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Environmental variation drives continental-scale synchrony of European beech reproduction

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Abstract

Spatial synchrony is the tendency of spatially separated populations to display similar temporal fluctuations. Synchrony affects regional ecosystem functioning, but it remains difficult to disentangle its underlying mechanisms. We leveraged regression on distance matrices and geography of synchrony to understand the processes driving synchrony of European beech masting over the European continent. Masting in beech shows distance-decay, but significant synchrony is maintained at spatial scales of up to 1500 km. The spatial synchrony of the weather cues that drive interannual variation in reproduction also explains the regional spatial synchrony of masting. Proximity played no apparent role in influencing beech masting synchrony after controlling for synchrony in environmental variation. Synchrony of beech reproduction shows a clear biogeographical pattern, decreasing from the northwest to southeast Europe. Synchrony networks for weather cues resemble networks for beech masting, indicating that the geographical structure of weather synchrony underlies the biogeography of masting synchrony. Our results support the hypothesis that environmental factors, the Moran effect, are key drivers of spatial synchrony in beech seed production at regional scales. The geographical patterns of regional synchronization of masting have implications for regional forest production, gene flow, carbon cycling, disease dynamics, biodiversity, and conservation.

Key words: geography of synchrony, mast seeding, Moran effect, network analysis, regression on distance matrices, plant reproduction, seed production, spatial synchrony,

Introduction

Spatial synchrony in ecology is the tendency of disjunct populations to display coincident changes in time-varying system state (Liebhold *et al.* 2004). Synchrony affects regional ecosystem functioning and results in large-scale outbreaks (Bjørnstad *et al.* 2002), shortages (Ostfeld & Keesing 2000), or extinctions (Earn *et al.* 2000). Synchrony is thought to arise from three mechanisms acting alone or in combination: dispersal between populations, correlated fluctuations in environmental drivers of population dynamics (Moran effect), and interactions with synchronized or mobile species (Liebhold *et al.* 2004; Lee *et al.* 2020; Walter *et al.* 2021). However, despite the pervasiveness of spatial synchrony in population dynamics in virtually every taxon, it remains difficult to disentangle its underlying mechanisms.

One ecological phenomenon with impressive scale of spatial synchrony and large socio-ecological importance is mast seeding (Koenig & Knops 2000). Masting is synchronous, annually variable seed production by plant populations (Silvertown 1980; Kelly 1994; Pearse *et al.* 2016). This is a phenomenon that occurs on all continents, and the spatial scale of synchrony of masting often encompasses entire species ranges (Sakai 2002; Norden *et al.* 2007; Ascoli *et al.* 2017b; Chechina & Hamann 2019). The variable allocation of resources associated with masting affects plant growth, the population dynamics of plants and animals, carbon stocks, and disease risk (Hackett-Pain *et al.* 2018; Ostfeld *et al.* 2018; Clark *et al.* 2019). Thus, understanding the drivers of masting synchrony can enable the prediction of widespread masting events and their ecological consequences, and indicate whether spatial synchrony may strengthen or weaken as a consequence of global changes.

Theory suggests two drivers of spatial synchrony in masting: regionally correlated weather variation (Fernández-Martínez *et al.* 2017; LaMontagne *et al.* 2020) and pollen dispersal (Satake & Iwasa 2002a, b). Weather has been recognized as a potentially important driver of spatial synchrony of plant reproduction due to patterns of spatial autocorrelation in temperature or rainfall similar to those exhibited by seed production (Koenig & Knops 2000; Kelly & Sork 2002). The Moran effect can synchronize masting by affecting resource acquisition, flower production, or fruit maturation (Liebhold *et al.* 2004; Bogdziewicz *et al.* 2020a). Independently, pollen dispersal has the potential to drive synchrony by means of phase-locking among populations of wind-pollinated species far more distant than the direct pollen exchange between plants (Satake & Iwasa 2002a). However, due to the scale at which synchrony of masting is observed, it is notoriously difficult to test which of these processes prevail.

We address this question using half century-long (1954 – 2014) datasets of seed production from across the range of a major European forest-forming species, European beech (*Fagus sylvatica*) (Appendix S1: Fig. S1). Annual variation in seed production in European beech correlates with a cold and wet weather in summer two years prior seedfall (Vacchiano *et al.* 2017). Hot and dry summers that follow the cold and wet summers lead to mast years (Vacchiano *et al.* 2017). High precipitation during flowering in spring correlates negatively with seedfall in autumn, possibly by interfering with pollination (Kasprzyk *et al.* 2014; Mund *et al.* 2020). Alongside weather variation, pollen limitation was repeatedly identified as an important driver of reproductive dynamics in masting species, including in European beech (Abe *et al.* 2016; Bogdziewicz *et al.* 2020b). Pollen dispersal distance is often fat-tailed and can potentially reach populations separated by hundreds of kilometres (Belmonte *et al.* 2008; Oddou-Muratorio *et al.* 2010), but even localized pollen transfer has the potential to induce long-distance reproductive synchronization (Satake & Iwasa 2002a). Thus, weather variation and pollen dispersal are the processes that can be responsible for observed synchronization of beech reproduction over vast distances (Ascoli *et al.* 2017b; Vacchiano *et al.* 2017). We use matrix regressions to isolate these effects. Matrix regressions provide a tool for isolating the drivers of population synchrony in that the effects of environmental forcing can be disentangled from non-environmental spatial processes, such as pollen dispersal (Haynes *et al.* 2013; Walter *et al.* 2017). Moreover, we use graph theory and network analyses to map spatial variation in synchrony of beech reproduction and link it with geography of synchrony in climate (Walter *et al.* 2017). The geography of synchrony approach builds a spatial network of sites, which are connected to other sites based on their degree of synchrony. Site-level measures incorporate information on all the synchronous interactions with other sites, creating a single measure which can be related directly to environmental and spatial gradients (Walter *et al.* 2017).

