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RESEARCH ARTICLE

First description and conservation implications of a unique stand of the Caucasian wingnut in Lapankuri (Georgia)

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Abstract

Many north-temperate tree species survived glacial periods in small, low-density populations in refugia. These refugia are located in eastern and western North America, South Europe, East Asia, and western Asia. As a part of western Asia, Georgia harbors two main refugia: the Colchis in western Georgia and the eastern Great Caucasus, where many Cenozoic relict plants still exist. In this article, we report a new population of Pterocarya fraxinifolia (the Caucasian wingnut) which was discovered in the eastern Great Caucasus, near the village Lapankuri. The Lapankuri P. fraxinifolia stand is unique because the species grows not only in a narrow strip of riparian vegetation, but is also occurring in a broad band up to 100 m away from the river. Pterocarya fraxinifolia is dominant in the stand and is represented by large and old trees. Many other relict trees such as Diospyros lotus and Juglans regia are also present in the Lapankuri stand. Although some Cenozoic relict species are widely cultivated and naturalized in Central and Western Europe, natural stands of these plants provide the only evidence of their past growing conditions; therefore, conservation of this place is strongly advocated.

KEYWORDS

Cenozoic plants, conservation, Georgia, Pterocarya fraxinifolia, Refugia, relict plants

1 | INTRODUCTION

The Cenozoic period (the past 66 million years, Myr) was characterized by a gradual cooling in both hemispheres with temperature changes at high latitudes being more pronounced than close to the equator (Moran et al., 2006). Increased cooling of the Northern Hemisphere from 15 Myr ago onward caused a drop in diversity of temperate and subtropical forest biomes in the Northern Hemisphere and their retreat from mid to high latitude circumboreal distributions southward to refugial regions that preserved a warm and wet climate (Tiffney & Manchester, 2001; White et al., 1997; Zachos et al., 2001). These refugia of warm temperate woody plants are today located in East Asia, south-eastern and western North America, south-eastern Europe, and western Asia (Denk et al., 2001; McIver & Basinger, 1999; Milne, 2006; Milne & Abbott, 2002; Tarkhnishvili et al., 2012; Wen, 1999).

The Caucasus region was designated as one of 36 global "biodiversity hotspots" (Myers et al., 2000; Venevsky & Venevskaia, 2005). The Caucasus biodiversity hotspot includes Georgia, Armenia, Azerbaijan, and small portions of Russia, Iran, and Turkey. The region is characterized by a unique flora; many endemic species and five endemic plant genera are known from the area (Gagnidze et al., 2002; Grossheim, 1936). In addition, the Caucasus is one of the most important Pleistocene glacial refugia in the Northern Hemisphere. This claim is well supported by several lines of evidence: The presence of extant survivors of plant lineages with a wide Cenozoic distribution such as Pterocarya fraxinifolia (Poir.) Spach., Zelkova carpinifolia (Pall.) K. Koch, Parrotia persica C.A. Mey., and the high level of endemism in both plants and animals (Grossheim, 1936; Ketskhoveli, 1959; Kolakovskyi, 1961; Milne, 2004; Sharifi & Assadian, 2004; Tarkhnishvili et al., 2000; Zohary, 1973). Several characteristics favored survival

of Cenozoic relicts in the Caucasus throughout the Pleistocene. The Caucasus is influenced by a warm and humid climate from the Black Sea, which supports the establishment of humid broad-leaved deciduous forests with an evergreen understory containing Cenozoic relict plants. Similarly, humid and warm winds coming from the Caspian Sea are captured by the eastern Great Caucasus range and Elburz mountain range promoting the formation of luxuriant mesophyllous vegetation with dominance of Cenozoic relict taxa (Akhani et al., 2010; Dagtekin et al., 2020; Denk et al., 2001; Martin-Benito et al., 2020).

Although a considerable number of Euxinian-Hyrcanian Cenozoic relict taxa is today cultivated and partly naturalized in Central and South Europe, the documentation of natural stands of relict trees is the only way to understand how these species or their congeneric extinct counterparts grew in the past. Moreover, descriptions of natural forest vegetation in the Caucasus and adjacent areas commonly are restricted to work from the early nineteenth century such as Engler and Drude's Vegetation of the Earth (Radde, 1899) or general works such as Kolakovskyi (1961). Thus, the aim of this work was to study the small-scale distribution patterns of a well-known Cenozoic relict tree, Pterocarya fraxinifolia, in Lapankuri, eastern Great Caucasus and to report a new P. fraxinifolia stand occurring near the village Lapankuri.

