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Introgression and Long-Term Naturalization of Archaeophytes into Native Plants – Underestimated Risk of Hybrids

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1. Introduction

1.1 Difficulties in the study of archaeophytes

Alien plants pose problems in the conservation of biodiversity, especially by invasion and successive mal-effects on local ecosystem and biodiversity (Pyšek et al., 1995; Ellstrand, 2003; Nentwig, 2007). Even if they are only in cultivation, they could affect by hybridization, vector of diseases and pests and other factors. Since an alien plant is defined as one whose distribution has expanded out of its native range under human influence, the history of alien plants begins with human migration, especially in association with agriculture. As most have spread with active migration since the Age of Discovery, alien plants can be delineated into archaeophytes (introduced before the Age of Discovery) and neophytes (introduced since) (Pyšek et al., 2002; Preston et al., 2004).

Although this classification is commonly used, particularly in Europe, it is difficult to distinguish these two categories (Pyšek et al., 2004; Willis & Birks, 2006). It is practically impossible to prove the non-nativeness of a plant, especially from morphological, ecological, or phytogeographical data. For example, most archaeophytes grow in or near human-made environments, for example, as agricultural weeds or ruderal plants. They have already extended into that ecological system and have been held in equilibrium. Therefore, although research tries to distinguish archaeophytes from true native plants, the two are usually treated the same in the practice of biodiversity conservation. In fact, some archaeophytes are listed in Red Lists (Cheffings & Farrell, 2005; Ministry of Environment, Japan, 2007), since exclusion of archaeophytes from native plants without distinct evidence would make their conservation value lower (Willis & Birks, 2006).

1.2 Biodiversity in Japan and archaeophytes

The Japanese archipelago is rich in biodiversity (Ohwi, 1965; Iwatsuki et al., 1993–2011). The climate of this region ranges widely from subarctic to subtropical, with high humidity and precipitation throughout. It lies near the Asian continent and has been connected with it several times in geological history (continental islands). This placement may have promoted

migration from north and south and produced flora with mixed boreal and temperate elements. By contrast, the archipelago was not connected with the continent during the last glacial maximum, and this isolation may have stimulated the phylogenetic differentiation of species or intraspecific taxa from the continental mother taxa. In addition, its mountainous topography with about twenty 3000-m-class peaks provides refugia for many alpine plants that are relicts of the glacial period.

However, this biologically affluent archipelago is also one of the most populous regions in the world. Although preservation measures beginning in the early modern age have maintained a high percentage of forest (about 70% of land) and protected this "green archipelago" (Totman, 1987), population pressure still poses threats. Therefore Japan is nominated in one of the biodiversity hotspots (Mittermeier et al., 2004).

Humans arrived in Japan relatively recently, ca. 35 000 years BP or later (Keally, 2009). Agriculture is estimated to have begun in Japan 3000 years BP or later (Shōda, 2007). The introduction of alien plants may have begun from this period. Maekawa (1943) first proposed the concept of "prehistorically naturalized plants", presumably introduced from the Asian continent before the beginning of written history (end of the 6th century CE). He listed about 120 ruderal plants, mainly agricultural weeds. Other plants, including trees, are now also included in this category (Shimizu, 2003). Of course, many plants were also introduced from the Asian continent in historic times before the Age of Discovery. However, since most of these plants are crops or ornamentals, only a few became completely naturalized. Therefore, most of the naturalized archaeophytes in Japan are prehistorically naturalized plants.