Methods

Data collection and materials

Seed production data. We used a long-term, continental-scale dataset of masting time series for European beech (MASTREE, Ascoli *et al.* 2017a). We extracted all records for annual production of beech seeds. We excluded records of annual flower or pollen production, or tree-ring-based mast year reconstructions. MASTREE contains ordinal and continuous time-series, but all records are also associated with a five-point ordinal measurement of masting intensity

(ORDindex), ranging from 1 (very poor masting) to 5 (very abundant masting). To obtain long masting series with a minimum number of missing years, individual masting series were aggregated into chronologies associated with NUTS-1 regions (Nomenclature of Territorial Units for Statistics version 2013). Data that could not be associated with an individual NUTS-1 region were excluded. Following the method described by Vacchiano et al (2017) and Ascoli et al (2017b), we aggregated records using the most frequently observed masting class (i.e. ORDindex) for each year. The highest masting class was used in the case of multi-modality. Analysis focused on the period 1954-2014, and NUTS-1 chronologies contained between 1 and 61 years of observations within this period. NUTS-1 chronologies with <5 observations were excluded from subsequent analysis, leaving 53 NUTS-1 (hereafter, sites) regional chronologies for this analysis, maximum distance between NUTS-1 equalled 2286.6 km. This sample size was chosen as a trade-off between the need for robustness and data inclusion.

Weather data. Weather time series for 1954-2014 were obtained for each NUTS-1 from the gridded CRU TS 3.23 database (Harris *et al.* 2014). We averaged monthly mean maximum daily temperature and monthly total precipitation for all gridcells within each NUTS-1.

Analysis of drivers of spatial synchrony in beech reproduction. To isolate the influences of weather and spatial proximity on the spatial synchrony of beech masting, we performed multiple regression on resemblance (or distance) matrices (MRMs) (Lichstein 2007; Haynes *et al.* 2013; Walter *et al.* 2017). This technique is an extension of the partial Mantel test, a procedure for determining the partial correlation between two distance or resemblance matrices while controlling for the influence of a third matrix. MRM is used to examine relationships between a dependent distance or resemblance matrix and any number of explanatory distance or resemblance matrices (Haynes *et al.* 2013). By using explanatory matrices for both spatial proximity and any measures of environmental similarity, variance in the dependent matrix can be partitioned into environmental or spatial sources. Significance of spatial proximity as a factor affecting synchrony after controlling for effects of environmental variation is interpreted as indicator of among-population dispersal (i.e. pollen dispersal) acting as potential synchronizing driver (Haynes *et al.* 2013).

To carry out the MRM, we created resemblance matrices where the elements were the similarities (synchrony in seed production and weather, and spatial distance) for all pair-wise

combinations of locations. Similarities were calculated as the Spearman pairwise correlation coefficients between masting and weather time series with at least 5 years of overlap. Spatial distance values were converted to indices of similarity by the formula $[1 - (\text{measure of distance} / \text{maximum distance})]$ (Haynes et al. 2013). We included environmental variables in the MRM models that correspond to key stages of the beech reproductive cycle: monthly mean daily maximum temperature and monthly total precipitation in summer (June - July), in spring (April - May), and during the growing seasons (May - August) (Vacchiano *et al.* 2017; Nussbaumer *et al.* 2018). To avoid including collinear covariates into the models (e.g. rainfall and temperature during summer), we combined weather variables that were based on the same time windows into principal components using principal component analysis (PCA) with varimax rotation (Appendix S1: Table S1). The data used in the PCA were the site-specific values of each weather variable in each year from 1954 to 2014. We then used the PCA scores to calculate resemblance matrices for environment across sites (Haynes *et al.* 2013).

Following Lichstein (2007) and Haynes *et al.* (2013), we investigated the roles of environmental versus spatial factors by fitting a ‘space model’, an ‘environment model’ and a ‘combined model’. The only explanatory matrix in the space model was spatial proximity. The environment model included the explanatory matrices for synchrony in weather (as listed above). The combined model included all of the explanatory matrices. The statistical significance of each explanatory matrix was determined by a permutation procedure appropriate for spatially structured data, whereby each observed regression coefficient was compared with a distribution of coefficients generated from 10000 permutations of the dependent matrix (Lichstein 2007). The MRM procedure was carried out using the *ecodist* package (Goslee & Urban 2007) in R. We visualized spatial synchrony of seed production and weather variables using Mantel correlograms.

Biogeography of synchrony. To explore geographical gradients in beech masting synchrony, we constructed separate, spatially-explicit synchrony networks of beech masting and weather, whereby sites were nodes and their pair-wise, long-term synchrony in masting or summer (June-July) weather PCA scores represented weighted edges. We used summer weather following the results of the MRM analysis (see Results). Between-site synchronies (edge weights) were similarity indices calculated using the formula $1 - (\text{dissimilarity measure between site } i \text{ and } j) / (\text{maximum dissimilarity})$, with dissimilarity measures being Euclidean distances calculated based on pair-wise Spearman correlation matrices of masting or summer (June-July) weather time

series with at least 5 years of overlap. Next, we assessed spatial patterns of masting synchrony across Europe using Generalised Linear Models (GLMs) with beta distribution and logit link, including site-level mean synchrony (of either masting or weather) as a response and sites' latitude, longitude, and their interaction fitted as natural cubic splines as explanatory terms. The response was normalised as $y_i = (y_i + 1)/2$. Models were fitted using R version 3.5.1 and *glmmTMB* package (Brooks *et al.* 2017). Because we detected a clear geographical gradient in beech masting synchrony (see Results), we performed community delineation analysis on the beech masting synchrony network, to assess whether it consisted of subgroups incorporating sites well-synchronized with each other, and less well synchronized with sites from different subgroups. To find the community structure, we used the fast greedy modularity optimization algorithm, which identifies communities by optimizing a modularity score (i.e., the number of edges falling within groups minus the expected number if edges were randomly distributed), providing a measure of the strength of the partition of a network into distinct modules (Clauset *et al.* 2004; Newman 2006). Community delineation was performed using *igraph* in R (Csardi & Nepusz 2006).

We tested whether the beech masting synchrony network follows the weather synchrony network using the multiple regression quadratic assignment procedure (MRQAP). The MRQAP is a modelling framework allowing investigation of the relationship between a dependent matrix and independent matrices, while considering the non-independence of network data by using permutation techniques to test the significance of effect sizes (Dekker *et al.* 2007). We fitted MRQAP model with the beech masting synchrony matrix (pair-wise similarity indices of seed production) as a dependent variable and the weather matrix (pair-wise similarity indices of weather PCA scores) as an explanatory term, and used the double-semi-partialling technique to perform permutations (Dekker *et al.* 2007). The model was fitted using the *asnipe* R package and statistical significance was assessed based on t-statistics and 1000 permutations (Farine 2013).