2 | MATERIALS AND METHODS

A floristic study was carried out in the surroundings of the village Lapankuri, eastern Great Caucasus (Figure 1), in 2015 and 2016. Identifications of plants were based

on Vascular Plants of Georgia (Gagnidze, 2005). Plant names and their authorities follow the International Plant Names Index (PNI, 2023).

3 | RESULTS

An impressive population of P. fraxinifolia, previously not mentioned in the literature, was discovered in eastern Georgia, in the surroundings of the village Lapankuri, located between 42°3′41.19″ N 45°32′24.99″ E and 42°3′47.52″ N 45°33′55.22″ E. The P. fraxinifolia stand was mapped using ArcGIS version 10.2.2 and the area of the stand was measured. The core area of the riparian forest with dominance of P. fraxinifolia is 35 ha (Figure 1). This place was characterized by the riverbed of the Lopota river, which forms a strongly braided river system. (Figure 2). The stand has a northern exposition; alluvial soils are widely distributed. The weather conditions prevailing in Lapankuri are characterized by a cold and moderate climate. The village of Lapankuri experiences a significant amount of rainfall, even during the month with historically low precipitation levels. The mean annual precipitation level amounts to 733mm. The majority of rainfall occurs in April and the maximum precipitation level is 110mm. The minimum precipitation level equals to 40mm. The average annual temperature in Lapankuri is 7.9°C. The temperatures are highest in August, at around 20.6°C. The minimum temperature is in January, the temperature registers at a minimum value of -4.3°C.

On gravels, the pioneer species *Salix alba* is forming small patches, whereas *Pterocarya fraxinifolia* is restricted to the deeper alluvial soils. On the right side of the river Lopota, cultivated land is present.



FIGURE 1 Distribution of riparian forest dominated by P. fraxinifolia (in light blue) near the village Lapankuri.



FIGURE 2 Braided river system of river Lopota (Google Earth image).

Mespilus germanica L.
Morus nigra L.
Populus alba L.
Populus nigra L.
Pyrus pyraster (L.) Burgsd.
<i>Quercus robur</i> subsp. <i>pedunculiflora</i> (K. Koch) Menitsky
Rosa sp.
Rubus sp.
Salix alba L.
Salix purpurea L.
Sambucus nigra L.
Smilax excelsa L.
Ulmus minor Mill.
Viburnum opulus L.

TABLE 1	List of common trees, shrubs, and lianas in Lapankur
P. fraxinifolia	-dominated riparian forest.

In Lapankuri, *Pterocarya* does not only grow along the main course of the river but forms an original and vast forest extending deep into the alluvial plain including natural levees. *Pterocarya fraxinifolia* is represented by old and large trees and is the dominant species. Close to the river Lopota, the sun-loving *Salix alba*, *Populus alba*, and *P. nigra* were restricted to gravels with shallow substrate. Sporadically, the riparian forest element *Quercus robur* subsp. *pedunculiflora* occurred (see Table 1, Figure 3). Other woody taxa like *Alnus barbata*, *Carpinus betulus*, *Acer campestre*, *Cornus mas, Diospyros lotus Crataegus pentagyna,* and *Juglans regia* were also present in the wingnut dominated forest (see Table 1; Figure 3).

4 | DISCUSSION

In the course of this study, natural populations of P. fraxinifolia were investigated throughout almost the whole distribution range of the species: in western Georgia -Colchis, eastern Great Caucasus, and in northern Iran, Hyrcanian forest region, and in the Zagros mountains. Not included in this survey were the regions south of the Black Sea. During the Cenozoic, the species, or its closely related ancestors, were widely distributed in western Eurasia extended to the north as far as Iceland (Mai, 1995).but nowadays it is restricted to the abovementioned regions. Pterocarya fraxinifolia is widely cultivated in Europe and is a moderately cold tolerant species. (see, e.g., Lintunen et al., 2015, for frost tolerance and hardiness, and POWO for a general distribution including regions where P. fraxinifolia has been introduced; https://powo.science.kew.org/taxon/44247 11?_gl=1*1npydcm*_ga*Njg3NzE3ODg5LjE2ODA1 MTU4NzQ.*_ga_ZVV2HHW7P6*MTY5Mzg5OTY0Ny4 zOC4xLjE2OTM4OTk2NjYuMC4wLjA.).

