



Resilient forests for the future

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Abstract

Forest ecosystems are of global importance, ecologically, economically and culturally. However, despite their fundamental role in mitigating the worst effects of climate change, to date there have been surprisingly few resources devoted to defining, conserving and planning resilient forests for the future. Progress in this field of research, which requires international and interdisciplinary cooperation, collaboration and communication, was presented and discussed at the second biannual conference of the European Research Group, Evoltree (<https://www.evoltree.eu>). Over four days more than 140 scientists met to share developments and to discuss forest ecology, genetics, genomics and evolution with a focus on realising “Resilient Forests for the Future”. From examining evolutionary dynamics and using the past to understand future responses, to evaluating breeding approaches and the sustainable use of forest genetic resources, the conference addressed critical themes with relevance to this topic. The role of genomics in conservation, investigation of biotic interactions and identifying climate resilient forests were also explored. Finally, innovative methods and approaches which promise to increase the scale and speed with which forest evolutionary research can progress were introduced and evaluated. The Evoltree network and conference series provides invaluable opportunities to share knowledge and increase collaboration on forest genetic research, the need for which has never been greater or more urgent.

Keywords Genetic diversity · Local adaptation · Resilience · Selection · Forest genetics · Phenotyping

Introduction

The importance of forests cannot be overstated. They cover almost a third of the Earth’s landmass and contribute to numerous vital processes, such as habitat and nutrition for

associated species, soil formation, water regulation and timber production. Their central role in supporting biodiversity and sequestering carbon means that they are at the forefront of global efforts to mitigate the impacts of rapidly advancing climate change (CC), but ironically the threat from CC is particularly acute for these large, long-lived, immobile species (Aitken et al. 2008; Dauphin et al. 2021). Furthermore, their oft-assumed role in climate mitigation relies on healthy, well-adapted tree populations, or on the active promotion of adaptation through forest management (Muys and Messier 2023). Natural disturbance events, such as prolonged drought periods, heat waves, wind throws, as well as pest and pathogen outbreaks, are also increasing in severity and frequency as a result of CC. The concept of ‘resilience’—the capacity of forest ecosystems to recover from such perturbations while maintaining similar functioning and structure (Fig. 1)—allows researchers to quantify and track the response of forests and to assess the impact of these perturbations across spatial and temporal scales (Seidl et al. 2016; Boyd et al. 2022).

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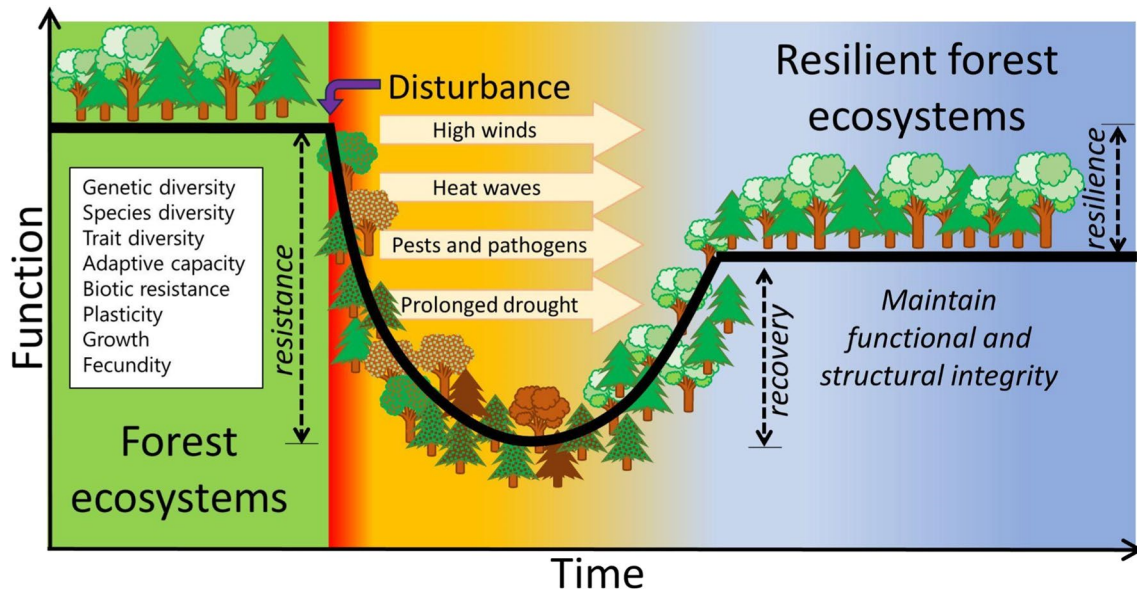