We tested whether the site-level synchrony of beech masting and weather are associated with the long-term mean values of our weather variables, i.e. long-term mean summer temperature and mean summer precipitation. We used GLMs with beta distribution and logit link, with either mean synchrony of masting or synchrony of summer temperature as a response, and average (1954-2014), site-level summer (June-July) temperature or precipitation as the explanatory term. We considered linear and quadratic effects. Since both predictors were correlated (Pearson's $r = -$

0.41, $t = -3.28$, $p = 0.002$), we tested for their effects in separate models and performed model selection following information-theoretic approach based on Akaike Information Criterion.

Results

Mean spatial synchrony in beech masting across all sites was significantly greater than zero (mean Spearman rank correlation and 95% CI: 0.32, 0.25 – 0.41). Weather PCA scores were slightly more synchronous than masting: summer weather (0.49, 95% CI 0.41 – 0.57), spring weather (0.44, 95% CI 0.37 – 0.51), growing season weather (0.48, 95% CI 0.41 – 0.54). The synchrony of masting and weather regressed to zero at distances ~ 1500 km (Fig. 1).

The MRM indicated spatial synchrony variation in weather as the main driver of spatial synchrony of beech mast seeding. In the space model, we detected a significant positive relationship between spatial proximity and synchrony (Appendix S1: Table S2). That model explained 11.5 % of the variance in the pair-wise synchrony of masting. The environment model explained about three times more variation in the masting synchrony as the space model (37.0%). In the environmental model, the only significant predictor of masting synchrony was synchrony in the summer weather (Appendix S1: Table S2), although growing season weather approached significance with $p = 0.07$. The combined model (space and environment) explained the same variance as the environment model (37.2%). Although proximity was a significant predictor of the synchrony of masting in the space model, proximity did not have a significant effect in the combined model. As in the environment model, masting synchrony in the combined model was significantly explained by synchrony in summer and, to a limited degree, by synchrony of growing season weather (Appendix S1: Table S2).

Network analysis revealed a clear biogeographical pattern in beech masting synchrony that decreased from the northwest to southeast Europe (Fig. 2, Appendix S1: Table S3). Fast greedy optimisation based on masting synchrony grouped sites into two clusters corresponding to the biogeographical gradient described above (Fig. 3) – highly synchronized northwest (mean within cluster synchrony = 0.57, 95%CI: 0.54–0.61, $n = 30$ sites) and poorly synchronised southeast (mean = 0.25, 95%CI: 0.21–0.29, $n = 23$ sites). The geographical pattern in masting synchrony corresponded to a matching pattern of synchrony of weather cues (Fig. 2, Appendix S1: Table S3). The resemblance of masting and weather synchrony maps indicate the key role of the Moran effect in driving the regional patterns of masting synchrony (Walter *et al.* 2017). Regressing the network of beech masting synchrony on the network of summer weather using the MRQAP indicated that

weather explains 41% of variation in biogeography of beech mast seeding synchrony ($\beta = 0.69$, $p < 0.001$). Among-sites synchronization of seed production was higher at warmer sites, but this reversed for sites with long-term mean temperatures above $\sim 20.5^{\circ}\text{C}$ (Fig. 4, Appendix S1: Table S4A). A relationship with similar curvature was observed between synchrony of weather cues and the local climate (Fig. 4, Appendix S1: Table S4B). The parallel relationships of weather and masting synchrony with local climate suggests that climate at particular sites shapes their weather synchronization with other sites, which in turn determines each site synchronization of seed production.

Discussion

Environmental variation drives regional (~ 1500 km) synchrony of seed production in European beech. Both exogenous factors, like environmental conditions, and endogenous factors, like flower abscission and pollination, have been considered as drivers of spatial synchrony in models of proximate drivers of masting (Satake & Iwasa 2002a; Lyles *et al.* 2015; Noble *et al.* 2018; Schermer *et al.* 2019). Depending on specific assumptions, these theoretical models may require some form of coupling of seed production of nearby plants to create synchrony (e.g. pollen coupling), alongside the effect of correlated environmental fluctuations (Satake & Iwasa 2002a; Noble *et al.* 2018; Bogdziewicz *et al.* 2020d). In our MRM analysis, proximity played no apparent role in influencing beech masting synchrony after controlling for synchrony in environmental variation. Lack of spatial proximity effects on masting synchrony after controlling for effects of environmental variation implies that among-population dispersal is not acting as potential synchronizing driver in the system (Haynes *et al.* 2013). This implies that pollen dispersal is not an important synchronising agent of beech masting synchrony at regional scales, and that the synchrony in weather is a main driver of spatial synchrony of beech seed production over the species range.

Similarly to our results, past studies on masting synchrony in other species employing MRM models found little evidence for non-environmental spatial process playing a significant role in synchronizing masting at regional scales. In California oaks, regional synchrony of acorn production appears to be driven by synchrony in annual rainfall (Koenig *et al.* 2017). Similarly, MRM models indicated that continental synchrony in white spruce masting is driven by synchrony in summer temperatures (LaMontagne *et al.* 2020), while synchrony in piñon pine masting by synchrony in drought (Wion *et al.* 2020). This limited pool of studies conducted so far point that

the role of pollen dispersal in regional synchronization of masting appears negligible. Potentially, pollen dispersal may be more important for synchronization of masting at local scales as effective pollen transfer is mostly localized (Sork *et al.* 2002; Chybicki & Burczyk 2010; Oddou-Muratorio *et al.* 2010). Whether synchrony in masting is due to the Moran effect or pollen coupling is difficult to determine, because both hypotheses generate similar patterns of spatial synchrony and are not mutually exclusive (Koenig & Knops 2013). The results presented here appear to lend further support against the hypothesis that dispersal plays an important role in synchronizing masting at regional scales.