A unique stand of this species occurs in Lapankuri, eastern Great Caucasus. The Lapankuri *P. fraxinifolia*-dominated forest is situated between the villages Lapankuri and Napareuli along the river Lopota. Caucasian wingnut is a relict monoecious tree species that requires deep soils and sufficient air humidity; it grows in riparian forests in the areas of partially flooded forests and running water from lowlands up to 1730 m



in the Zagros Mountains (Akhani & Salimian, 2003; Gulisashvili, 1961). This fast-growing anemophilous species prefers alluvial and clay soils with a humus layer, semi-deep to shallow soils with medium nutrient requirement (Gulisashvili, 1961; Hoseinpour et al., 2013; Sheykholislami & Ahmadi, 2009). Although being a thermophilous plant, it can stand short lasting winter frosts reaching -25°C (Gulisashvili, 1961; Lintunen et al., 2015).

The *P. fraxinifolia* stand in Lapankuri is composed of trees of different age, saplings, young trees, and old trees are present here. Special interest deserves the appearance of tall trees up to 30 m tall, which are well represented in the Caucasian wingnut stand in Lapankuri and distinguish it from all other known populations in the whole distribution range of the species (Figure 4). Gulisashvili (1961) reported that *Pterocarya fraxinifolia* never forms monodominant populations. However, the Lapankuri stand is characterized by the dominance of Caucasian wingnut. The presence of seedlings suggests that the Lapankuri Caucasian wingnut-dominated forest is a self-sustaining population (Figure 5).

Pterocarya fraxinifolia is an important component of the riparian forests in the eastern Great Caucasus and northern Iran and usually grows in small groups along rivers (Gulisashvili, 1961). The Lapankuri Caucasian wingnut stand is unique since the species distributed here not only directly along the river and adjacent channels as in all other known stands of the eastern Great Caucasus, for example, in Ninigori 41°50′57″ N 46°13′52″ E (Kakheti; personal observation), but also forms a vast forest growing 100 m away from the river bank. The establishment of this P. fraxinifolia stand appears to depend on the natural fluctuation of the water level of the river Lopota, which creates appropriate ecological conditions for the species' growth and also enables transportation of P. fraxinifolia seeds further away from the river, where they germinate and seedlings grow. A similar situation, in which P. fraxinifolia grows away from the river, was found in North Iran - Khan Bebin population 36°58'01.4" N; 55°01'40.4" E (personal observation).



FIGURE 4 Tall P. fraxinifolia tree in Lapankuri riparian forest.

Here the Caucasian wingnut, similar to the Lapankuri stand, grows not only along the river, but also at some distance from the river. However, large and old individuals are absent and *Pterocarya* is not dominant but part of a mixed forest.

It should be mentioned that also in the Colchis region of western Georgia, *Pterocarya* grows not only along rivers but also in the adjacent alluvial forest. This can be explained by the presence of high groundwater levels. But in the Colchis region, Caucasian wingnut is represented by young and juvenile trees (personal observation) because of intensive logging of the Colchic lowland forest. To the best of our knowledge,



FIGURE 5 Seedling of *P. fraxinifolia* in Lapankuri riparian forest.

the Lapankuri *P. fraxinifolia* stand is unique throughout the species distributional range, because (i) the tree is dominant in the riparian forest, (ii) is represented by large and old trees in addition to the presence of seedlings, and (iii) grows not only along the river, but further away from the river in alluvial lowland forest. We assume that this situation might reflect the natural condition of *Pterocarya*-dominated lowland forests in prehistoric times. Therefore, conservation actions are of utmost importance to protect this unique Caucasian wingnut stand.

Besides P. fraxinifolia, other important relict taxa are well presented there. Among them are: Quercus robur subsp. pedunculiflora which is a relict taxon with distribution in south-eastern Europe, from the Balkan Peninsula across Crimea to the Caucasus and northern part of Anatolia. In southeastern and eastern Georgia, this sun-loving species grows along rivers forming riparian forests together with willow and poplar species. Vicariant species of Quercus robur subsp. pedunculiflora in western Georgia is Quercus robur subsp. imeretina (Steven ex Woronow) Menitsky. Both taxa are closely related to the strictly European species Q. robur L. s.str. All these taxa are members of section Quercus and recent leaf morphological and genetic research shows that there is limited difference between Q. robur and Quercus robur subsp. pedunculiflora (Curtu et al., 2011).