Fig. 1 Conceptualisation of resilience in forest ecosystems over time following a disturbance event, adapted from Lloret et al. (2011). The black line represents variation in a function relating to forest eco-

systems over time, with a disturbance event indicated. Examples of parameters which can be used to assess resilience in forest ecosystems are listed in the white box

The European Research Group Evoltree (<https://www.evoltree.eu>) started in 2006 with the aim of linking the research fields of ecology, genetics, genomics and evolution in a European forest context. The self-supporting network of research institutes and Universities promotes collaboration and facilitates research in these fields through the provisioning of resources, training and dissemination activities such as the here-presented Evoltree biannual conference. The first biannual conference in 2021 impressively demonstrated the progress being achieved in relation to genomic approaches and adaptation in forest ecosystems, highlighting both important limitations and promising areas of future research (Neophytou et al. 2022).

The second biannual Evoltree conference, ‘Resilient Forests for the Future’, was hosted by the Transilvania University of Braşov in September 2023 in the Romanian city Braşov. Over four days, 143 researchers from 31 countries attended the hybrid event where 36 talks and 68 posters (Table S1) were presented across six topical sessions, including two teaching lectures on applications of remote sensing in genomics by Mihai Daniel Niţă and adaptive silviculture by Valeriu Norocel Nicolescu (second biannual Evoltree conference book of abstracts: Curtu and Ciocîrlan 2023). The majority of talks were filmed, professionally edited and the videos made available on YouTube (www.youtube.com/@evoltreenetwork2096).

Session 1: Climate resilient forests

Understanding the complex underlying factors, mechanisms and processes affecting forest resilience under CC is crucial to develop suitable mitigation and adaptation strategies. Forest resilience may be influenced by the type, duration and severity of natural disturbance events, as well as other factors including species-specific characteristics, biotic interactions and management practices.

Jill Hamilton (keynote) opened the conference asking if interspecific genetic exchange might facilitate adaptation in a changing climate. By studying natural hybrid zones between black cottonwood (*Populus trichocarpa*) and balsam poplar (*P. balsamifera*) in North America, pairing whole-genome resequencing and clonally replicated common garden experiments, she showed that phenotypic plasticity tended to be higher in individuals with admixed ancestry, indicating a possible fitness advantage across a broad array of environments. Cigdem Kansu presented another aspect of the same project showing signatures of positive selection in range-wide populations of *P. trichocarpa* and *P. balsamifera* collected along transects following major drainage systems across East–West mountain barriers. She revealed overlaps in candidate genes for adaptation in both species and in different provenances of *P. trichocarpa*.

Christian Rellstab continued with a study on the suitability of regional versus continental seed sources for CC mitigation of oaks in Europe. Preliminary results showed that provenances of pedunculate oak (*Quercus robur*) and downy oak (*Q. pubescens*) differed in drought adaptive traits on continental as well as on regional scales. A similar study was presented by Madeline Toomey, who investigated the suitability of seed sources for restoration practices of silver banksia (*Banksia marginata*) in Australia. They combined genotype–environment associations (GEA) with common-garden experiments and revealed candidate loci for local adaptation to differences in temperature and water availability.

Niels Müller presented a whole-genome resequencing study of European beech (*Fagus sylvatica*) trees from a range-wide provenance trial (Müller et al. 2023). The team performed GEA and could show that adaptive gene variants were typically common throughout the whole species distribution with varying allele frequencies. Furthermore, they estimated genomic offset to future climate and observed strong differences even between populations originating from the same region.

Finally, Debojyoti Chakraborty presented a complex modeling approach using harmonized provenance trial data in Europe to evaluate the effect of assisted migration of provenances and/or species on carbon sequestration under future climate conditions. The model suggested that carbon sequestration decreases with CC, however the decline would be less pronounced under assisted migration scenarios of species and seed sources compared to local seed source scenarios.