The key role of environmental variation as a driver of regional patterns in masting synchrony is further supported by the geography of synchrony analysis. Network analysis indicated that spatial patterns in the synchrony of weather underlie the geography of synchrony of beech masting over the European continent. The northwest-southeast gradient in beech masting synchrony matched synchrony network of summer weather, providing exceptional evidence for the role of environmental variation as a driver of regional synchronization of forests reproduction (Walter *et al.* 2017). Moreover, the relationship between synchrony of both weather and masting was non-linearly related to local climate, which may drive the divergence in beech masting synchrony between colder northwest and warmer southeast Europe. The non-linear relationship between local climate and sites synchronization indicates that climate warming may induce changes in the spatial synchrony of weather cues that will translate to changes in regional synchronization of masting – as already shown for other ecological phenomena (Koenig & Liebhold 2016; Sheppard *et al.* 2016; Shestakova *et al.* 2016; Manzanedo *et al.* 2020). If the lower synchrony in the southeast is due to warmer mean temperature in the southeast, then warming climate has the potential to increase the synchrony of both weather and trees seed production, but this will reverse once a tipping point of ~ 20.5 °C is passed. Under such scenario, we can expect further declines in masting synchrony in the already poorly synchronized southeast, and that synchrony in northwest will eventually decline as warming continues.

The northwest-southeast gradient in weather and masting synchrony was related to local climate, but also resembles the northwest to southeast gradient of correlation between summer temperatures and the Summer North Atlantic Oscillation (SNAO). SNAO is a major large-scale climate mode influencing both weather and masting patterns in the European Atlantic region (Folland *et al.* 2009; Bladé *et al.* 2012; Ascoli *et al.* 2017b). The geographical divide that SNAO exerts on summer temperatures along a ridge extending from 45°N-3°W to 50°N-26°E parallels

the borderline between positive to negative synchrony in both weather and masting revealed by our network analysis (Folland *et al.* 2009; Bladé *et al.* 2012). The influence of the Atlantic climate circulation, coupled with the relatively homogeneous geomorphology in northwest Europe, could be an important environmental feature for beech masting synchronization in this region. In contrast, in the southeast region SNAO loses the role of weather synchronizer, while multiple interacting climate modes (Zhu *et al.* 2017; Barcikowska *et al.* 2020), and the complex geomorphology (water bodies, mountain ranges), diversify local weather patterns through space and time (Casanueva *et al.* 2014; Sun *et al.* 2019), decreasing beech masting synchronization.

While the mechanisms driving the northwest-southeast gradient in weather synchrony remain to be established, the ecological consequences of such gradient for beech forests are diverse and potentially great. The highly synchronized northwest is characterized by regional boom-and-bust masting dynamics with taxonomically and ecologically diverse consequences for community dynamics (Ostfeld & Keesing 2000; Bogdziewicz *et al.* 2016). In contrast, at poorly synchronized southeast, each site maintains its own schedule of high and low seed years. From a forest regeneration perspective, lowered regional synchrony can influence recruitment by disrupting the satiation mechanism for mobile seed predators (Curran & Leighton 2000). High synchrony in northwest Europe can also allow higher gene flow across sites of that region compared to southeast, contributing to homogeneous genetic structure of beech populations in the north compared to the south (Magri *et al.* 2006; Kremer *et al.* 2012). Other consequences of desynchronization involves a reduced ability to produce regional mast forecasts for planning of natural forest regeneration, and regional risk forecasts for Lyme disease and hantavirus by rodents dependent on beech seeds (Ostfeld *et al.* 2018; Bregnard *et al.* 2020).

A limitation of our study is that it was based on ordinal rather than continuous seed production data. However, the rapid accumulation of long-term data on plant reproduction promise further improvements that will allow us to better understand the spatiotemporal patterns of seed production and to hint at processes that may govern those patterns (Fernández-Martínez *et al.* 2019; Pearse *et al.* 2020; Pesendorfer *et al.* 2020; Clark *et al.* 2021). These datasets already indicate changes in masting intensity and synchrony that are possibly related to climatic change (Redmond *et al.* 2012; Bogdziewicz *et al.* 2020c; Shibata *et al.* 2020; Hackett-Pain & Bogdziewicz 2021). In that context, our study warns that as the climate changes so will regional synchronization of masting (Hansen *et al.* 2020; Bogdziewicz *et al.* 2020c), which will have implications for

regional forest production, carbon cycling, disease dynamics, evolutionary dynamics, and conservation (Elliott & Kemp 2016; Vacchiano *et al.* 2018; Bogdziewicz *et al.* 2020b).

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Literature

Abe, T., Tachiki, Y., Kon, H., Nagasaka, A., Onodera, K., Minamino, K., *et al.* (2016).

Parameterisation and validation of a resource budget model for masting using spatiotemporal flowering data of individual trees. *Ecology Letters*, 19, 1129–1139.

Ascoli, D., Maringer, J., Hacket-Pain, A., Conedera, M., Drobyshev, I., Motta, R., *et al.* (2017a). Two centuries of masting data for European beech and Norway spruce across the European continent. *Ecology*, 98, 1473-1473

Ascoli, D., Vacchiano, G., Turco, M., Conedera, M., Drobyshev, I., Maringer, J., *et al.* (2017b). Inter-annual and decadal changes in teleconnections drive continental-scale synchronization of tree reproduction. *Nature Communications*, 8, 2205.

Barcikowska, M.J., Kapnick, S.B., Krishnamurty, L., Russo, S., Cherchi, A. & Folland, C.K. (2020). Changes in the future summer Mediterranean climate: contribution of teleconnections and local factors. *Earth System Dynamics*, 11, 161–181.

Belmonte, J., Alarcón, M., Avila, A., Scialabba, E. & Pino, D. (2008). Long-range transport of beech (*Fagus sylvatica* L.) pollen to Catalonia (north-eastern Spain). *Int J Biometeorol*, 52, 675–687.

Bjørnstad, O.N., Peltonen, M., Liebhold, A.M. & Baltensweiler, W. (2002). Waves of larch budmoth outbreaks in the European Alps. *Science*, 298, 1020–1023.

Bladé, I., Liebmann, B., Fortuny, D. & van Oldenborgh, G.J. (2012). Observed and simulated impacts of the summer NAO in Europe: implications for projected drying in the Mediterranean region. *Clim Dyn*, 39, 709–727.

Bogdziewicz, M., Ascoli, D., Hacket-Pain, A., Koenig, W.D., Pearse, I., Pesendorfer, M., *et al.* (2020a). From theory to experiments for testing the proximate mechanisms of mast seeding: an agenda for an experimental ecology. *Ecology Letters*, 23, 210–220.