Carpinus betulus commonly occurs on well-drained soils. This species is not only a relict plant component of beech and oak forest but it also grows in lowland riparian forests of western Georgia in better drained soils (Denk et al., 2001). Similarly to western Georgia, *C. betulus* is well presented in the riparian forest of Lapankuri. It is noteworthy that this species is often referred to as *C. caucasica* Grossh. in the literature, but considered a synonym of *C. betulus* in modern taxonomic accounts (e.g., Govaerts, 2003). Nevertheless, as in *Pterocarya* (Maharramova et al., 2018), *Fagus* (Kurz et al., 2023), and other tree species, there might be some hidden, cryptic species in western Eurasia. These will only be detected by thorough phytogeographical investigations and renewed efforts in the morphological monitoring of widespread tree taxa.

Diospyros lotus is native to the Balkans, Turkey, Caucasia, Central Asia to China, and Japan. It is closely related to the Japanese species *D. kuroiwai* Nakai (Yonemori et al., 2007). It occurs on foothills in the Colchic refugium and in riparian forests of the eastern Great Caucasus.

Acer campestre is a very common accessory element in well-drained forests and riparian stands in Europe and western Asia (Grimm & Denk, 2014). The species is typically found along forest-edges in fully humid, warm-temperate climates. Recently, populations of A. campestre occurring in western Georgia were described as a new species A. orthocampestre Grimm & Denk (2014). The populations from eastern Georgia have not been investigated and the species distribution toward the east is unknown. However, based on the distributional pattern of A. campestre in the North Caucasus, East Georgia, Azerbaijan, and North Iran, where it is confined to humid temperate climates, following strictly the river valleys, we assume that all populations of A. campestre to the east might belong to A. orthocampestre (Grimm & Denk, 2014).

Alnus barbata is a Euxino-Hyrcanian species which occurs frequently in riparian forests of eastern Georgia and almost everywhere in the Colchic refugium. This pioneer species is tolerant to frequent flooding, and grows even in shallow standing water (Denk et al., 2001). It is closely related to *A. glutinosa* (L.) Gaertn.

4.1 | Implications for conservation

Due to habitat loss, construction of roads, and establishment of settlements, of agricultural land and of hydropower plants, natural riparian forests are very rarely found in western Eurasia. Moreover, especially in Central and Western Europe, natural water level fluctuation is regulated by dams and channels, which prevent the formation of riparian forest. Therefore, in situ conservation of naturally grown riparian forest, especially when dominated by rare Cenozoic relict plant species, is one of the most important aims in conservation biology. Pterocarya fraxinifolia is included in the Georgian Red Data Book (Kacharava, 1982) as a rare arboreal Cenozoic relict. However, logging of this tree was observed in different Caucasian wingnut-dominated places of the eastern Great Caucasus. P.fraxinifolia is listed in the IUCN Red List as vulnerable (Betrisey et al. 2019). Pterocarya fraxinifolia is protected in Lagodekhi Nature Reserve (Kakheti, eastern Georgia) and in Colchic National Park in western Georgia; however, the species is still under the threat of human influence and ongoing climate change coupled with anthropogenic environmental

change. The unique Caucasian wingnut stand of Lapankuri requires a special protection status in order to prevent further damages, especially logging, establishing of maize field plantations, and pastures.

4.2 | Concluding remarks

A considerable number of Cenozoic relict trees are today planted and naturalized in Central and Western Europe (e.g., Syringa, Aesculus, Pterocarya, Juglans, and others). Natural stands of these taxa are threatened by human activities in combination with a warming climate. In this article, we document a newly discovered natural stand of Caucasian wingnut, Pterocarya fraxinifolia, in eastern Georgia and emphasize its uniqueness. Unlike previously reported natural stands of *Pterocarya* fraxinifolia, the here reported one is a dominant stand of large and old trees of Pterocarya extending across a wide alluvial plane away from the river bed. With a rich second tree layer and shrub layer and seedlings of Pterocarya, this stand might well resemble forests of Caucasian wingnut from prehistoric times. Protection of this alluvial forest is strongly recommended.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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REFERENCES