1.3 Archaeophytic naturalized useful trees in Japan

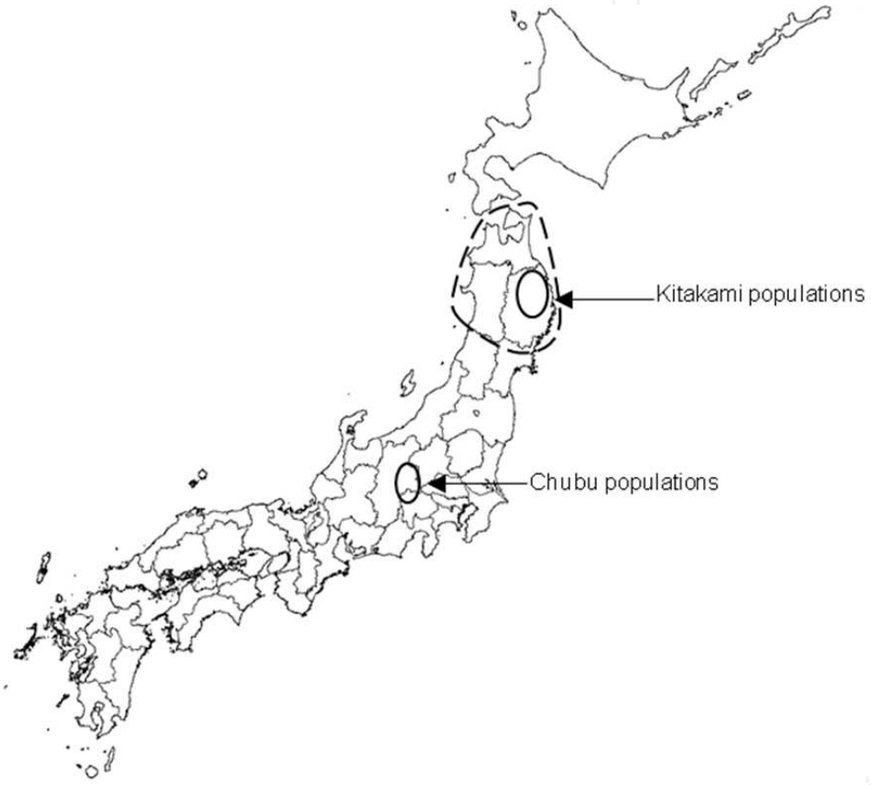
Several fruit trees and a few industrial crop trees were introduced into Japan prehistorically. Representative examples are pear (*Pyrus pyrifolia* Nakai), peach (*Prunus persica* L.), plum (*Prunus salicina* L.), apricot (*Prunus armeniaca* L.), persimmon (*Diospyros kaki* Thunb.), loquat (*Eriobotrya japonica* Lindl.), and princess tree (*Paulownia tomentosa* Steud.). These plants now grow more or less wild and can reproduce without human intervention. Some have extended their wild distribution into the upper temperate deciduous forest zone (1000–1600 m a.s.l. in central Japan), where human settlement has been rare and many native flagship species of Japanese biodiversity grow. Whereas some or all of these species were formerly regarded as native, archaeological and phytogeographical research now estimates that they are introduced; for example, the remains, usually seeds or stones, of these fruit trees are found only at archaeological sites dating after the beginning of agriculture, in contrast to native edible fruit species such as wild grape (*Vitis coignetiae* Planch.) and raspberries (*Rubus* spp.) (Kobayashi, 1990).

2. Introgression of archaeophytic *Pyrus pyrifolia* into native *Pyrus ussuriensis* in NE Japan

2.1 Problems in the classification of Japanese *Pyrus*

Among these naturalized useful trees, only *Pyrus pyrifolia* has intercrossable wild relatives in the flora of Japan, namely *Pyrus calleryana* and *Pyrus ussuriensis*. *Pyrus calleryana* is doubtlessly native because it has a very distinctive distribution in common with other

famous endangered plants such as *Magnolia stellata* (Ueda, 1989). On the other hand, the status of *P. ussuriensis* in the flora of Japan has been obscure. This plant was originally described in the early 20th century as two new native species from remote regions (Nakai, 1918): namely, *Pyrus hondoensis* in central Japan (Chubu region) and *Pyrus aromatica* in northeastern Japan (Kitakami Mountains; Fig. 1). However, since then, trees morphologically intermediate between these plants and *P. pyrifolia* were reported, and many of them were described as distinct species. As a result, more than 70 "species" of *Pyrus* were described throughout Japan. Since most of them exist only sporadically in human areas, modern taxonomists treat them as synonyms of either *P. pyrifolia* or *P. ussuriensis* (Ohwi, 1965; Kitamura, 1979; Iketani & Ohashi, 2001).