Bogdziewicz, M., Kelly, D., Tanentzap, A.J., Thomas, P.A., Lageard, J.G.A. & Hacket-Pain, A. (2020b). Climate Change Strengthens Selection for Mast Seeding in European Beech. *Current Biology*, 30, 3477-3483.e2.

Bogdziewicz, M., Kelly, D., Thomas, P.A., Lageard, J.G.A. & Hacket-Pain, A. (2020c). Climate warming disrupts mast seeding and its fitness benefits in European beech. *Nature Plants*, 6, 88–94.

Bogdziewicz, M., Pesendorfer, M., Crone, E.E., Pérez-Izquierdo, C. & Bonal, R. (2020d). Flowering synchrony drives reproductive success in a wind-pollinated tree. *Ecology Letters*, 23, 1820–1826.

Bogdziewicz, M., Zwolak, R. & Crone, E.E. (2016). How do vertebrates respond to mast seeding? *Oikos*, 125, 300–307.

Bregnard, C., Rais, O. & Voordouw, M.J. (2020). Climate and tree seed production predict the abundance of the European Lyme disease vector over a 15-year period. *Parasites & Vectors*, 13, 408.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., *et al.* (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R journal*, 9, 378–400.

Casanueva, A., Rodríguez-Puebla, C., Frías, M.D. & González-Reviriego, N. (2014). Variability of extreme precipitation over Europe and its relationships with teleconnection patterns. *Hydrology and Earth System Sciences*, 18, 709–725.

Chechina, M. & Hamann, A. (2019). Climatic drivers of dipterocarp mass-flowering in South-East Asia. *Journal of Tropical Ecology*, 35, 108–117.

Chybicki, I.J. & Burczyk, J. (2010). Realized gene flow within mixed stands of *Quercus robur* L. and *Q. petraea* (Matt.) L. revealed at the stage of naturally established seedling. *Molecular Ecology*, 19, 2137–2151.

Clark, J.S., Nuñez, C.L. & Tomasek, B. (2019). Foodwebs based on unreliable foundations: spatiotemporal masting merged with consumer movement, storage, and diet. *Ecological Monographs*, 89, e01381.

Clark, J.S., Andrus, R., Aubry-Kientz, M. et al. (2021) Continent-wide tree fecundity driven by indirect climate effects. *Nature Communications* 12, 1242, <https://doi.org/10.1038/s41467-020-20836-3>

Clauset, A., Newman, M.E.J. & Moore, C. (2004). Finding community structure in very large networks. *Phys. Rev. E*, 70, 066111.

Curran, L.M. & Leighton, M. (2000). Vertebrate Responses to Spatiotemporal Variation in Seed Production of Mast-Fruiting Dipterocarpaceae. *Ecological Monographs*, 70, 101–128.

Csardi, G. & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal Complex Systems*, 1695.

Dekker, D., Krackhardt, D. & Snijders, T.A.B. (2007). Sensitivity of MRQAP Tests to Collinearity and Autocorrelation Conditions. *Psychometrika*, 72, 563–581.

Earn, D.J.D., Levin, S.A. & Rohani, P. (2000). Coherence and Conservation. *Science*, 290, 1360–1364.

Elliott, G. & Kemp, J. (2016). Large-scale pest control in New Zealand beech forests. *Ecological Management & Restoration*, 17, 200–209.

Farine, D.R. (2013). Animal social network inference and permutations for ecologists in R using asnipe. *Methods in Ecology and Evolution*, 4, 1187–1194.

Fernández-Martínez, M., Pearse, I., Sardans, J., Sayol, F., Koenig, W.D., LaMontagne, J.M., et al. (2019). Nutrient scarcity as a selective pressure for mast seeding. *Nature Plants*, 5, 1222–1228

Fernández-Martínez, M., Vicca, S., Janssens, I.A., Espelta, J.M. & Peñuelas, J. (2017). The North Atlantic Oscillation synchronises fruit production in western European forests. *Ecography*, 40, 864–874.

Folland, C.K., Knight, J., Linderholm, H.W., Fereday, D., Ineson, S. & Hurrell, J.W. (2009). The Summer North Atlantic Oscillation: Past, Present, and Future. *Journal of Climate*, 22, 1082–1103.

Goslee, S.C. & Urban, D.L. (2007). The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software*, 22, 1–19.

Hacket-Pain, A.J., Ascoli, D., Vacchiano, G., Biondi, F., Cavin, L., Conedera, M., *et al.* (2018). Climatically controlled reproduction drives interannual growth variability in a temperate tree species. *Ecology Letters*, 21, 1833–1844.

Hacket-Pain, A.J., Bogdziewicz M. (2021) Climate change and plant reproduction: trends and drivers of mast seeding change. *Philosophical Transactions of the Royal Society B*, 10.1098/rstb.2020-0379

Hansen, B.B., Grøtan, V., Herfindal, I. & Lee, A.M. (2020). The Moran effect revisited: spatial population synchrony under global warming. *Ecography*, 43, 1591-1602.

Harris, I., Jones, P.D., Osborn, T.J. & Lister, D.H. (2014). Updated high-resolution grids of monthly climatic observations – the CRU TS3.10 Dataset. *International Journal of Climatology*, 34, 623–642.

Haynes, K.J., Bjørnstad, O.N., Allstadt, A.J. & Liebhold, A.M. (2013). Geographical variation in the spatial synchrony of a forest-defoliating insect: isolation of environmental and spatial drivers. *Proceedings of the Royal Society B: Biological Sciences*, 280, 20122373.

Kasprzyk, I., Ortyl, B. & Dulaska-Jeż, A. (2014). Relationships among weather parameters, airborne pollen and seed crops of *Fagus* and *Quercus* in Poland. *Agricultural and Forest Meteorology*, 197, 111–122.

Kelly, D. (1994). The evolutionary ecology of mast seeding. *Trends in Ecology & Evolution*, 9, 465–470.

Kelly, D., Geldenhuis, A., James, A., Penelope Holland, E., Plank, M.J., Brockie, R.E., *et al.* (2013). Of mast and mean: differential-temperature cue makes mast seeding insensitive to climate change. *Ecology Letters*, 16, 90–98.

Kelly, D. & Sork, V.L. (2002). Mast seeding in perennial plants: why, how, where? *Annual Review of Ecology and Systematics*, 33, 427–447.

