue light receptor CRY. Then, we analyzed the phylogenetic structures with habitat types, spatial scales, times, succession stages and vertical structures. The assembly process of forest vertical structure is mainly driven by light, while horizontal community assembly is determined by multiple biotic and abiotic factors (Tang and Dubayah 2017). Therefore, we hypothesis that CRY's phylogeny is more closely related to vertical structure rather than horizontal assembly. The previous study using DNA barcodes had comprehensively interpreted the horizontal community assembly of Dinghushan forest (Pei, Lian et al. 2011). In this paper, we compared the generated results to previous DNA barcode results. By exploring the community assembly mechanism of south subtropical evergreen broadleaf forest, we aimed to provide introduction to protection of *in situ* biodiversity. Also, this study provided a new point of view to analyses of community assembly in future.

Materials and methods

1. Study site and sample collection

The study site is the 20 ha Dinghushan subtropical forest dynamics plot (DHS FDP) located in Dinghushan National Nature Reserve (23°09′21″-23°11′30″N, 112°30′30″-112°33′41″E), Zhaoqing city, Guangdong Province, China. The DHS FDP is a member of Chinese Forest Biodiversity Monitoring Network (CForBio) and the Center for Tropical Forest Science (CTFS) global network of forest dynamics plots. In the plot, all trees with a diameter at breast height ≥1 cm (DBH) were measured, mapped and tagged every 5 years since 2005. Fresh leaves of each species were

collected from 2 tagged individuals located within the plot during 2015 census. Leaf tissue was dried immediately in silica-gel and stored in -20°C freezer.

2. DNA sequencing and community phylogenetic reconstruction

Genomic DNA sequences were extracted from freeze-dried leaf samples using a DNA extraction Kit (TransGen Biotech). Then, a pair of degenerate primer (5'-TCWCCDCTTCTNCCICCTAA-3' and 5'-TGTRTCCCARAARTACTTCA-3') was utilized to amplify *Cry* sequences. The obtained fragments covered the most conserved region of FAD-binding domain of cryptochrome. The PCR cycling template. PCR cycling was started at 95 °C for 10 min, followed by 40 cycles of 95 °C, 54 °C and 72 °C for 1 min, and then extension at 72 °C for 10 min. The DNA sequencing were conduct using the same pair of degenerate primer. Then, DNA sequences of cryptochrome were translate into protein. The amino acid dataset was aligned using MUSCLE v. 3.8.31 (Edgar 2004). Also, all CRY sequences used in this study were submitted to GenBank (https://www.ncbi.nlm.nih.gov/) and the accession numbers were listed in Table S1.

The phylogenetic reconstruction was performed using CRY protein sequences. The most appropriate model of amino acid substitutions for our dataset was determined according to the Akaike information criterion (AIC) and using ProtTest v.3.0 (Akaike 1981, Darriba, Taboada et al. 2011). Based on the test, the fittest substitution model of CRY sequences is GTR with gamma distribution and proportion of invariable sites (GTR + G + I, $\alpha = 0.86$, p-inv = 0.20). Then we used the Bayesian method as implemented in BEAST v.2.4.3 (Drummond and Rambaut 2007) to reconstruct the phylogeny of plant CRYs. The length of the MCMC chain was set for 10 million with trees sampled every 1000 steps. The maximum clade credibility tree was determined from the generated 10,000 trees (burnin = 10%) using TreeAnnotator v.2.1.2 from the BEAST software package. Also, the phylogenetic tree was calibrated according to molecular time estimates (Table 1) (Wikstrom, Savolainen et al. 2001, Muellner-

Riehl, Weeks et al. 2016).

3. Habitat types, spatial scales, vertical structure classification and community phylogenetic structure analyses

In this study, the 20-ha plot was divided into five hundred 20 m x 20 m and twenty 100 m x 100 m quadrats. These quadrats are adjacent and non-overlapping. The analyses were conducted by two different spatial scales. The classification of habitat types and spatial scales was followed the methods of Pei et al. (2011). Five types of habitat in the DHS FDP were classified including high-gully (HG), high-slope (HS), low-slope (LS), ridge-top (RT) and valley (V) (Table 2). In addition, the plot consisted of two types of forests including early successional (ES, ~60y) and late successional (LS, ~400y) stands according (Chen, Zhang et al. 2015, Lian, Chen et al. 2015). Also, we analyzed the patterns of community assembly of forest vertical structures including shrub (1.4 – 5 m of tree height), understory (5.1 – 10 m), canopy (10.1 - 15 m) and emergent (> 15 m) layers. The net relatedness index (NRI) and nearest taxon index (NTI) were utilized to estimate the patterns of community assembly (Webb, Ackerly et al. 2008).