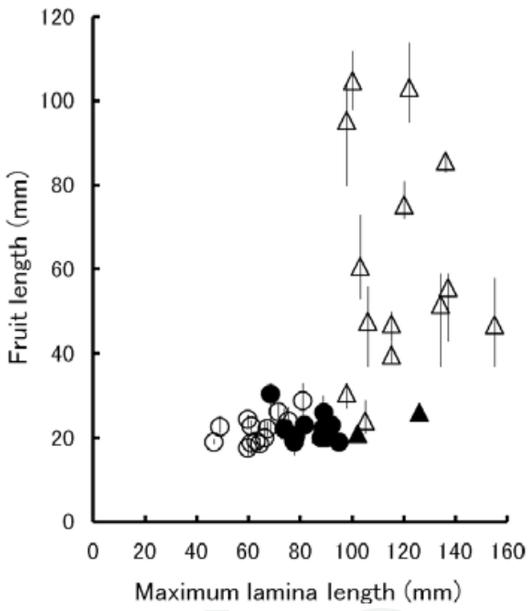
Solid ellipses indicate the distribution site of the populations in the Kitakami Mountains and the Chubu region. The dashed line indicates the region where wild trees other than the true native type are common. Prefectural boundaries are also shown.

Fig. 1. Localities of two native populations of *Pyrus ussuriensis* in Japan

This taxonomic confusion leads to doubt about the nativeness of wild populations of *P. ussuriensis* (Kitamura, 1979), which is heightened for other reasons. First, this species is edible and is cultivated in northeastern China and Korea. Therefore, *P. ussuriensis* could also have been introduced and naturalized. Second, species of *Pyrus* easily hybridize with each other. Third, morphological distinction between species is obscure: only the presence/absence of calyx lobes in mature fruits is the discriminative character in floristic and taxonomic works (Yü & Ku, 1974; Ku & Sponberg, 2003). Finally, the original sites of discovery are in the lower mountain zone, not far from human settlements.

2.2 Approaches from phytogeography and morphology

As one of the main reasons for this suspicion may be a lack of understanding of the true wild populations of *P. ussuriensis*, my group performed extensive field investigations (Iketani & Ohashi, 2003). We found this species both near the original places of discovery and in more elevated places, which correspond to the upper temperate deciduous forest zone. In contrast to the sporadic distribution of trees growing in human areas at lower elevation, the wild trees grew more densely at higher elevation. They were also morphologically distinct from other seemingly wild or cultivated trees. The fruits and leaf laminae are small in the former but vary in the latter from as small as in wild trees to as large as in edible cultivars (Fig. 2). In addition, the disjunctive geographical distribution at higher elevations of the Chubu region and the Kitakami Mountains is one of the distinctive patterns of endemic taxa in the flora of Japan (Ohashi, 1987). These findings support the indigenousness of the wild populations.



