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# Selective extinction within a Tertiary relict genus in the Japanese Pleistocene explained by climate cooling and species-specific cold tolerance

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ABSTRACT

The Pleistocene floristic change in the Northern Hemisphere is marked by extensive extinctions of Tertiary relicts in middle to high latitudes, which are thought to have been moderate in East Asia. However, species losses from geographically isolated areas in East Asia were comparatively heavy. In this study, we report a selective extinction event within the relict genus *Staphylea* (Staphyleaceae) from the Japanese Pleistocene. We described two species, *Staphylea bumalda* DC. and *S. spinosa* Y. Huang et A. Momohara sp. nov. (Staphyleaceae), based on seed remains from the middle early Pleistocene (ca. 1.7–1.2 Ma) Shobudani Formation in the northern Kii Peninsula of southwestern Honshu. According to the fossil records and modern distributions of *Staphylea*, we presumed that *S. bumalda* emerged in Japan at least by the early Pliocene and has persisted until today, whereas *S. spinosa* was exterminated after the middle early Pleistocene. To explain the different fates of the two species, we estimated their climate tolerance by observing the climate requirements of their nearest living relatives. Our results indicate that *S. bumalda* could tolerate colder climates, particularly in winter, than *S. spinosa*. Floristic compositional changes at the study area reveal a cooling trend followed by a glacial stage after the last occurrence of *S. spinosa*. The cold winter temperature in the glacial stage was probably beyond the cold tolerance of *S. spinosa*, which ultimately led to its demise. Surrounding geomorphological changes, such as the uplift of the Kii Mountains, might also have played a role in the way of preventing plant migration when climate deteriorated. This selective extinction event adds a new episode into our knowledge of the Pleistocene plant extinctions along with their possible underlying mechanisms in the Northern Hemisphere.



## 1. Introduction

Regional extinctions are important factors that have shaped modern floras, phytogeographic patterns, and phylogenies (Wen, 1999; Svenning, 2003; Eiserhardt et al., 2015). The last extensive natural extinctions of plants took place in the Pleistocene, characterized by regional losses of Tertiary relict taxa caused mainly by climate instability between glacial and interglacial stages (Follieri et al., 1986; Jackson and Weng, 1999; Svenning, 2003). The species losses are observed to have been heavier in middle to high latitudes, such as in Europe (Martinetto, 2001, 2015; Svenning, 2003; Hampe and Petit, 2005), but are considered to have been far less severe in East Asia (Svenning, 2003). However, in geographically isolated areas of East Asia (e.g., islands), the Pleistocene plant extinctions might have been comparably remarkable due to curtailed migration.

Japan, in the northeast of East Asia, is an archipelago chiefly composed of four main islands. The Pleistocene floristic changes in Japan are featured by widespread extinctions of Tertiary elements, many of which are now endemic only to central and southern China (Momohara et al., 1990; Momohara, 1992, 1994, 2016). Such local species extinctions were first noted by Miki (1948) on the basis of abundant extinct taxa recognized from lowland fossil floras in and around Osaka, southwestern Honshu. More examples of extinctions have been reported in recent decades (Momohara et al., 1990, 2017; Momohara, 1994, 2016).

Besides the extinction event itself, there is increasing interest in studying the possible mechanisms behind the plant extinctions in the Japanese Pleistocene. From the end of the late Pliocene to the middle Pleistocene, the Japanese main islands underwent several stages during which plant species were eliminated. These stages correspond well to the timing of the major phases when cold climates occurred associated with a global cooling trend, and thus the cooling trend is thought to have been the key force driving plant extinctions in Japan (Momohara, 1994, 1999, 2016). The fact that most of the regionally extinct species or their closest modern relatives are now growing in lower latitudes of

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East Asia with warm climates further supports the presumed relation between plant extinctions and the climate cooling. Other than declining temperatures, geomorphological changes such as mountain uplift are also considered likely to have played a role in the extinctions (Momohara, 1994, 2011). Japan has undergone active topographic uplift since the late Pliocene (Sangawa, 1977; Kazaoka et al., 1986; Oikawa, 2003; Suganuma et al., 2003). The mountain uplift adversely affected plant habitats, e.g., alluvial landforms as habitats for *Glyptostrobus* and *Metasequoia* (Yamakawa et al., 2008, 2017). Moreover, the uplifted mountains might have served as biogeographic barriers, hindering plant migration when the local environment became unsuitable (Momohara, 1994, 2005, 2011). Despite equivalent environmental changes they experienced, most of the plant species found in the fossils are still encountered today in the wild. Therefore, inherent cold tolerance and ecological adaptation of plants are also important in determining their fates in the face of harsh conditions.

In this study, we report a selective extinction event within a Tertiary relict genus, *Staphylea* L. (Staphyleaceae), from the Japanese Pleistocene. We first described two species, *S. bumalda* DC. and *S. spinosa* Y. Huang et A. Momohara sp. nov., based on seed fossil remains from the middle early Pleistocene Shobudani Formation in Hashimoto City of the northern Kii Peninsula, southwestern Honshu, Japan. We then extracted the climate tolerance of the two species by looking at the climate requirements of their nearest living relatives. We finally discuss on possible mechanisms to explain the survival of *S. bumalda* but the extinction of *S. spinosa* in Japan.

## 2. Materials and methods

### 2.1. Modern distribution of Staphylea

*Staphylea* L. is a Tertiary relict genus in the bladdernut family Staphyleaceae and includes 10 species of large shrubs to small trees (Li et al., 2008). It is native mainly to subtropical areas of the Northern Hemisphere, but a few species also extend into temperate zones, with disjunctive ranges in East Asia, South Asia, eastern and western North America, and the Mediterranean (Spongberg, 1971; Weaver, 1980; Sosa, 1988; Li et al., 2008; Harris et al., 2017). In Japan of East Asia, *S. bumalda* represents the only living species of this genus (Ohashi et al., 2016).