$$NRI = -1 \times (MPD - rndMPD)/sdrndMPD$$

$$NTI = -1 \times (MNTD- rndMNTD)/sdrndMNTD$$

MPD is mean phylogenetic distance, MNTD is mean nearest phylogenetic taxon distance and sd is standard deviation, mean pairwise distances are weighted by species abundance. We compared the observed values of MPDs and MNTDs to the null distributions. The null models were obtained by shuffling the species names across the tips of the phylogeny with 999 random assemblages. The analyses conducted by Picante package as implement in R (Team 2009, Kembel, Cowan et al. 2010). Finally, two-tailed tests were run for the statistical significance of NRI/NTI results with R software (Team 2009).

Results

1. Phylogenetic analyses

The phylogeny of DHS FDP was constructed by Bayesian method using CRY sequences with posterior possibility (Figure 2 and Figure S1). This study included 96 species, corresponding to 94.73% of total orders, 82.61% of families, 57.14% of existing angiosperm species and 92.67% of tree individuals in DHS FDP according to 2015 census data. Generally, we found the statistic support for major nodes is quite strong (most posterior possibility > 0.9, Figure 2). Also, we compared the CRY tree and the DNA barcoding tree (species tree). The CRY and species phylogenetic trees demonstrated consistent topology (Figure 2). On the other hand, the CRY tree manifested longer branch lengths as compared to species tree, indicating that plant light receptor genes evolved much faster as compared to genomic DNA fragments used for barcoding (Figure 2).

2. Community phylogenetic structure analyses

In this study, we investigated community phylogenetic structure using NRI and NTI indices. Results demonstrated that barcode and CRY manifested similar pattern of phylogeny (Figure 3). Mean abundance-weighted NRI values showed overdispersal structure, while NTI results were generally phylogenetically clustered. In other words, NRI values were negative in most habitats of all years and NTI values tended to be positive. Moreover, barcoding results were more habitat-specific as compared to CRY values; valley displayed the highest level of NRI and lowest NTI. But for CRY results, the differences among habitats were not statistically significant in 2005 and 2015.

For phylogenetic structure in a larger special scale (100 m x 100 m), values of CRY NRI were tend to be negative in all years while values of NTI were positive (Figure

4). Both indices of CRY demonstrated increasing trends through time, suggesting the phylogeny tend to be more clustering. On the other hand, no significant variation in phylogenetic structure among years was detected.

Values of NRI and NTI differed significantly between the two succession stages of Dinghushan forest community (Figure 5). The NRI values are on average phylogenetically overdispersed or random. Also, the two indices showed different trends during the succession. The late succession stage NRI results are more overdispersed as compared to early stage values. But for NTI analyses, the phylogenetic structure of the late succession stage is more clustering than early stage.

Based on the temporal patterns of 2010 and 2015, NRI values of CRY became more clustering in upper canopy layers (Figure 6). Conversely, DNA barcoding NRI pattern manifested a shift towards phylogenetic overdispersion in forest vertical structure. Understory and canopy layers displayed the highest level of CRY NTI based on 2010 census data. Regarding 2015 data, CRY NTI results showed no significant difference among the layers.

Discussion

In relation to our first aim, phylogenetic tree of CRY is compared to the species tree generated by DNA barcodes (Figure 2). The CRY tree demonstrates consistent topology as compared to the species tree with strong node statistic support, suggesting that the phylogeny is reliable for further study. On the other hand, the CRY tree manifests longer branch lengths as compared to species tree, indicating that plant light receptor genes evolved much faster as compared to genomic DNA fragments used for barcoding. Plants are surrounded by an altering light environment that light intensity, spectrum and day length are changing frequently (Trewavas 2017). In the long evolutionary history, plants evolved a set of light receptors to sense signal then adjust

physiology, regulate gene expression to match ambient conditions (Zhang and Folta 2012). This means that plant light receptors are very sensitive to environmental changes (Galvao and Fankhauser 2015). Therefore, analyzing phylogenetic structure of a community utilizing information generating from photoreceptor gene sequences is an effective way to study relationship between community assembly and heterogeneity of light environment.