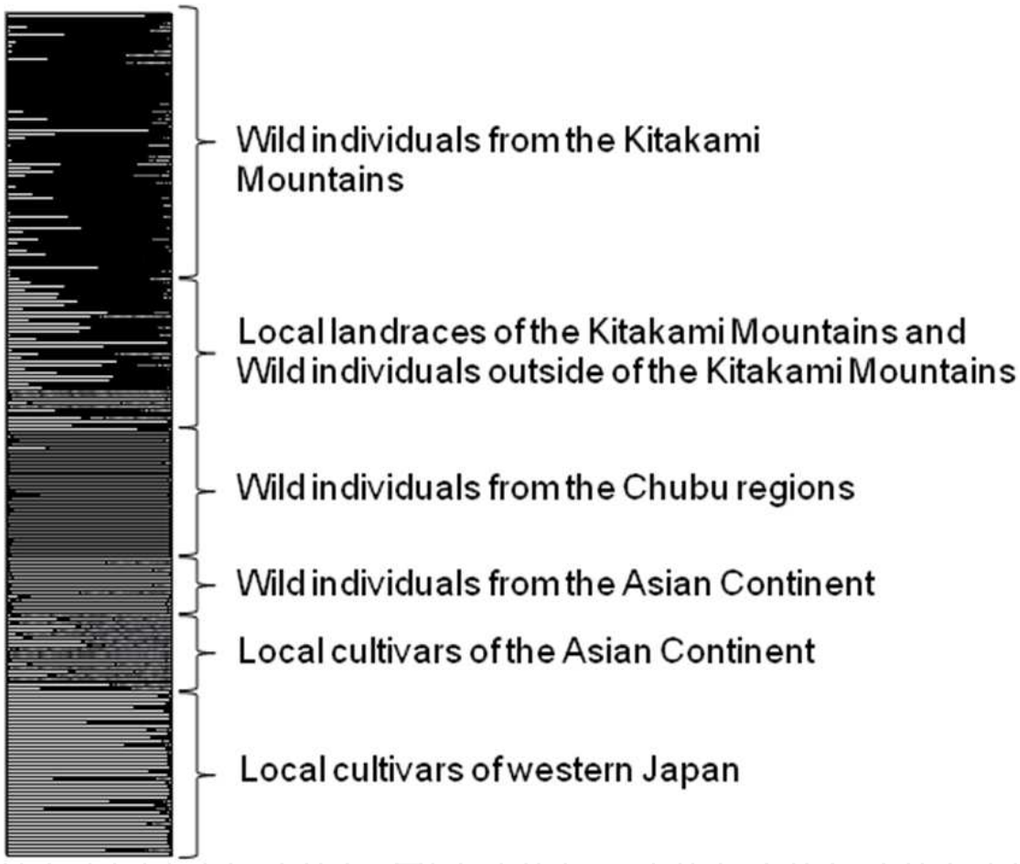
● *Pyrus ussuriensis* from northeastern Japan. ○ *P. ussuriensis* from central Japan. ▲ *P. ussuriensis* from Asian continent. ▵ Cultivars of *P. ussuriensis* and naturalized *Pyrus*. Vertical lines show the maximum and minimum values of fruit length. (From Iketani & Ohashi, 2003)

Fig. 2. Relation between fruit length and maximum lamina length in *Pyrus* accessions

2.3 Molecular approach reveals introgression between native and prehistorically naturalized plants

Traditional methods made the presence of true native populations plausible. However, the evidence was not conclusive, and the reason for the appearance of morphologically intermediate trees between *P. ussuriensis* and *P. pyrifolia* remained in doubt. Worse, many pear trees with wide morphological variations were discovered in the Kitakami Mountains and surrounding region (Katayama & Uematsu, 2006). To resolve these difficulties, we investigated population genetics using microsatellite loci and with Bayesian statistical inference (Iketani et al., 2010).

The analysis of 226 individuals from six regions implied five hypothetical ancestral populations (Fig. 3; Iketani et al., 2010). These results were at least partly predictable, but not entirely expected. The two true native populations of *P. ussuriensis* in Japan showed genetic distinctiveness, and both were much differentiated from wild plants of *P. ussuriensis* in the Asian continent. These results show that the Japanese populations of *P. ussuriensis* are truly native. Similarly, the introduction of *P. pyrifolia* from China was also supported, since the genetic structure of old Japanese cultivars and local landraces shows a partially common element with Chinese pear cultivars.



Five hypothetical ancestral populations are shown with different shadings. Modified based on Iketani et al., (2010)

Fig. 3. Bayesian statistical inference of population structure of *P. ussuriensis* and *P. pyrifolia*.

Populations from northeastern Japan were more or less genetically admixed with *P. pyrifolia*. This phenomenon was more conspicuous in local landraces and wild individuals collected from outside of the Kitakami Mountains, but was also evident in wild individuals in that region. This result and the ubiquity of intermediate trees clearly show introgression between native *P. ussuriensis* and prehistorically naturalized *P. pyrifolia* trees. In addition, truly native trees proved to be much rarer than introgressed trees and should be protected. *Pyrus ussuriensis* has now been added to the Japanese National Red List of Threatened Plants (Ministry of Environment, Japan, 2007).