To summarise: first results indicate that natural hybridisation might facilitate adaptation in a changing environment, especially in extreme environments. Furthermore, genomic offset studies reveal regions and populations with potential elevated mortality risk due to CC highlighting possible management priorities. Further research is needed to understand the suitability of regional and continental seed sources for CC mitigation.

Session 2: Tree genomics and biotic interactions under climate change

Individuals, populations and species interact and form complex communities. The rapid development of high throughput sequencing methods and bioinformatic tools over the last decade open up new opportunities to analyse these relationships, which is especially urgent given the challenges increasingly being imposed by CC.

Nathan Swenson initiated the session, giving an exciting insight into a fundamental problem in trait-based tree ecology—functional traits can only be a poor imitation of the real dynamic responses of organisms to a changing

environment. Nonetheless, transcriptomics is a good tool to approach and overcome this problem: these data revealed more precise results compared to analyses of functional traits. Transcriptome data can also be used to identify genes associated with defence responses of trees against herbivorous insects, as presented by Hilke Schroeder who identified differentially expressed genes correlated with phenotypically tolerant and susceptible pedunculate oaks against insect herbivory. As well as specialist responses, they also observed a general defence response of oaks when comparing herbivory by both specialists and generalists.

A further important tool to investigate biotic interactions between trees and pest species are metabolomics and the analysis of leaf specialized metabolites which play a key role in plant resistance (Erb and Reymond 2019). Domitille Coq--Etchegaray used whole-genome low-coverage sequencing to genotype sessile oaks (*Q. petraea*) within an experimental common garden and then performed a genome-wide association study (GWAS) on 219 specialized metabolites identified through untargeted metabolomics (Coq--Etchegaray et al. 2023). She demonstrated a simple genetic architecture of the metabolomic variation in sessile oak where a small number of loci were generally associated with metabolites, with little evidence for local adaptation.

Although some oak species are predicted to be less affected by CC than other temperate forest tree species (Hanewinkel et al. 2012; Kremer and Hipp 2020), they will nonetheless have to adapt to future climate conditions. One of the options available when attempting to ensure healthy and productive oak forests in Northern Europe may be either assisted gene flow or assisted selection. Using a landscape genomics framework, Jill Olofsson identified candidate gene variants correlated with drought tolerance that could enhance the adaptive potential of Northern European sessile oaks. An urgent need for help has long been identified in ash (*Fraxinus excelsior*), which is strongly suffering from ash dieback. Erik Dahl Kjaer found that unaffected trees produce more and healthier offspring than affected trees (Eisen et al. 2023), providing hope that selection acting against susceptible trees will result in lower susceptibility in subsequent generations. Modeled forecasts under different scenarios suggested an optimistic outcome for ash, with populations comprising up to 60% healthy trees in the future.

Overall, this session highlighted the possibilities and challenges when using and combining “-omics” approaches. The already intensive effort in this area will lead us to a better understanding of the multiple abiotic and biotic threats that forests are increasingly facing.

Session 3: Evolutionary genomics

The use of genomic data to study evolutionary processes (Savolainen and Pyhäjärvi 2007) has advanced our

understanding of adaptation (Isabel et al. 2020). In turn, it has significant implications for the management and conservation of forest trees, their associated organisms, and hence entire forest ecosystems in a changing climate (Plomion et al. 2016).

Brandon Lind led the session with a compelling case for the limits of predicting maladaptation to future climate using genomic data (i.e. genomic offset). Several genomic offset methods were evaluated using simulations designed to vary in evolutionary history (Lotterhos 2023) and experimental design of the training and validation datasets. Results he presented suggest that performance is primarily (positively) influenced by the degree of local adaptation, but also declines with increasing climate novelty. He called for more variation in training datasets in future studies to reflect how evolutionary history varies across landscapes. He also proposed that genomic offset methods might be better suited for near-term assisted migration than for predicting maladaptation to future climates. Santiago C. González-Martínez and Juliette Archambeau presented a study characterising genetic variation for height within and among rangewide populations of maritime pine (*Pinus pinaster*). They found that extreme climates rather than environmental heterogeneity reduce genetic diversity for this trait. They then evaluated genomic offset estimations using empirical data and found that different GEA methods identified predominantly different sets of genetic markers associated with climate. Together, these presenters convincingly called for care in the interpretation and application of genomic offset approaches to predict future population maladaptation. Octávio Paulo highlighted the utility of genomic data for characterising species diversity, population structure and differentiation and local adaptation in oak species (*Q. suber*, *Q. ilex* and *Q. rotundifolia*), within a CC hotspot in the Mediterranean.