In this study, NRI and NTI are utilized to estimate the phylogenetic patterns of a subtropical tree community (Figure 3-6). Generally, NRI is more sensitive to tree-wide phylogenetic patterns, while NTI has greater power to analyze patterns of the phylogeny tips (Webb, Ackerly et al. 2002, Kraft, Cornwell et al. 2007). Firstly, NRI and NTI values of CRY are compared to results generated by DNA barcodes. Results generated by CRY are consistent, NRI values of all five habitats are negative, indicating an overall phylogenetic overdispersal pattern. The overdispersal results specifies the convergent evolution of light sensing system of plant in local adaptation (Cavender-Bares, Ackerly et al. 2004). On the contrary, all NTI results manifest a clustering distribution of phylogenetic closely-related taxa (Singer, Kosakyan et al. 2018). The closely-related species (e.g., *Ficus* and *Ilex* species) may be settled by environmental filtering such as limitation of light, water and nutrients (Liu, Chen et al. 2018). Several previous works indicate that NRI is more effective to detect nonrandom patterns of community phylogenetic structure as compared to NTI (Letcher 2010, Letcher, Chazdon et al. 2012, Muscarella, Uriarte et al. 2014). But in our study, NTI values display more clustering results than NRI of all analyses (Figure 3-6). Previous works report that NTI showing higher level of clustering than NRI indicates recent diversifications within the region (Brunbjerg, Cavender-Bares et al. , Qian and Jiang 2014). However, this is contrary to Pei's work which study the same forest dynamics plot using DNA barcodes (Pei, Lian et al. 2011), suggesting that phylogenetic structures of gene and species levels are quite different.

In addition, the CRY NRI and NTI results are not significantly different among habitats, suggesting that the habitats may not has significant effect on changes in light environment thus influence plant light sensing systems (Figure 3). On the other hand, NRI and NTI values of 2015 exhibit broader ranges as compared to 2005 and 2010 results (Figure 3). This may be a consequence of tree recruitment after disturbance. The forest is rarely suffered from anthropogenic disturbance since the establishment of Dinghushan Nature Reserve in 1956 (Ouyang, Ye et al. 2013). On the other hand, the community assembly is impacted by natural disturbance such as typhoon (Sui, Wang et al. 2017). Forest gap generated by typhoon disturbance is one of the main factor that drives the recruitment of a forest community that created high light conditions (Saito 2002, Comita, Uriarte et al. 2018). Also, understorey phylogenetic structure is determined by overstorey species identity rather than species richness(Coppi, Lazzaro et al. 2019). In the DHS FDP, one of the dominant tree species *Schima superba* decreased 69.31% during 2010-2015, while abundance of light-demanding species such as *Aidia canthioides* and *Ormosia glaberrima*, increased dramatically.

There are many reported works about phylogenetic pattern of temperate, subtropical and tropical forests during succession generated inconsistent conclusion that phylogenetic patterns are tend to be: clustering (Letcher 2010, Whitfeld, Kress et al. 2012, Chai, Yue et al. 2016) or overdispersed (Ding, Zang et al. 2012, Mo, Shi et al. 2013, Purschke, Schmid et al. 2013, Liu, Chen et al. 2018) as succession proceeds. For the analysis of a larger special scale (100 m x 100 m) in this study, both NRI and NTI values increase through the time, suggesting that the phylogenetic structure of tree community becomes more overdispersion as succession proceeds (Figure 4). These results are in agreement with to NTI results of different successional stages, phylogenetic structure of late successional (LS) forests is more clustering as compared to early successional (ES) forests (Figure 5d-f). But for NRI results, the older forests are more phylogenetic overdispersed (Figure 5a-c). Previous studies

suggest that the overdispersion is caused by disturbance and forest gaps (Prescott 2002, Jin, Qian et al. 2015); gaps generate microenvironment similar to primary stage of forest succession and forest understory is not subjected to limitation of light resource. Also, forest gaps are likely to harbor phylogenetically distantly related species rather than enclosed forest (Jin, Qian et al. 2015).

The heterogeneity of light environments along forest vertical structures influence the phylogenetic pattern (Coppi, Lazzaro et al. 2019). Overstorey and understorey species are more specialized to high and low light availability gradient respectively (Dupuy and Chazdon 2006). With canopy closure, understorey light-demanding seedling tend to decrease and take over by shade-tolerant species (Wagner, Fischer et al. 2011). In this study, we found that the NRI tend to be more clustering in upper canopy layers (Figure 6). Our results are consistent with a previous study on subtropical forest (Jin, Qian et al. 2015). On the other hand, the prevalent positive NTI values of canopy layers suggest that phylogenetically related species tend to coexist and adapted to similar light conditions.

