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Living on the Edge: Various Modes of Persistence at the Range Margins of Some Far Eastern Species

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1. Introduction

Present-day patterns of plant distribution have been formed under the influence of various biotic and abiotic factors. Plant distribution reflects the habitat preferences of species and the outcome of their competition as well as the complex evolutionary processes resulting in the specificity of mating systems, the genetic structure of different species and other aspects of species biology. Together, these factors determine the current ranges and distributions of plant species. At the edge of a species' range, the significance of particular interactions with the environment becomes more pronounced. However, our understanding of this class of interactions is limited. There is debate about whether these interactions represent a distinct and ordered set of related phenomena or whether they are unrelated and without order. Different approaches to this problem are needed in different situations. Understanding the processes of microevolution in species at the edges of their ranges is of great interest, particularly in view of the continuing decline in worldwide biodiversity and ongoing and future climate changes. When the area of a plant's habitat is sufficient, most populations exist in a relatively stable condition, and changes in their genetic structure follow slow processes, such as gene flow and genetic drift. However, in populations growing at the edge of their range, the rates of genetic processes can change dramatically. At the limits of the climatic and ecological tolerance of species, populations usually become smaller and more fragmented. These populations are generally less genetically diverse than those living at the center of the range because they exist in less favorable habitats and at lower densities, and consequently, they may be more prone to extirpation (Hampe & Petit, 2005; Vucetich & Waite, 2003). However, some species may have existed as groups of isolated populations for thousands of generations. The long-term survival and evolution of a species depends on the maintenance of sufficient genetic variability within and among populations. Patterns of population genetic diversity have been shown to be generally shaped by past climate-driven range dynamics, rather than solely by stochastic demographic and genetic processes (Hewitt, 2004). Given the enormous variety of plant life forms and their habitats as well as the complexity of their evolutionary histories, it is difficult to accept as a general rule that all marginal populations will exhibit lower genetic diversity than those from the center of a

species' range. Moreover, this rule would not hold true for all rare plants, which are associated with different causes underlying their rarity. A comparison of rare species belonging to different plant families and with different evolutionary histories may aid in inferring a number of scenarios under which a species may persist at the edge of its range. These scenarios may include common principles that do not correspond well to the "center-periphery" hypothesis.

2. The region and the species selected

The southern part of East Asia together with tropical Asia, is considered one of the centers of the origin and diversification of many plant taxa. The southern region of the Russian Far East (Primorsky Territory, Primorye) is located at the eastern edge of the Asian continent. The majority of this region is mountainous, with the Sikhote Alin Mountains extending throughout most of the area. The geographic location of the region accounts for the variety of its flora: it includes mountainous tundra areas, coniferous forests and coniferous-deciduous forests, and part of the lowlands surrounding Khanka Lake is occupied by forest-steppe. The flora of the region is unique and is characterized by a very complex mix of representatives of different kinds of vegetation. Unlike many other regions at the same latitude, most of this area was not glaciated during the Pleistocene; glaciers were limited to the highest peaks of Sikhote Alin, and the vegetation has undergone uninterrupted development since the Pliocene. The modern species complexes of Sikhote Alin have been formed during numerous migration processes under the influence of global climate change, the specific impact of the region's proximity to the ocean and marine transgressions. The region maintains a large number of rare and endangered species that originated in earlier epochs. Unfortunately, many of the previously abundant plants of the area have already become rare and are disappearing as a result of increasing anthropogenic pressure. The removal of rare and disappearing plants from their native habitats has led to the disruption of natural ecosystems and has significantly impoverished the biodiversity of the region.

Over 2,500 vascular plant species are represented in the flora of the southern part of the Russian Far East, and more than 340 species are listed in the Red Data Book of Primorsky Krai (2008) as endemic, rare or endangered. A large number of rare species are endemic, restricted to certain habitats, or their northern distribution limits are located in the region. Some of these species are relics of Tertiary flora with extremely limited ranges, whereas others exhibit range habitat preferences occupying tiny areas at specific locations. We have chosen a number of rare Far Eastern species (Figure) characterized by different life history traits for the present study. All of these species are listed in the Rare Plant Species of the Soviet Far East and Their Conservation (Kharkevich & Kachura, 1981), Red Data Book of Primorsky Krai (2008) and the Red Data Book of the Russian Federation (1988). The genetic diversity and population structure of each of these species have been studied using the following markers: allozymes, dominant DNA markers (random amplified polymorphic DNA, RAPD, and/or inter simple sequence repeat, ISSR) and sequences of noncoding regions of the chloroplast genome (cpDNA). Some life history traits and the main parameters related to genetic diversity and population structure in these species are presented in Table. Below, we provide a detailed description each of these species.