3. Implications for biological conservation

3.1 Long-term hybridization and naturalization?

At present we have almost no empirical evidence to infer the historical introgression of *P. pyrifolia* into native *P. ussuriensis*. Although agriculture began later in northeastern Japan than in western Japan, the introduction of *P. pyrifolia* into this region would have also begun prehistorically, or early in historical times at the latest. Since *P. pyrifolia* itself is not widely escaped and naturalized even now, hybridization might have occurred first, and naturalization of hybrid offspring might have followed. Acceleration of naturalization due to hybridization between alien and native species, which is a well-known conservation problem (Ellstrand, 2003; Fitzpatrick & Shaffe, 2007), might have happened.

However, there are still many unclear points in the above scenario. Neither *P. ussuriensis* nor *P. pyrifolia* is very invasive. When assessed for invasiveness, they are judged as posing no or limited risk. For example, their weed risk factor (Food and Agriculture Organization of the United Nations [FAO], 2005) is 4 at most, against a critical score of 6. Even if the fitness of hybrids is better than that of the parents, it is unlikely that they would have expanded like other invasive plants. Therefore, we have to ascribe the cause of this limited expansion to the long passage of time, perhaps more than a thousand years. Kowarik (1995) and Pyšek & Jarošík (2005) studied the time-lag between the introduction and naturalization of alien plants in terms of centuries. The case of *Pyrus* could be appended as an example in terms of millennia.

A long residence time must raise the chance of successful naturalization (Pyšek & Jarošík, 2005). However, human activities such as repeated secondary release would promote invasion beyond the threshold of naturalization (Kowarik, 2003). As both *Pyrus* species bear edible fruits, ancient peoples in northeastern Japan might have grown and propagated hybrid pear trees, which would have become the source of secondary release, although there is no supportive evidence from history, ethnology, archaeology, or demography. Thus, research in these fields will be necessary.

3.2 Negative effect of archaeophytes through hybridization

How should we treat these hybrid pears? On one hand, they now grow widely in northeastern Japan but are not very invasive. The number of individuals is not very large and they are perhaps held in equilibrium in nature. Therefore, they could be treated similarly as native plants, as many other prehistorically naturalized plants (archaeophytes) are.

However, we cannot ignore these pears, because the plant that now grows widely is not an archaeophyte itself. Instead, an archaeophyte has hybridized with a native plant, and the hybrid offspring grow better than their native parent. In this case, hybrid plants should be controlled for the conservation of native plants, especially if the latter are threatened.

This case shows that archaeophytes that are themselves not invasive could still pose a risk to native plants in the long term. The negative effects of alien plants on natural ecosystems are already known. For example, there is much evidence that crops and other domesticated plants can hybridize with their wild relatives while still in cultivation (Ellstrand, 2003). Reproductive interference, which is the depression of fitness by interspecific pollination

interactions such as competition for limited pollinators and pollen loss by interspecific pollen transfer, has recently been recognized (Matsumoto et al., 2010; Takakura et al., 2011). In both phenomena, negative effects could become evident on the human timescale if a plant was cultivated extensively, such as agricultural crops. Even with ornamental use, the effect could appear on such a timescale.

Sukopp & Sukopp (1993) expressed concern about the naturalization ("becoming feral") of cultivated plants ("cultigens") and long-term ecological effects such as hybridization with related wild plants. They listed several pairs of cultivated and wild plants in Central Europe which could hybridize. Since then, several actual cases among these pairs have been reported; e.g., *Daucus carota* ssp. *sativus* and ssp. *carota* (Magnussen & Hause, 2007), *Beta vulgaris* ssp. *vulgaris* and ssp. *maritima* (Arnauld et al., 2003; Fénart et al., 2008), and *Brassica napus* and *Brassica rapa* (Andersen et al., 2009).

In conservation policy, introduced cultivated plants which prove not to be invasive are not usually regard as dangerous. However, in the conservation of threatened plants, their crossable relatives should not be grown near natural habitat. The International Union for Conservation of Nature and Natural Resources [IUCN] (2000) recommended: "Since the impacts on biological diversity of many alien species are unpredictable, any intentional introductions and efforts to identify and prevent unintentional introductions should be based on the precautionary principle." The case of *Pyrus* supports this policy. We have to control even archaeophytes if they could harm native plants, once they prove to be truly naturalized alien plants. This is why we should distinguish archaeophytes and true native plants more precisely.