Generally, our NRI and NTI results are quite near average values of East Asia summarized by Feng et al (Feng, Mi et al. 2015). The community assembly of south subtropical forest community is mainly driven by stochastic processes.

This study has some limitations. Firstly, all NRI and NTI results generated in this study are not significantly different as compared to null model, suggesting a randomness of phylogenetical structure. This study was conducted on a narrow geographical range and involved only limited number of species. Also, there are multiple copies of CRY occurs in plants (Mei and Dvornyk 2015), only one CRY1 homolog of each species was use in the analyses to simplify the phylogeny. Furthermore, light is not the only essential environmental factor shapes the community, community assembly is the consequence of complicated abiotic and

biotic processes (Kraft, Adler et al. 2015). Influence by other environmental factors (functional diversity of other genes) is yet to be well studied.

Figures

Figure 1. The spatial distribution of habitats and successional stages in the 20-ha DHS FDP. (a) The five habitat types (Pei, Lian et al. 2011); (b) early successional (left of blue line) and late successional (right of blue line) stands, quadrats from youngest to oldest: T1 - T5.

Figure 2. A comparison of the phylogenetic structures of DHS FDP. The gene tree (a) is inferred by CRY with Bayesian algorism (node support below 0.5 are not shown) and the species tree (b) is reconstructed by DNA barcode sequences via ML analysis (Pei, Lian et al. 2011)

Figure 3 The net relatedness index (NRI) and nearest taxon index (NTI) varied by time and habitat types in 20 m x 20 m quadrats. (a) 2005 NRI, (b) 2010 NRI, (c) 2015 NRI, (d) 2005 NTI, (e) 2010 NTI and (f) 2015 NTI. Five types of habitat in the DHS FDP including high-gully (HG), high-slope (HS), low-slope (LS), ridge-top (RT) and valley (V) were classified by Pei, Lian et al. (2011). Letters indicate significant differences among the habitat types * symbols indicate significant differences between two methods ($p < 0.05$).

Figure 4 The NRI (a) and NTI (b) of a larger spatial scale (100 m x 100 m). * symbols indicate significant differences between two methods ($p < 0.05$).

Figure 5 The NRI (a) and NTI (b) varied by successional stages of forest. # symbols indicate significant differences between successional stages and * symbols indicate significant differences between two methods ($p < 0.05$).

Figure 6 The NRI and NTI varied by canopy layers. (a) 2010 NRI, (b) 2015 NRI, (c) 2010 NTI and (d) 2015 NTI. Results of 2005 census cannot be calculated because lack of height data. Letters indicate significant differences among the canopy layers and * symbols indicate significant differences between two methods ($p < 0.05$).

Tables

Table 1 Calibration points used in molecular phylogenetic tree.

Taxa	Divergent age estimates (Mya)
Angiosperms	150-140
Eudicots	147-131
Asterids	128-122
Rosids	109-104
Laurales	114-108
Ericales	92-85
Malpighiales	81-77
Malvales	71-67
Fabales	79-74
Rosales	79-73
Sapindales	110.5-99
Myrtales	79-75
Gentianales	94-88

Table 2 Habitats of DHS FDP

Habitats	DHS Plot	High-slope	Low-slope	Ridge-top	High-gully	Valley
Number of	500	73	115	62	77	173

quadrats						
Area (ha)	20	2.92	4.60	2.48	3.08	6.92

Acknowledgements

We would like to thank Prof. Jie Yang (XTBG, CAS) for her help with data analysis, and graduate students of SCBG, CAS for their help with sample collection.

Authors' contributions

QM designed methodology, finished the field survey and lab work, performed data analysis and wrote the manuscript. JL performed data analysis and wrote the manuscript. YW, ML and XG assisted field survey and lab work. ZW performed data analysis and reviewed the paper. HC assist the field survey. WY conceived the ideas and reviewed the manuscript.

Data accessibility statement

All sequences used in this study have been submitted to GenBank database. Accession numbers were listed in supplementary file Table S1.