The subsequent group of presenters focussed on the role of hybridisation and introgression in adaptation to novel environments. Ovidiu Paun explained that hybridisation and the resulting introgression of adaptive alleles, as well as transposable element proliferation, may have contributed to adaptive radiation in the radiating group of persimmon trees (*Diospyros* spp.) in New Caledonia. Louise Gathercole also reported on extensive introgression in the north and west of Britain between the two native oak species, with alleles from *Q. robur* being incorporated into *Q. petraea*.

Finally, another source of novel genetic variation to populations was reported by Niklas Tysklind, who demonstrated that somatic mutations in tropical tree species, although abundant only at low frequency, are heritable (Schmitt et al. 2024). It was proposed that somatic mutations may play a role in plant evolution through their contribution to standing genetic variation.

In summary, the use of genomic data has significant power to enhance our understanding of adaptation but, as a tool to inform management, it should be used with caution and must be supported by validation using independent data.

Session 4: Innovative methods and approaches

In the recent past, forest evolutionary research has applied various new approaches mostly facilitated by the availability of new sequencing and phenotyping techniques, high-performance computers, and machine learning methods. Keynote speaker Meredith Schuman emphasized that intensive monitoring of genetic diversity is needed to protect biodiversity. Her research group uses remote sensing techniques to characterize genetic variation without genotyping individual trees, or doing so only on a small scale for validation. For example, they could show that two beech species (*F. sylvatica* and *F. orientalis*) can be distinguished by spectral analyses of top canopy leaves (D'Odorico et al. 2023). They also showed that leaf spectroscopy could even describe a limited part of genetic variation within species (Czyż et al. 2023).

Jing Xu presented an innovative study that aims at using laser scanners, gas analyzers, and thermal and multispectral cameras mounted on drones to measure phenotypic traits related to drought resistance in Nordmann fir (*Abies nordmanniana*). Similarly, Marcela van Loo presented a novel high-throughput multi-sensor phenotyping platform to study drought adaptation in Norway spruce (*Picea abies*) in a greenhouse experiment under controlled conditions. The ground-based platform allows for the measurement of over 50 phenotypic traits in seedlings, which are then complemented by transcriptomic and metabolomic profiles, as well as stem anatomy data. Finally, Jan Stejskal compared a contact and optical non-contact hyperspectral phenotyping method in seedlings of Scots pine (*Pinus sylvestris*). Both methods delivered valuable trait information but targeted different regions of the spectral range (Stejskal et al. 2023).

The second group of studies looked at advances in genomic approaches. Pangenomic analyses describe the structural variation among genomes of different individuals and the role of this variation in trait characteristics and adaptation. Ludovic Duvaux presented a new workflow to efficiently assemble genomes from long-read sequencing. Using graph methods he demonstrated that pangenomes can be analysed for highly heterogeneous genomes of trees, and plans to use this knowledge in a collaborative project characterising the pangenome of European white oaks (*Quercus* spp). Another new and popular approach is low-coverage whole-genome sequencing. Using down-sampling of sequencing reads, Ourania Grigoriadou-Zormpa showed that population genomic outcomes strongly depend on the

underlying sequencing coverage; compared to high coverage, genetic diversity is under-estimated and inbreeding and differentiation are over-estimated with low coverage. Using genotype likelihoods instead of traditional variant calling could correct such biased estimations.

This session efficiently highlighted how the combination of high-throughput phenotyping and sequencing will greatly advance our knowledge on how forests will react to future environmental changes.

Session 5: Conservation genomics

The combined effects of CC and habitat degradation have led to a dramatic acceleration of biodiversity loss, forming one of the world's greatest contemporary challenges (Allendorf et al. 2022). Conservation genetics and biological conservation are the two sides of the same coin, and genomic methods introduce an unprecedented power in data and tools to manage genetic resources.