- Akhani, H., Djamali, M., Ghorbanalizadeh, A., & Ramezani, E. (2010). Plant biodiversity of Hyrcanian relict forests, N Iran: An overview of the flora, vegetation, palaeoecology and conservation. *Pakistan Journal of Botany*, 42, 231–258.
- Akhani, H., & Salimian, M. (2003). An extant disjunct stand of *Pterocarya fraxinifolia* (Juglandaceae) in the central Zagros Mountains, W Iran. *Willdenowia*, 33, 113–120.
- Bétrisey, S., Song, Y., Yousefzadeh, H., & Kozlowski, G. (2019). Pterocarya fraxinifolia. The IUCN Red List of Threatened Species 2019: e.T66815986A66816002. https://dx.doi.org/10.2305/IUCN. UK.20193.RLTS.T66815986A66816002.en
- Curtu, A. L., Sofletea, N., Toader, A. V., & Enescu, M. C. (2011). Leaf morphological and genetic differentiation between *Quercus robur* L. and its closest relative, the drought-tolerant

Quercus pedunculiflora K Koch. Annals of Forest Science, 68, 1163–1172.

- Dagtekin, D., Şahan, E. A., Denk, T., Köse, N., & Dalfes, H. N. (2020). Past, present and future distributions of oriental beech (*Fagus orientalis*) under climate change projections. *PLoS One*, *15*(11), e0242280.
- Denk, T., Frotzler, N., & Davitashvili, N. (2001). Vegetational patterns and distribution of relict taxa in humid temperate forests and wetlands of Georgia (Transcaucasia). *Biological Journal of the Linnean Society*, 72, 287–332.
- Gagnidze, R. (2005). Vascular plants of Georgia. A nomenclatural checklist (p. 248). Georgian Academy of Sciences.
- Gagnidze, R., Gviniashvili, T., Shetekauri, S., & Margalitadze, N. (2002). Endemic genera of the Caucasian flora. *Feddes Repertorium*, *113*, 616–630.
- Govaerts, R. (2003). *World checklist of selected plant families database in ACCESS: 1–216203.* The Board of Trustees of the Royal Botanic Gardens.
- Grimm, G. W., & Denk, T. (2014). The Colchic region as refuge for relict tree lineages: Cryptic speciation in field maples. *Turkish Journal of Botany*, *38*, 1050–1066.
- Grossheim, A. A. (1936). *Analysis of the flora of the Caucasus* (p. 260). Proceedings of the Botanical Institute of Azerbaijan.
- Gulisashvili, V. (1961). *Dendroflora of the Caucasus*. Publishing House of the Academy of Sciences of Georgia.
- Hoseinpour, M., Payam, H., & Fallahchai, M. M. (2013). Considering the quantitative characteristic of *Pterocarya fraxinifolia* (lam.) Spach species in north forests of Iran. *Bulletin of Environment, Pharmacology and Life Sciences*, 2(9), 65–70.
- Kacharava, W. (Ed.). (1982). *Red data book of the Georgian SSR* (p. 255). Tbilisi.
- Ketskhoveli, N. (1959). *Vegetation of Georgia*. Publishing House of the Academy of Sciences of Georgia.
- Kolakovskyi, A. A. (1961). *The plant world of Colchis*. Publishing House of the Moscow University.
- Kurz, M., Koelz, A., Gorges, J., Carmona, B. P., Brang, P., Vitasse, Y., & Csillery, K. (2023). Tracing the origin of oriental beech stands across Western Europe and reporting hybridization with European beech–implications for assisted gene flow. *Forest Ecology and Management*, 531, 120801.
- Lintunen, A., Paljakka, T., Riikonen, A., Lindén, L., Lindfors, L., Nikinmaa, E., & Hölttä, T. (2015). Irreversible diameter change of wood segments correlates with other methods for estimating frost tolerance of living cells in freeze-thaw experiment: A case study with seven urban tree species in Helsinki. *Annals of Forest Science*, 72(8), 1089–1098.
- Maharramova, E., Huseynova, I., Kolbaia, S., Gruenstaeudl, M., Borsch, T., & Muller, L. A. (2018). Phylogeography and population genetics of the riparian relict tree Pterocarya fraxinifolia (Juglandaceae) in the South Caucasus. *Systematics and Biodiversity*, *16*(1), 14–27.
- Mai, D. H. (1995). Tertiäre Vegetationsgeschichte Europas. Gustav Fischer Verlag.
- Martin-Benito, D., Pederson, N., Lanter, C., Köse, N., Doğan, M., Bugmann, H., & Bigler, C. (2020). Disturbances and climate drive structure, stability, and growth in mixed temperate old-growth rainforests in the Caucasus. *Ecosystems*, 23, 1170–1185.
- McIver, E. E., & Basinger, J. F. (1999). Early tertiary floral evolution in the Canadian high Arctic. *Annals of the Missouri Botanic Garden*, 86, 523–545.
- Milne, R. I. (2004). Phylogeny and biogeography of rhododendron subsection Pontica a group with a tertiary relict distribution. *Molecular Phylogenetics and Evolution*, 33, 389–401.
- Milne, R. I. (2006). Northern hemisphere plant disjunctions: A window on tertiary land bridges and climate change? *Annals of Botany*, 98, 465–472.