Funding information

This study supported by Strategic Priority Research Program of the Chinese Academy of Sciences (XDB31030000), National Natural Science Foundation of China (Grant No. 31600341), Key Special Project for Introduced Talents Team of Southern Marine

Science and Engineering Guangdong Laboratory (Guangzhou) (GML2019ZD0408), the National Key R&D Program of China (grand No. 2017YFC0505802) and Chinese Forest Biodiversity Monitoring Network

Reference

Akaike, H. (1981). "Citation Classic - a New Look at the Statistical-Model Identification." Current Contents/Engineering Technology & Applied Sciences(51): 22-22.

Brunbjerg, A. K., J. Cavender-Bares and W. L. Eiserhardt "Multi-scale phylogenetic structure in coastal dune plant communities across the globe." Journal of Plant Ecology **7**: 101–114.

Cavender-Bares, J., D. D. Ackerly, D. A. Baum and F. A. Bazzaz (2004). "Phylogenetic overdispersion in Floridian oak communities." Am Nat **163**(6): 823-843.

Cavender-Bares, J., K. H. Kozak, P. V. A. Fine and S. W. Kembel (2009). "The merging of community ecology and phylogenetic biology." Ecology Letters **12**(7): 693-715.

Chai, Y., M. Yue, X. Liu, Y. Guo, M. Wang, J. Xu, C. Zhang, Y. Chen, L. Zhang and R. Zhang (2016). "Patterns of taxonomic, phylogenetic diversity during a long-term succession of forest on the Loess Plateau, China: insights into assembly process." Sci Rep **6**: 27087.

Chen, J., H. Zhang, W. Liu, J. Lian, W. Ye and W. Shen (2015). "Spatial distribution patterns of ammonia-oxidizing archaea abundance in subtropical forests at early and late successional stages." Sci Rep **5**: 16587.

Comita, L. S., M. Uriarte, J. Forero-Montana, W. J. Kress, N. G. Swenson, J. Thompson, M. N. Umana and J. K. Zimmerman (2018). "Changes in Phylogenetic Community Structure of the Seedling Layer Following Hurricane Disturbance in a Human-Impacted Tropical Forest." Forests **9**(9).

Coppi, A., L. Lazzaro, E. Ampoorter, L. Baeten, K. Verheyen and F. Selvi (2019). "Understorey phylogenetic diversity in thermophilous deciduous forests: overstorey species identity can matter more than species richness." Forest Ecosystems **6**.

Darriba, D., G. L. Taboada, R. Doallo and D. Posada (2011). "ProtTest 3: fast selection of best-fit models of protein evolution." Bioinformatics **27**(8): 1164-1165.

Ding, Y., R. G. Zang, S. G. Letcher, S. R. Liu and F. L. He (2012). "Disturbance regime changes the trait distribution, phylogenetic structure and community assembly of tropical rain forests." Oikos **121**(8): 1263-1270.