Koenig, W.D. & Knops, J.M.H. (2000). Patterns of Annual Seed Production by Northern Hemisphere Trees: A Global Perspective. *The American Naturalist*, 155, 59–69.

Koenig, W.D. & Knops, J.M.H. (2013). Large-scale spatial synchrony and cross-synchrony in acorn production by two California oaks. *Ecology*, 94, 83–93.

Koenig, W.D., Knops, J.M.H., Pesendorfer, M.B., Zaya, D.N. & Ashley, M.V. (2017). Drivers of synchrony of acorn production in the valley oak (*Quercus lobata*) at two spatial scales. *Ecology*, 98, 3056–3062.

Koenig, W.D. & Liebhold, A.M. (2016). Temporally increasing spatial synchrony of North American temperature and bird populations. *Nature Climate Change*, 6, 614–617.

Kremer, A., Ronce, O., Robledo-Arnuncio, J.J., Guillaume, F., Bohrer, G., Nathan, R., *et al.* (2012). Long-distance gene flow and adaptation of forest trees to rapid climate change. *Ecology Letters*, 15, 378–392.

LaMontagne, J.M., Pearse, I.S., Greene, D.F. & Koenig, W.D. (2020). Mast seeding patterns are asynchronous at a continental scale. *Nature Plants*, 6, 460–465.

Lee, A.M., Sæther, B.-E. & Engen, S. (2020). Spatial covariation of competing species in a fluctuating environment. *Ecology*, 101, e02901.

Lichstein, J.W. (2007). Multiple regression on distance matrices: a multivariate spatial analysis tool. *Plant Ecology*, 188, 117–131.

Liebhold, A., Koenig, W.D. & Bjørnstad, O.N. (2004). Spatial synchrony in population dynamics. *Annual Review of Ecology and Systematics*, 35, 467–490.

Lyles, D., Rosenstock, T.S. & Hastings, A. (2015). Plant reproduction and environmental noise: How do plants do it? *Journal of Theoretical Biology*, 371, 137–144.

Magri, D., Vendramin, G.G., Comps, B., Dupanloup, I., Geburek, T., Gömöry, D., *et al.* (2006). A new scenario for the Quaternary history of European beech populations: palaeobotanical evidence and genetic consequences. *New Phytologist*, 171, 199–221.

Manzanedo, R.D., HilleRisLambers, J., Rademacher, T.T. & Pederson, N. (2020). Evidence of unprecedented rise in growth synchrony from global tree ring records. *Nature Ecology & Evolution*, 4, 1622–1629.

Mund, M., Herbst, M., Knohl, A., Matthäus, B., Schumacher, J., Schall, P., *et al.* (2020). It is not just a ‘trade-off’: indications for sink- and source-limitation to vegetative and regenerative growth in an old-growth beech forest. *New Phytologist*, 226, 111–125.

Newman, M.E.J. (2006). Modularity and community structure in networks. *PNAS*, 103, 8577–8582.

Noble, A.E., Rosenstock, T.S., Brown, P.H., Machta, J. & Hastings, A. (2018). Spatial patterns of tree yield explained by endogenous forces through a correspondence between the Ising model and ecology. *PNAS*, 115, 1825–1830.

Norden, N., Chave, J., Belbenoit, P., Caubère, A., Châtelet, P., Forget, P.-M., *et al.* (2007). Mast Fruiting Is a Frequent Strategy in Woody Species of Eastern South America. *PLOS ONE*, 2, e1079.

Nussbaumer, A., Waldner, P., Apuhtin, V., Aytar, F., Benham, S., Bussotti, F., *et al.* (2018). Impact of weather cues and resource dynamics on mast occurrence in the main forest tree species in Europe. *Forest Ecology and Management*, 429, 336–350.

Oddou-Muratorio, S., Bontemps, A., Klein, E.K., Chybicki, I., Vendramin, G.G. & Suyama, Y. (2010). Comparison of direct and indirect genetic methods for estimating seed and pollen dispersal in *Fagus sylvatica* and *Fagus crenata*. *Forest Ecology and Management*, The ecology and silviculture of beech: from gene to landscape, 259, 2151–2159.

Ostfeld, R.S. & Keesing, F. (2000). Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology & Evolution*, 15, 232–237.

Ostfeld, R.S., Levi, T., Keesing, F., Oggenfuss, K. & Canham, C.D. (2018). Tick-borne disease risk in a forest food web. *Ecology*, 99, 1562–1573.

Pearse, I.S., Koenig, W.D. & Kelly, D. (2016). Mechanisms of mast seeding: resources, weather, cues, and selection. *New Phytologist*, 212, 546–562.

Pearse, I.S., LaMontagne, J.M., Lordon, M., Hipp, A.L. & Koenig, W.D. (2020). Biogeography and phylogeny of masting: do global patterns fit functional hypotheses? *New Phytologist*, 227, 1557–1567.

- Pesendorfer, M.B., Bogdziewicz, M., Szymkowiak, J., Borowski, Z., Kantorowicz, W., Espelta, J.M., *et al.* (2020). Investigating the relationship between climate, stand age, and temporal trends in masting behavior of European forest trees. *Global Change Biology*, 26, 1654–1667.
- Redmond, M.D., Forcella, F. & Barger, N.N. (2012). Declines in pinyon pine cone production associated with regional warming. *Ecosphere*, 3, art120.
- Sakai, S. (2002). General flowering in lowland mixed dipterocarp forests of South-east Asia. *Biol J Linn Soc*, 75, 233–247.
- Satake, A. & Iwasa, Y. (2002a). Spatially limited pollen exchange and a long-range synchronization of trees. *Ecology*, 83, 993–1005.
- Satake, A. & Iwasa, Y. (2002b). The Synchronized and Intermittent Reproduction of Forest Trees Is Mediated by the Moran Effect, Only in Association with Pollen Coupling. *Journal of Ecology*, 90, 830–838.
- Schermer, É., Bel-Venner, M.-C., Fouchet, D., Siberchicot, A., Boulanger, V., Caignard, T., *et al.* (2019). Pollen limitation as a main driver of fruiting dynamics in oak populations. *Ecology Letters*, 22, 98–107.
- Sheppard, L.W., Bell, J.R., Harrington, R. & Reuman, D.C. (2016). Changes in large-scale climate alter spatial synchrony of aphid pests. *Nature Climate Change*, 6, 610–613.
- Shestakova, T.A., Gutiérrez, E., Kirilyanov, A.V., Camarero, J.J., Génova, M., Knorre, A.A., *et al.* (2016). Forests synchronize their growth in contrasting Eurasian regions in response to climate warming. *PNAS*, 113, 662–667.
- Shibata, M., Masaki, T., Yagihashi, T., Shimada, T. & Saitoh, T. (2020). Decadal changes in masting behaviour of oak trees with rising temperature. *Journal of Ecology*, 108, 1088–1100.
- Silvertown, J.W. (1980). The evolutionary ecology of mast seeding in trees. *Biol J Linn Soc*, 14, 235–250.
- Sork, V.L., Davis, F.W., Smouse, P.E., Apsit, V.J., Dyer, R.J., Fernandez-M, J.F., *et al.* (2002). Pollen movement in declining populations of California Valley oak, *Quercus lobata*: where have all the fathers gone? *Mol. Ecol.*, 11, 1657–1668.