3.3 Potential problems in the Pyrinae

The invasiveness and other negative ecological effects of *Pyrus* and related plants are also relevant to the case for distinguishing archaeophytes and true native plants more precisely. The genus *Pyrus* belongs to the subtribe Pyrinae of the tribe Pyreae (formerly subfamily Maloideae) in the family Rosaceae (Potter et al., 2007). Since the reproductive barriers between the members of this tribe are low, interspecific hybrids which are usually fertile are common in nature; even intergeneric hybrids are not rare. This is one of the most extreme cases in higher plants, even though plants produce hybrids much more easily than animals. Previously this character has been a problem only in taxonomy (Kovanda, 1965; Robertson et al., 1991), but it could also become a problem in conservation. Species of this subtribe naturalize commonly in the temperate zones of both hemispheres; e.g., *Malus pumila* (apple), *Pyrus communis* (common pear), *P. pyrifolia*, *Cotoneaster* spp., and *Crataegus* spp. (hawthorn).

So far, only a few species of the Pyrinae are nominated in national and other lists of invasive plants (Table 1). This list shows the obvious invasiveness of some species in Oceania and the Pacific islands, where no native species of the Pyrinae grow (except for *Osteomeles*). *Eriobotrya japonica*, *Pyracantha* spp., and *Sorbus* spp. are also naturalized in the temperate zone of Europe and Japan (Tutin et al., 1968; Shimizu, 2003), but they are not recognized as invasive. However, hybridization between introduced plants and their wild relatives would happen in the long term even without naturalization.

Recently, the invasiveness of *Pyrus calleryana*, which was introduced from East Asia and has been widely propagated in the USA as an ornamental during the past 50 years, has been

Species	Nominated list[a]
Amelanchier spicata	EMPPO
Cotoneaster franchettii	AWC, CIPC
Cotoneaster glaucophyllus	AWC, MoE NZ
Cotoneaster lacteus	CIPC
Cotoneaster pannosus	AWC, HER, CIPC
Cotoneaster salicifolius	AWC
Cotoneaster simonsii	AWC, MoE NZ
Crataegus monogyna	AWC, CIPC
Crataegus sinaica	AWC
Eriobotrya japonica	MoE NZ, HER
Pyracantha angustifolia	AWC, HER, MoE NZ
Pyracantha coccinea	AWC
Pyracantha fortuneana	AWC
Sorbus aucuparia	MoE NZ
Sorbus spp.	AWC

a: AWC, Australian Weeds Committee (2011). CIPC, California Invasive Plant Council (2006). EMPPO, European and Mediterranean Plant Protection Organization (2011). HER, Hawaiian Ecosystems at Risk (2011). MoE NZ, Ministry of Environment, New Zealand (2011).

Table 1. Species of the Pyrinae nominated in national and other lists of invasive plants.

recognized (Vincent, 2005). This is perhaps the first case of a species of *Pyrus* being recognized as invasive. This sudden realization of invasion is explained as the overcoming of self-incompatibility owing to the planting of different cultivars and the Allee effect (Culley & Hardiman, 2009; Hardiman & Culley, 2010). However, since there are no native species of *Pyrus* in North America, negative genetic effects on native relatives would not occur.

In Europe, in contrast, although Sukopp & Sukopp (1993) stated that *Pyrus communis* became feral in Europe in the absence of wild relatives, in fact there are many wild species in this continent (Tutin et al., 1968; Aldasoro et al., 1996), some possibly of hybrid origin, either wild × wild or wild × cultivated. Introgression between cultivated apple (*Malus pumila*, syn. *M.* ×*domestica*) and a wild relative (*Malus sylvestris*) in Europe is already known (Coart et al., 2003, 2006; Larsen et al., 2006). These cases are comparable to our case of *Pyrus ussuriensis* in terms of introgression between archaeophytic cultivated fruit trees and wild relatives.