Drummond, A. J. and A. Rambaut (2007). "BEAST: Bayesian evolutionary analysis

by sampling trees." Bmc Evolutionary Biology **7**.
Dupuy, J. M. and R. L. Chazdon (2006). "Effects of vegetation cover on seedling and sapling dynamics in secondary tropical wet forests in Costa Rica." Journal of Tropical Ecology **22**: 65-76.
Edgar, R. C. (2004). "MUSCLE: multiple sequence alignment with high accuracy and high throughput." Nucleic Acids Res **32**(5): 1792-1797.
Fankhauser, C. and A. Batschauer (2016). "Shadow on the Plant: A Strategy to Exit." Cell **164**(1-2): 15-17.
Feng, G., X. Mi, W. L. Eiserhardt, G. Jin, W. Sang, Z. Lu, X. Wang, X. Li, B. Li, I. Sun, K. Ma and J. C. Svenning (2015). "Assembly of forest communities across East Asia--insights from phylogenetic community structure and species pool scaling." Sci Rep **5**: 9337.
Fortunato, A. E., R. Annunziata, M. Jaubert, J. P. Bouly and A. Falciatore (2015). "Dealing with light: the widespread and multitasking cryptochrome/photolyase family in photosynthetic organisms." J Plant Physiol **172**: 42-54.
Galvao, V. C. and C. Fankhauser (2015). "Sensing the light environment in plants: photoreceptors and early signaling steps." Curr Opin Neurobiol **34**: 46-53.
Gerhold, P., J. F. Cahill, M. Winter, I. V. Bartish and A. Prinzing (2015). "Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better)." Functional Ecology **29**: 600-614.
Heckenhauer, J., K. Abu Salim, M. W. Chase, K. G. Dexter, R. T. Pennington, S. Tan, M. E. Kaye and R. Samuel (2017). "Plant DNA barcodes and assessment of phylogenetic community structure of a tropical mixed dipterocarp forest in Brunei Darussalam (Borneo)." PLoS One **12**(10): e0185861.
Jin, Y., H. Qian and M. Yu (2015). "Phylogenetic Structure of Tree Species across Different Life Stages from Seedlings to Canopy Trees in a Subtropical Evergreen Broad-Leaved Forest." PLoS One **10**(6): e0131162.
Kembel, S. W., P. D. Cowan, M. R. Helmus, W. K. Cornwell, H. Morlon, D. D. Ackerly, S. P. Blomberg and C. O. Webb (2010). "Picante: R tools for integrating phylogenies and ecology." Bioinformatics **26**(11): 1463-1464.
Kraft, N. J., W. K. Cornwell, C. O. Webb and D. D. Ackerly (2007). "Trait evolution, community assembly, and the phylogenetic structure of ecological communities." Am Nat **170**(2): 271-283.
Kraft, N. J. B., P. B. Adler, O. Godoy, E. C. James, S. Fuller and J. M. Levine (2015). "Community assembly, coexistence and the environmental filtering metaphor." Functional Ecology **29**: 592– 599.
Kress, W. J., D. L. Erickson, F. A. Jones, N. G. Swenson, R. Perez, O. Sanjur and E. Bermingham (2009). "Plant DNA barcodes and a community phylogeny of a tropical forest dynamics plot in Panama." Proceedings of the National Academy of Sciences of the United States of America **106**(44): 18621-18626.
Letcher, S. G. (2010). "Phylogenetic structure of angiosperm communities during tropical forest succession." Proc Biol Sci **277**(1678): 97-104.
Letcher, S. G., R. L. Chazdon, A. C. S. Andrade, F. Bongers and M. van Breugel (2012). "Phylogenetic community structure during succession: evidence from three

neotropical forest sites." Perspectives in Plant Ecology, Evolution and Systematics **14**: 79–87.

Lian, J. Y., C. Chen, Z. L. Huang, H. L. Cao and W. H. Ye (2015). "Community Composition and Stand Age in a Subtropical Forest, Southern China." Biodiversity Science **23**(2): 174-182.

Liu, B., H. Y. H. Chen and J. Yang (2018). "Understory Community Assembly Following Wildfire in Boreal Forests: Shift From Stochasticity to Competitive Exclusion and Environmental Filtering." Front Plant Sci **9**: 1854.

Mayfield, M. M. and J. M. Levine (2010). "Opposing effects of competitive exclusion on the phylogenetic structure of communities." Ecol Lett **13**(9): 1085-1093.

McClung, C. R. (2006). "Plant circadian rhythms." Plant Cell **18**(4): 792-803.

Mei, Q. and V. Dvornyk (2015). "Evolutionary History of the Photolyase/Cryptochrome Superfamily in Eukaryotes." PLoS One **10**(9): e0135940.

Mo, X. X., L. L. Shi, Y. J. Zhang, H. Zhu and J. W. Slik (2013). "Change in phylogenetic community structure during succession of traditionally managed tropical rainforest in southwest China." PLoS One **8**(7): e71464.

Muellner-Riehl, A. N., A. Weeks, J. W. Clayton, S. Buerki, L. Nauheimer, Y. C. Chiang, S. Cody and S. K. Pell (2016). "Molecular phylogenetics and molecular clock dating of Sapindales based on plastid rbcL, atpB and trnL-trnF DNA sequences." Taxon **65**(5): 1019-1036.

Muscarella, R., M. Uriarte, D. L. Erickson, N. G. Swenson, J. K. Zimmerman and W. J. Kress (2014). "A well-resolved phylogeny of the trees of Puerto Rico based on DNA barcode sequence data." PLoS One **9**(11): e112843.

Ouyang, X. J., W. H. Ye, M. Hockings, C. L. Luk and Z. L. Huang (2013). "Developing phase of China's system of nature reserves in perspective." Forest Science Practice **15**: 340-348.

Pei, N. C., J. Y. Lian, D. L. Erickson, N. G. Swenson, W. J. Kress, W. H. Ye and X. J. Ge (2011). "Exploring Tree-Habitat Associations in a Chinese Subtropical Forest Plot Using a Molecular Phylogeny Generated from DNA Barcode Loci." Plos One **6**(6).