Sun, Z., Ouyang, Z., Zhang, X. & Ren, W. (2019). A new global dataset of phase synchronization of temperature and precipitation: Its climatology and contribution to global vegetation productivity. *Geoscience Data Journal*, 6, 126–136.

Vacchiano, G., Ascoli, D., Berzaghi, F., Lucas-Borja, M.E., Caignard, T., Collalti, A., *et al.* (2018). Reproducing reproduction: How to simulate mast seeding in forest models. *Ecological Modelling*, 376, 40–53.

Vacchiano, G., Hackett-Pain, A., Turco, M., Motta, R., Maringer, J., Conedera, M., *et al.* (2017). Spatial patterns and broad-scale weather cues of beech mast seeding in Europe. *New Phytologist*, 215, 595–608.

Walter, J.A., Hallett, L.M., Sheppard, L.W., Anderson, T.L., Zhao, L., Hobbs, R.J., *et al.* (2021). Micro-scale geography of synchrony in a serpentine plant community. *Journal of Ecology*, 109, 750–762.

Walter, J.A., Sheppard, L.W., Anderson, T.L., Kastens, J.H., Bjørnstad, O.N., Liebhold, A.M., *et al.* (2017). The geography of spatial synchrony. *Ecology Letters*, 20, 801–814.

Wion, A.P., Weisberg, P.J., Pearse, I.S. and Redmond, M.D. (2020), Aridity drives spatiotemporal patterns of masting across the latitudinal range of a dryland conifer. *Ecography*, 43: 569–580.

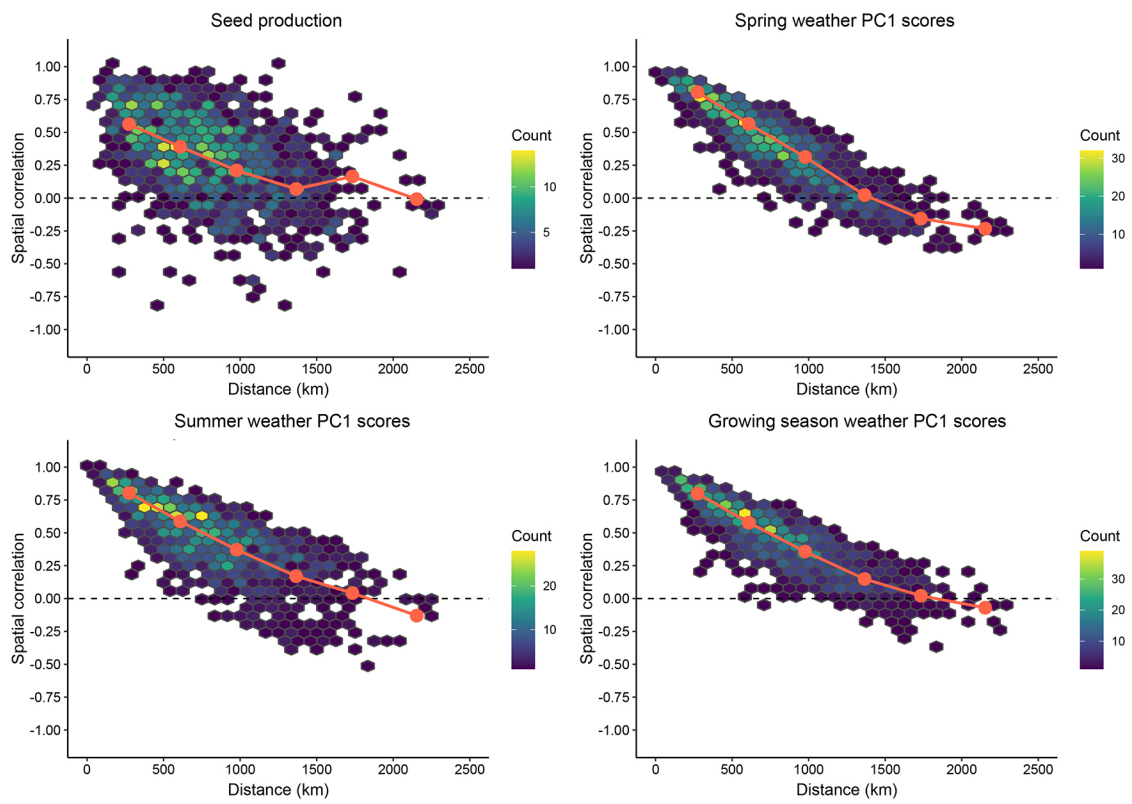
Zhu, Z., Piao, S., Xu, Y., Bastos, A., Ciais, P. & Peng, S. (2017). The effects of teleconnections on carbon fluxes of global terrestrial ecosystems. *Geophysical Research Letters*, 44, 3209–3218.

Figure 1. Spatial correlation in European beech masting and seasonal weather PCA scores. Red lines show Mantel correlograms, while hexes are pair-wise Spearman correlations between all sites. Circles indicate significant Mantel correlations. Hex colour is scaled to the number of observations within each hex.