Keynote speaker Ivan Scotti proposed a novel analytical framework that links population dynamics and resilience, using survival and reproduction (i.e. the fitness components) computed for individual genotypes. Konstantin Krutovsky highlighted dendrogenomics that integrate dendrosciences and genomics (Krutovsky 2022). The combined analysis of dendrological and genomic data facilitates the study of the molecular basis of growth and resilience traits, adaptive potential, spatial and temporal population structure and population dynamics. Examples using *Larix sibirica* (Novikova et al. 2023), *P. sibirica* and *Tsuga mertensiana*, underscored the utility of this framework.

The estimation of N_e is a paramount parameter in conservation and the focus of scientific debate, not least after being proposed as a genetic indicator in the frame of the Convention on Biological Diversity (Hoban et al. 2020). Marjana Westergren presented empirical estimates of contemporary N_e based on nuclear SSRs, using different methods and sampling designs for *F. sylvatica* and *Abies alba* and concluding that N_e estimates are highly dependent on sampling design. Anna-Maria Farsakoglou argued that high-throughput genomic data can be employed to estimate N_e indirectly, using the mean and standard deviation of expected heterozygosity (H_e) and the standard deviation of the inbreeding coefficient (F_{IS}) allowing comparisons of relative N_e across populations to be made. She proposed a particular theoretical framework, which she then applied using single-nucleotide polymorphism (SNP) data from five species (*A. alba*, *P. cembra*, *P. halepensis*, *P. nigra*, *Taxus baccata*).

The last group of studies focused on the conservation value of marginal/peripheral populations. Adelaide Theraroz presented SNP data from the widely, but disjunctly distributed *P. pinaster* to examine the genetic

processes operating in marginal populations and to test the Centre–Periphery Hypothesis. Theraroz found some significant correlations between population genetic parameters and geographical marginality indices (Picard et al. 2022) suggesting that marginal populations keep similar levels of adaptive capacity as central populations, and therefore they may be a valuable source of pre-adapted alleles to atypical environmental conditions. Sam Belton analyzed the *Q. robur*–*Q. petraea* complex at its northwestern limit in Ireland. He found that nuclear DNA diversity was amongst the highest across the entire distribution range of the species, potentially as a result of frequent introgressive hybridization.

Three important (and perpetual) conservation genomics challenges were addressed in this session: assessment of adaptive potential, estimation of effective population size (N_e) and value of marginal populations. Genomic tools provide new insights in these complex issues, taking advantage of the outstanding potential that genomic data can offer.

Session 6: Tree breeding and sustainable use of forest genetic resources

Climate change calls for more breeding for increasing resistance to biotic and abiotic stress factors and creates a demand for tree genetic knowledge in the management of forests. Keynote speaker Leopoldo Sánchez-Rodríguez gave an overview of activities and results from the B4EST EU Horizon 2020 project (Ray et al. 2022). B4EST aimed to enhance European forest resilience and productivity under CC while preserving genetic diversity. The project developed decision tools (see <https://b4est.eu/tools>) and genetic analysis techniques, including SNP arrays for six major forest tree species. Later, Sanna Olsson presented the application of a SNP array from B4EST in the breeding and conservation of *P. pinea*. Limited genetic diversity in this species has resulted in difficulties when using existing SSR markers to separate clones. The array improved clonal identification and enhanced genetic characterization of Iberian populations compared to the use of SSRs, and accurately estimated kinship relationships, thereby facilitating breeding programmes and enabling conservation activities.

Richard Buggs and coworkers have, via GWAS in European ash, identified numerous SNPs associated with resistance to the aforementioned ash dieback, and genomic predictions have successfully assessed resistance in planted trials and ancient woodlands. This genomic knowledge can expedite breeding programs to combat ash dieback (and, potentially, another threat to European ash: the emerald ash borer). Charalambos Neophytou presented how his group studied relict sessile oak stands in arid sites to understand

their adaptation to CC and associated drought events. Despite a homogeneous gene pool, they found genomic and physiological differences attributed to local adaptation, which holds promise for a climate-resilient oak breeding program.

Genomic selection (GS) has been applied in various conifer species using different SNP sources and was summarized by Harry Wu. Cross-validation GS has around 90% efficiency compared to phenotype selection. However, efficiency is lower in cross-population and cross-generation selection: reasons and mitigation strategies were discussed.