Prescott, C. E. (2002). "The influence of the forest canopy on nutrient cycling." Tree Physiol **22**(15-16): 1193-1200.

Purschke, O., B. C. Schmid, M. T. Sykes, P. Poschlod, S. G. Michalski, W. Durka, I. Kuhn, M. Winter and H. C. Prentice (2013). "Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: insights into assembly processes." Journal of Ecology **101**(4): 857-866.

Qian, H. and L. Jiang (2014). "Phylogenetic community ecology: Integrating community ecology and evolutionary biology." Journal of Plant Ecology **7**: 97–100.

Ruban, A. V. (2009). "Plants in light." Commun Integr Biol **2**(1): 50-55.

Saito, S. (2002). "Effects of a severe typhoon on forest dynamics in a warm-temperate evergreen broad-leaved forest in Southwestern Japan." Journal of Forest Research **7**: 137–143.

Sercu, B. K., L. Baeten, F. van Coillie, A. Martel, L. Lens, K. Verheyen and D. Bonte (2017). "How tree species identity and diversity affect light transmittance to the understory in mature temperate forests." Ecol Evol **7**(24): 10861-10870.

Shapcott, A., P. I. Forster, G. P. Guymer, W. J. McDonald, D. P. Faith, D. Erickson and W. J. Kress (2015). "Mapping biodiversity and setting conservation priorities for SE Queensland's rainforests using DNA barcoding." PLoS One **10**(3): e0122164.

Singer, D., A. Kosakyan, C. V. W. Seppey, A. Pillonel, L. D. Fernandez, D. Fontaneto, E. A. D. Mitchell and E. Lara (2018). "Environmental filtering and phylogenetic clustering correlate with the distribution patterns of cryptic protist species." Ecology **99**(4): 904-914.

Somers, D. E., P. F. Devlin and S. A. Kay (1998). "Phytochromes and cryptochromes in the entrainment of the Arabidopsis circadian clock." Science **282**(5393): 1488-1490.

Sui, D. D., Y. Wang, J. Y. Lian, J. Zhang, J. B. Hu, X. Y. Ouyang, Z. J. Fan, H. L. Cao and W. H. Ye (2017). "Gap distribution patterns in the south subtropical evergreen broad-leaved forest of Dinghushan." Biodiversity Science **25**: 382-392.

Tang, H. and R. Dubayah (2017). "Light-driven growth in Amazon evergreen forests explained by seasonal variations of vertical canopy structure." Proc Natl Acad Sci U S A **114**(10): 2640-2644.

Team, R. D. C. (2009). R: A Language and Environment for Statistical Computing. Vienna, Austria, R Foundation for Statistical Computing.

Thery, M. (2001). "Forest light and its influence on habitat selection." Plant Ecology **153**(1-2): 251-261.

Trewavas, A. (2017). "The foundations of plant intelligence." Interface Focus **7**(3): 20160098.

Vellend, M. (2010). "Conceptual synthesis in community ecology." Q Rev Biol **85**(2): 183-206.

Wagner, S., H. Fischer and F. Huth (2011). "Canopy effects on vegetation caused by harvesting and regeneration treatments." European Journal of Forest Research **130**: 17–40.

Webb, C. O., D. D. Ackerly and S. W. Kembel (2008). "Phylocom: software for the analysis of phylogenetic community structure and trait evolution." Bioinformatics **24**(18): 2098-2100.

Webb, C. O., D. D. Ackerly and M. A. McPeek (2002). "Phylogenies and community ecology." Annual Review of Ecology and Systematics **33**: 475–505.

Webb, C. O., J. B. Losos and A. A. Agrawal (2006). "Integrating phylogenies into community ecology." Ecology **87**(7): S1-S2.

Whitfeld, T. J. S., W. J. Kress, D. L. Erickson and G. D. Weiblen (2012). "Change in community phylogenetic structure during tropical forest succession: evidence from New Guinea." Ecography **35**: 821–830.

Wikstrom, N., V. Savolainen and M. W. Chase (2001). "Evolution of the angiosperms: calibrating the family tree." Proceedings of the Royal Society B-Biological Sciences **268**(1482): 2211-2220.

Zhang, T. and K. M. Folta (2012). "Green light signaling and adaptive response."

Plant Signal Behav **7**(1): 75-78.