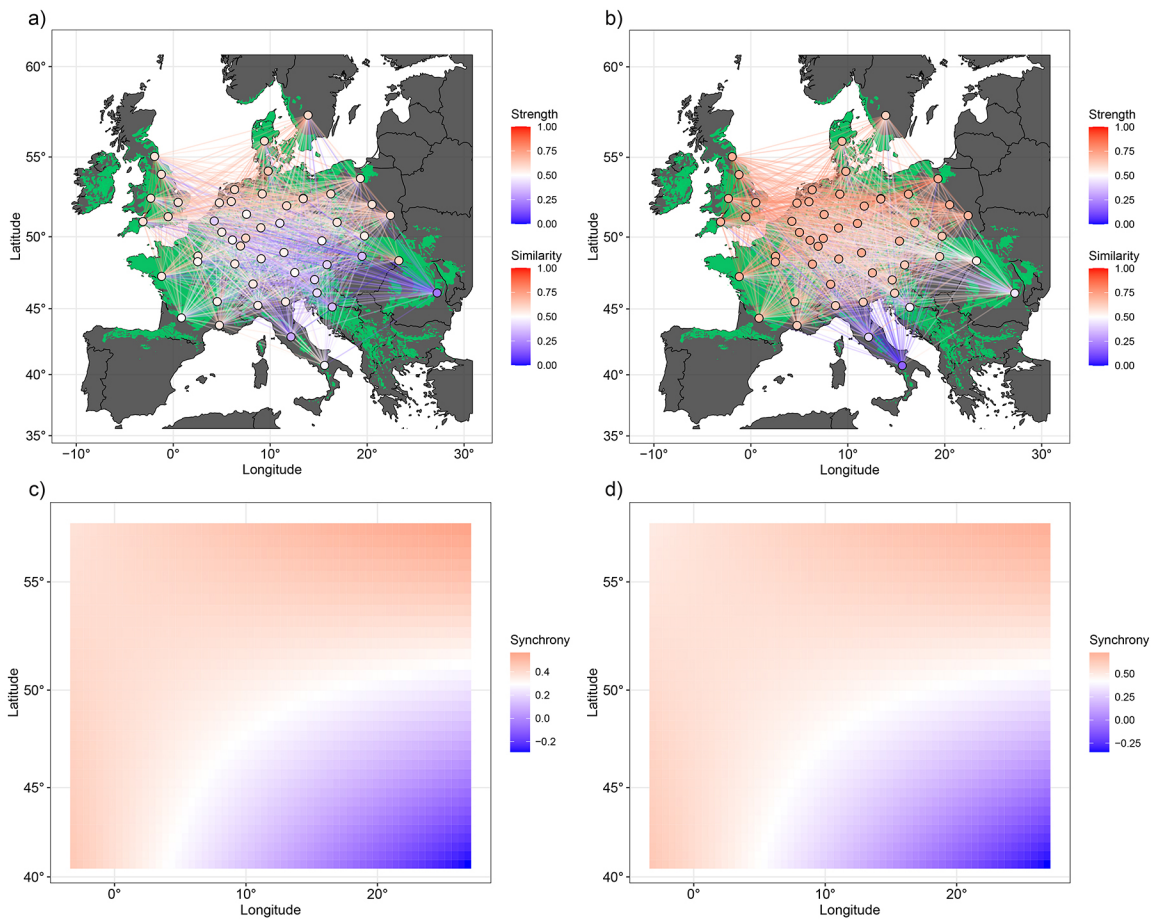
Figure 2. Geography of synchrony of beech masting and of summer weather. Maps show the site-level contributions to the synchrony network of (A) beech masting and (B) summer weather in terms of strength (points) and similarity (lines), with warmer (redder) colours indicating larger values. Network analysis based on seed production for 1954-2014, and 53 NUTS-1 regional chronologies that contained between 5 and 61 years of observations within this period. The lower panel shows modelled geographical patterns of (C) masting and (D) summer weather synchrony for European beech based on generalised models (Table S3). The circles are the 53 sites representing the 53 NUTS-1 chronologies.

Figure 3. Clusters within beech masting synchrony network delineated using the fast greedy modularity optimisation algorithm. Cluster-wide synchrony in northwest (yellow circles) Europe equalled 0.57 (95%CI: 0.54–0.61), while in southeast (blue circles) Europe it equalled 0.25 (95%CI: 0.21–0.29).

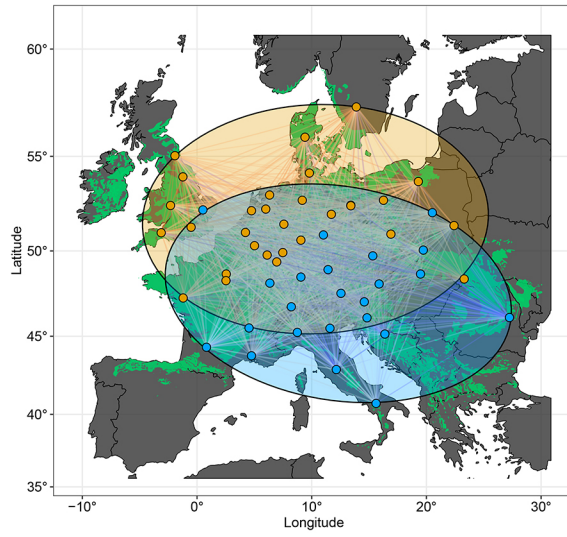
Figure 4. Synchrony of beech masting (blue points) and weather (red squares) as a function of site-level mean long-term (1954-2014) summer (June-July) maximum temperature. Points show mean synchronisation of particular sites with all other sites. The lines are based on the significant GLM predictions, while shading indicates the 95% confidence intervals.



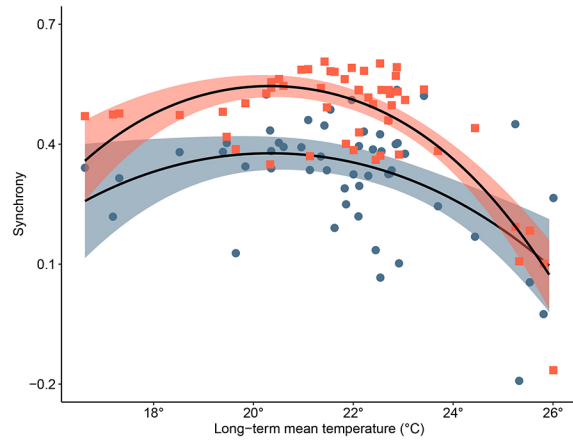
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