Katharina Liepe stated that the altered future climate requires new provenance recommendations, but traditional species distribution models may fail to take habitat changes fully into account. A new trait-based model, using Norway spruce trials, predicts a northern retreat due to CC (Liepe et al. 2022). Seed selection recommendations are provided by the model, but seed transfer alone cannot fully counteract the projected range decline.

Another changing environmental factor is increased deposition of nitrogen and phosphorus in ecosystems leading to eutrophication. In relation to that, Emilia Pers-Kamczyc presented a long-term study on *T. baccata* and *Juniperus communis* (Pers-Kamczyc et al. 2022), revealing that prolonged exposure to higher nutrient availability significantly reduces reproductive potential.

The oral presentations and posters in this session emphasised the increasing importance of genomics and modelling tools when breeding for and managing resilient forests, both now and in the future.

Conclusion and perspectives

The breadth and depth of research presented at the Evoltree conference clearly demonstrates the complexity in tackling the issue of resilience in forest ecosystems and the leading role of the Evoltree network in advancing scientific progress in this area. Overall, the conference showcased the development of novel empirical and modeling tools for breeding and management recommendations for future resilient forests. The conference also revealed the increased accuracy and precision of data collected, analyses performed and the subsequent predictive power being achieved as a result of these approaches, although many presenters also cautioned of overinterpretation in the absence of robust validation using independent data. Importantly, and despite a European focus for both the Evoltree network and the majority of the presenters and audience, the challenges discussed and addressed within the conference are global in nature and therefore possible solutions and strategies need to be disseminated and implemented beyond the European scale. In particular, many important European forest tree

species extend into northern Africa, the Middle East and beyond (www.euforgen.org is an invaluable resource in this regard) which means that results presented have relevance to audiences across more than the European continent.

Researchers conveyed the importance of exploring the evolutionary history of extant species to understand what processes might facilitate and promote adaptation to the changing climate (for example, several studies indicated that natural hybridisation between closely related species with distinct habitat preferences might facilitate adaptation to CC, especially in extreme environments), while others demonstrated cutting edge tools and analytical approaches.

Novel approaches, combining “-omics” (genomics, transcriptomics, metabolomics and phenomics) were presented in Braşov and discussed in relation to the power they have to support and inform conservation and management activities. However, management recommendations for forest tree species based on a single “-omics” data type need to be interpreted with caution and should be supported by validation using different independent data types. Similarly, several genomic offset studies highlighted difficulties in conveying general management guidance. Minor differences in the expected genomic offset between populations indicated that assisted gene flow approaches would need to be highly targeted and recommendations should be based on multiple approaches, including the use of local seed sources. Progress is also being made, and was explored at the conference, in understanding the usefulness of low-tech estimators of genetic diversity (most prominently N_e and adaptive potential). Their use in long-lived tree species was discussed, with speakers highlighting their role in evaluating declining trends in genetic diversity while emphasising the need for careful validation in order to identify populations with conservation needs.

Technological advances in genomics (and other “-omics”) and high-throughput phenotyping methods will increase our capacity to make and evaluate decision-making in this area. Furthermore, the use of machine learning for analyses combining large datasets (Korfmann et al. 2023) will certainly be an increasingly significant part of future research in this field and may dramatically improve management recommendations.

It is clear that defining, conserving and planning resilient forests for the future is a massive task of global significance, which requires international and interdisciplinary cooperation and collaboration. Ideally, researchers outside of Europe who are working either with the same species but in different environments, or in similar environments but with unrelated species, should also test these novel approaches and methods presented here to increase our understanding of their power and limitations within a global context.

Despite important incremental improvements in knowledge and tools, many of which were presented and discussed at Braşov, there are numerous tree species which have not yet been studied and an increase in urgency as CC begins to impact standing forests. The fundamental role that trees and forests are increasingly expected to play in mitigating the impacts of CC is strongly juxtaposed by the relatively low availability of resources and comparatively few researchers in this field. In this context, the role of the Evoltree network in supporting collaboration and providing resources, training and dissemination activities, such as the Evoltree conferences, is more important than ever.

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Data availability All data referenced in this short communication are available within the paper and its Supplementary Information.

Declarations

Conflict of interest The authors declare no competing interests.

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