### 2.2. Study area, geological horizon, and age control

Fossil seeds for the present study were collected from the Shobudani Formation outcropping along the Shobudani River at Miyukitsuji, northern Hashimoto City in the northern Kii Peninsula on the Pacific side of Honshu, Japan (Fig. 1). The Shobudani Formation in the study area consists of ca. 100 m thick fluvial sediments, which unconformably lie over the Sanbagawa crystalline schists and are unconformably overlain by terrace deposits (Momohara et al., 1990). Gravel in the lower part of the formation is composed mainly of subangular pebbles of the Izumi sandstone derived from the Izumi Range in the northern part of the sedimentary basin. Gravel in the upper part of the formation is dominated by a mixture of subrounded pebble-cobble including chert distributed in the Kii Mountains in the southern part of the basin. Six volcanic ash layers, Sh1–Sh6 in ascending order, are included within the Shobudani Formation. The Sh1 tephra is correlated with the Eb-Fukuda tephra, which is widespread across central and western Honshu (Satoguchi and Nagahashi, 2012) and positioned in the lower part of Marine Isotope Stage (MIS) 61 of the oxygen isotope record (ca. 1.73 Ma) in a marine section in southern Kanto (Nozaki et al., 2014). Another time control in the upper part of the deposits is the Sh6 tephra, which has been dated to 0.93 $\pm$ 0.21 Ma by fission track methods (Suzuki, 1988). Large amounts of plant macrofossils are contained in 41 sedimentary layers in the Shobudani Formation. According to stratigraphic changes in floristic composition, Momohara et al. (1990) established six assemblage zones, numbered from SB-I to SB-VI in ascending order. Fossil seeds of *Staphylea* for the present study were obtained from the assemblage P-23 in zone SB-III, which is correlated to the middle early Pleistocene (ca. 1.7–1.2 Ma) based on its position between the Sh1 and Sh6 tephras.

### 2.3. Morphological observations and comparisons

Plant macrofossils were previously obtained by sieving macerated sediments within water, while some larger ones were collected directly from outcrops at the study area. Herein, a total of 37 fossil seeds and seed fragments of *Staphylea* were recognized from the existing fossil collection kept at the Graduate School of Horticulture, Chiba University. They were separated into two groups based on morphology, which were considered to belong to two different taxa. Digital images of the fossils were taken under a stereomicroscope (Nikon SMZ18). To improve visualization, a software named Sensiv Measure (Mitani Corporation) was used to overlap a set of images captured at different focus planes for each specimen. Comparative materials of two extant species of *Staphylea*, *S. bumalda* and *S. holocarpa*, were observed from collections stored at the Graduate School of Horticulture, Chiba University. They were also digitally photographed under the Nikon stereomicroscope following the

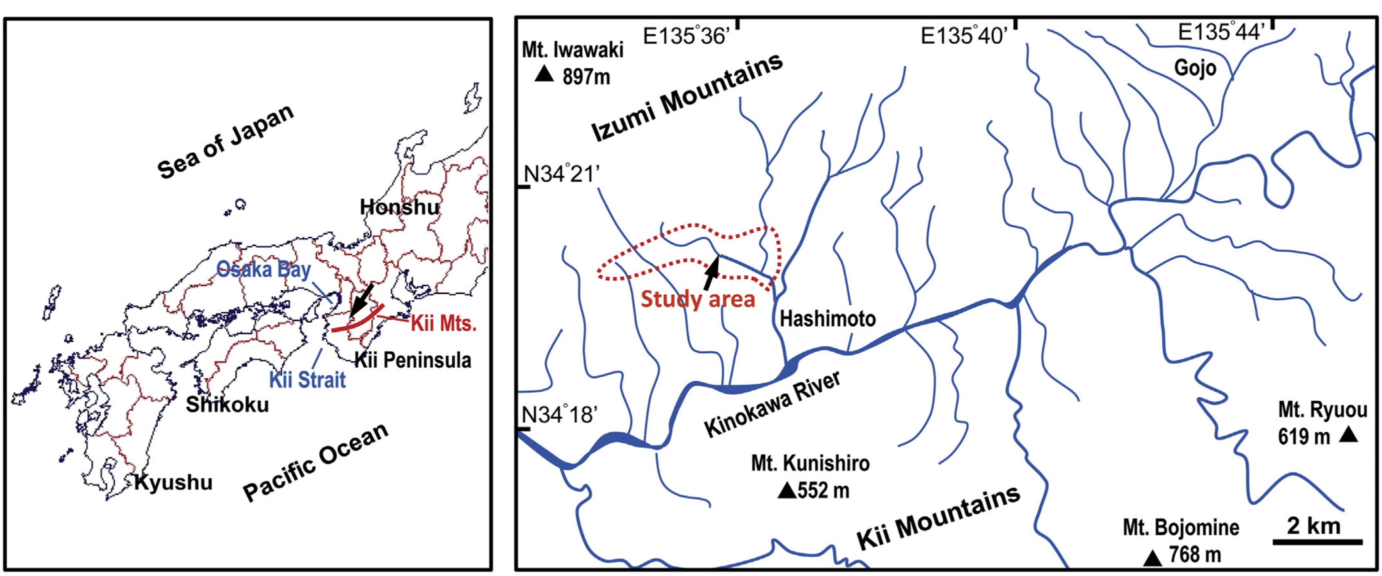


**Fig. 1.** Maps showing the study area in the northern Kii Peninsula where the fossil seeds of *Staphylea* were collected.