- Milne, R. I., & Abbott, R. J. (2002). The origin and evolution of tertiary relict floras. Advances in Botanical Research, 38, 281–314.
- Moran, K., Backman, J., Brinkhuis, H., Clemens, S. C., Cronin, T., Dickens, G. R., Eynaud, F., Gattacceca, J., Jakobsson, M., Jordan, R. W., Kaminski, M., King, J., Koc, N., Krylov, A., Martinez, N., Matthiessen, J., McInroy, D., Moore, T. C., Onodera, J., ... Kristoffersen, Y. (2006). The Cenozoic palaeoenvironment of the Arctic Ocean. *Nature*, 441, 601–605.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 854–858.
- IPNI. (2023). International Plant Names Index. The Royal Botanic Gardens, Kew, Harvard University Herbaria & Libraries and Australian National Herbarium. Published on the Internet https://www.ipni.org
- Radde, G. (1899). Grundzüge der Pflanzenverbreitung in den Kaukasusländern von der unteren Wolga über den Manytsch-Scheider bis zur Scheitelfläche Hocharmeniens. In A. Engler & O. Drude (Eds.), Vegetation der Erde (Vol. 3). Engelmann.
- Sharifi, M., & Assadian, S. (2004). Distribution and conservation status of *Neurergus microspilotus* (Caudata: Salamandridae) in Western Iran. Asiatic Herpetological Research, 10, 224–229.
- Sheykholislami, A., & Ahmadi, T. (2009). The study of Caucasian walnut ((lam.) Spach) in forests of Mashelak (Noshahr, Iran). *Botany Research Journal*, 2(2–4), 28–33.
- Tarkhnishvili, D., Gavashelishvili, A., & Mumladze, L. (2012). Paleoclimatic models help to understand current distribution of Caucasian forest species. *Biological Journal of the Linnean Society*, 105, 231–248.
- Tarkhnishvili, D., Thrope, R. S., & Arntzen, J. W. (2000). Pre-Pleistocene refugia and differentiation between populations

of the Caucasian salamander (*Mertensiella caucasica*). *Molecular Phylogenetics and Evolution*, 14, 414–422.

- Tiffney, B. H., & Manchester, S. R. (2001). The use of geological and paleontological evidence in evaluating plant phylogeographic hypotheses in the northern hemisphere tertiary. *International Journal of Plant Sciences*, *162*, S3–S17.
- Venevsky, S., & Venevskaia, I. (2005). Hierarchical systematic conservation planning at the national level: Identifying national biodiversity hotspots using abiotic factors in Russia. *Biological Conservation*, 124, 235–251.
- Wen, J. (1999). Evolution of the eastern Asian and eastern north American disjunct distribution in flowering plants. Annual Review of Ecology and Systematics, 30, 421–455.
- White, J. M., Ager, T. A., Adam, D. P., Leopold, E. B., Liu, G., Jette, H., & Schweger, C. E. (1997). An 18 million year record of vegetation and climate change in North-Western Canada and Alaska: Tectonic and global climatic correlates. *Palaeogeography Palaeoclimatology Palaeoecology*, 130, 293–306.
- Yonemori, K., Honsho, A. H., Kanzaki, S., Ino, H., Ikegami, A., Kitajima, A., Sugiura, A., & Parfitt, D. E. (2007). Sequence analyses of the ITS regions and the matK gene for determining phylogenetic relationships of *Diospyros kaki* (persimmon) with other wild Diospyros (Ebenaceae) species. *Tree Genetics & Genomes*, 4, 149–158.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E., & Billups, K. (2001). Trends, rhythms and aberrations in global climate - 65 Mya to present. *Science*, 292, 686–693.
- Zohary, M. (1973). *Geobotanical foundations of the Middle East*. G. Fischer Verlag.