The most crucial but incompletely understood situation occurs in East Asia, the center of differentiation of both *Pyrus* and *Malus*, as well as of many other genera of the Pyrinae. About 20 species of *Pyrus* and 30 of *Malus* are now recognized in this region (Iketani & Ohashi, 2001; Ohashi, 1993; Wu et al., 2003). Some species, especially those now found only in cultivation, might have a hybrid origin. These hybridizations might have occurred among native species, although some might have occurred between alien and native. For example, the Chinese pear cultivars we studied proved to be admixtures between *P. ussuriensis* and *P. pyrifolia* (Fig. 3). These cultivars originated in northern China (Yü, 1979), where *P. ussuriensis*

is native but *P. pyrifolia* is alien. Thus, the hybridization would have occurred between wild trees or local landraces of the former and introduced plants of the latter. The time of hybridization is uncertain, but is perhaps not recent. Floristic studies show that trees referred to as *P. ussuriensis* with fairly large fruits occur in nature (Yü & Ku, 1974; Ku & Sponberg, 2003). They are perhaps hybrids, as found in Japan.

4. Future research possibilities

Our case of *Pyrus* suggests that whether a plant is native or alien could be inferred from molecular data. However, studies based on this strategy are rare. In Japan, Sasanuma et al. (2002) and Hori et al. (2006) reported the genetic uniformity of *Elymus humidus* and *Lycoris radiata*, respectively, both of which are prehistorically naturalized plants, in comparison with a certain level of genetic diversity among their wild relatives. European studies have focused on cultivated plants and their relatives. In addition to the abovementioned studies of *Daucus*, *Beta*, *Brassica*, and *Malus*, there are several studies of *Triticum* and *Aegilops* (e.g., Zaharieva & Monneveux, 2006; Arrigo et al., 2011). However, investigations in Europe would be difficult, because Europe is contiguous with the true native habitats of many archaeophytes, and archaeophytes could have been introduced much earlier (from the 6th millennium BCE) than in Japan. Nevertheless, as there are many more archaeophytes in Europe than in Japan and as many putative hybrids between native and alien plants have already been reported (Vila et al., 2000; Pyšek et al., 2002), many opportunities for research remain. For example, English elm (*Ulmus minor* var. *vulgaris*) was proved to be a 2000-year-old Roman clone (Gil et al., 2004).

The importance of research in East Asia and other parts of Eurasia is obvious (Castri, 1989). In research on alien plants, basic biological data such as floristic and ecological status and phytogeography are necessary. Research in historical documents and archaeological data is important for the assessment of archaeophytes. Fortunately, East Asian countries are rich in these resources. Traditional Eastern herbalism, which originated in China and was also developed in Japan and Korea, may provide plant records. Although research in the East still has many constraints compared with that in the West, our long historical cultural heritage offers one important advantage.

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Topics in Conservation Biology

Edited by Dr. Tony Povilitis

ISBN 978-953-51-0540-4
Hard cover, 110 pages
Publisher InTech
Published online 02, May, 2012
Published in print edition May, 2012

Conservation biology is called a "crisis discipline." In a world undergoing rapid change, this science informs us about research, technologies, management practices, and policies that can help protect the earth's naturally-occurring biological diversity. The six chapters of this book provide insightful analysis on managing protected areas (Middle East), conserving biochemical and genetic diversity of carob tree (Tunisia) and wild pear (Japan), determining the health status of Amazon manatee, manipulating sex ratios to benefit wildlife, and narrowing the gap between religion and conservation. The authors approach threats to biological diversity from varied angles, reflecting the interdisciplinary nature of the field. This book offers room for reflection on the definition and utility of the word 'natural' on a planet now overwhelmingly dominated by people.

How to reference

In order to correctly reference this scholarly work, feel free to copy and paste the following:

Hiroyuki Iketani and Hironori Katayama (2012). Introgression and Long-Term Naturalization of Archaeophytes into Native Plants - Underestimated Risk of Hybrids, Topics in Conservation Biology, Dr. Tony Povilitis (Ed.), ISBN: 978-953-51-0540-4, InTech, Available from: http://www.intechopen.com/books/topics-in-conservation-biology/introgression-and-long-term-naturalization-of-archaeophytes-into-native-plants-underestimated-risk-o

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