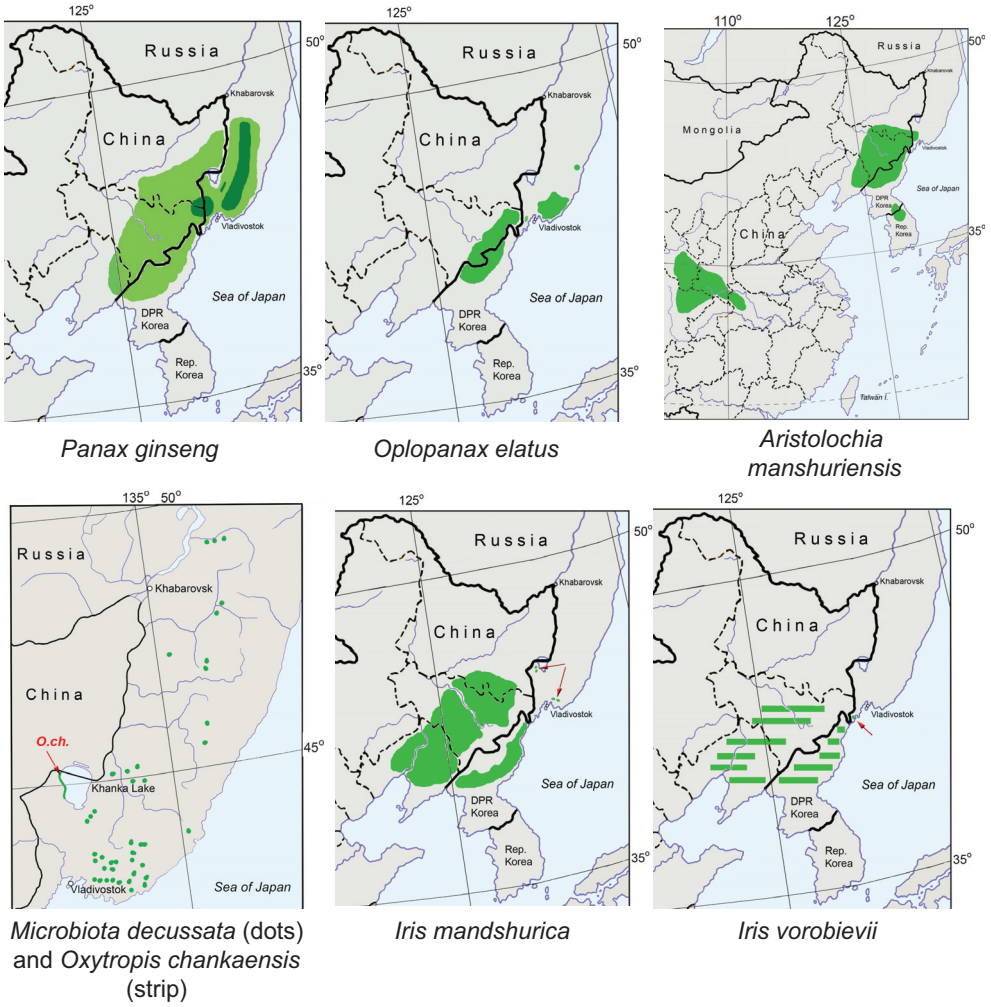

Fig. 1. Geographic ranges of rare Far Eastern species under study (according to Alexeeva, 2008; Huang et al., 2003; Kharkevich & Kachura, 1981; Shu, 2000; Xiang & Lowry, 2007; Zhu et al., 2010).

2.1 Ginseng (oriental ginseng), *Panax ginseng* C.A. Meyer

Ginseng, *Panax ginseng* C.A. Meyer, is a representative of the *Panax* L. genus related to an ancient family of angiosperms, the Araliaceae, members of which have been found in Cretaceous deposits. Most members of the Araliaceae are distributed in tropical and subtropical regions, with some species reaching the temperate zone. The *Panax* genus consists exclusively of herbaceous perennial plants, and all species in this genus are distinguished by the peculiar structure of an aboveground shoot that dies annually, whereas most members of the Araliaceae are trees or shrubs (Grushwitsky, 1961). The uniqueness of

Species*	Life-hystory traits					
	Life form	Life-span (years)	Clonality	Mating system	Pollination	Seed dispersal
Panax ginseng, E	PH	140	NC	S, A	I	G, A
Oplopanax elatus, V	S	300	C	S	I	G, A
Aristolochia manshuriensis, E	WL	50	NC	S	I	W, Wa
Microbiota decussata, V	S	250	C	S	W	G
Oxytropis chankaensis, V	PH	50	NC	S	I	W, Wa, G
Iris vorobievii, E	PH	≤7	PC	S	I	G, A
*Iris mandshurica,*V	PH	25	C	S	I	G, A

Species*	Genetic diversity parameters at population level								
	Allozymes			Dominant markers			Chloroplast DNA		
	P_{95}	*He*	F_{ST}	P_{95}	*He*	G_{ST}	$\pi \cdot 10^{-3}$	*h*	G_{ST}
Panax ginseng, E	7.6	0.022	0.204	4.0	0.013	0.249	–	–	–
Oplopanax elatus, V	25.0	0.113	–	23.5	0.088	0.293	–	–	–
Aristolochia manshuriensis, E	25.0	0.108	0.065	36.2	0.141	0.112	–	–	–
Microbiota decussata, V	–	–	–	45.1	0.249	0.352	0.603	0.954	0.090
Oxytropis chankaensis, V	37.1	0.294	0.025	66.9	0.290	0.135	0.480	0.703	0.146
Iris vorobievii, E	–	–	–	32.5	0.104	–	0.587	0.912	–
*Iris mandshurica,*V	–	–	–	31.3	0.108	–	0.285	0.733	–
Mean values for species with restricted ranges**	29.9	0.095	0.206	–	0.280	0.210	–	–	0.637a 0.165g

Table 1. Life-history traits and parameters of genetic variation in populations of rare Far Eastern species studied. *, Categories of rarity are given with the species name according to the Red Data Book of Primorsky Krai (2008): E, endangered; V, vulnerable. Life form: S, shrub; WL, woody liana; PH, perennial herb. Clonality: C, clonal; PC, poor clonal; NC, non-clonal. Mating system: S, sexual; A, apomixis. Pollination: W, wind; I, insect. Seed dispersal: W, wind; Wa, water; A, animal; G, gravity. Genetic diversity parameters at population level: P_{95}, percentage of polymorphic loci (95% criterion); *He*, expected genetic diversity; π, nucleotide diversity; *h,* haplotype diversity; F_{ST}, and G_{ST}, indices of genetic differentiation among populations; –, not determined. **, Mean values of genetic variation parameters in species with restricted ranges are cited from Gitzendanner & Soltis, 2000 (for allozyme data) and Nybom, 2004 (for dominant DNA marker data); G_{ST} based on chloroplast DNA data are cited from Petit et al. (2005): a, for angiosperms; g, for gymnosperms.

The genus *Panax* makes it difficult to ascertain its alliances with other genera of Araliaceae. The range of *Panax* is divided by the Pacific Ocean into two parts: an East Asian and a North American region (Grushwitsky, 1961). The intrageneric systematics of *Panax* has been revised as a result of the similarity of different *Panax* species habitus and the presence of intermediate forms that complicate species discrimination. Most *Panax* species are found in Eastern and Southeastern Asia, with the exception of *P. quinquefolium* L. and *P. trifolius* L.,

which inhabit North America. *P. ginseng* and *P. quinquefolium* have a chromosome number of 2n = 48, whereas most other *Panax* species exhibit 2n = 24.

In the past, *P. ginseng* was distributed throughout a wide territory in the forests of the Far East. It was estimated in the 1950s that in the first half of the 20th century, wild-growing ginseng plants could be found in large forestlands from 40° to 48° northern latitude and from 125° to 137° eastern longitude, covering approximately 500,000 square kilometers (Grushwitsky, 1961). At that time, the ginseng populations growing in Russia represented the northeastern boundary of the species' geographic range, whereas its main habitat area was located south and west of this territory, covering Heilongjiang, Jilin and Liaoning Provinces in China and the northern part of Korea. The natural range of ginseng is now drastically reduced (Figure). Wild-growing ginseng had disappeared completely from Korea and Liaoning Province in China by the 1930s and almost completely from Heilongjiang and Jilin Provinces in China by the 1990s (Zhuravlev & Kolyada, 1996). The distribution of ginseng has currently narrowed to a few patches in Russia and China (Zhuravlev & Kolyada, 1996; Zhuravlev et al., 2008). The largest patch of this species is located in the southern part of the Sikhote Alin mountain range; another population inhabits the southwest region of Primorye and Jilin and Heilongjiang Provinces (Changbai Mountains) in China; and a third population is located in the western part of Primorsky Territory (Figure, dark green). Reports of wild ginseng in China have become rare. In Russia, ginseng has been listed in the Red Book since 1975 as a federally threatened species (Red Data Book of the Russian Federation, 1988), and at present, Primorsky Territory in Russia is the only place in the world where natural ginseng populations exist, representing a remnant gene pool of wild-growing ginseng.

Ginseng is an herbaceous perennial species with an annually moribund shoot. It grows in certain special habitats and persists only in remote locations. It is very difficult to estimate the actual abundance of wild-growing ginseng in nature because of its ability to undergo lengthy dormancy, which may last from one to several dozen years; therefore, the recorded number of vegetative ginseng plants does not correspond to their true abundance. I.V. Grushwitsky investigated natural ginseng habitats in the 1950s and wrote that this plant did not exhibit a tendency toward extinction for the most part, despite its relic origin and low rate of regeneration (Grushwitsky, 1961). However, he also noted that human activity has a destructive influence on natural ginseng populations, reducing them to potentially threatened levels. In addition, logging, fires and the shallowing of rivers hamper the restoration of ginseng populations. Poaching and overexploitation of ginseng resources appear to be the most important and most obvious reasons for the reduction and exhaustion of ginseng populations today (Zhuravlev & Kolyada, 1996).

Ginseng reproduces exclusively through seeds and is nearly incapable of vegetatively reproducing (Grushwitsky, 1961; Zhuravlev & Kolyada, 1996). This species is characterized by a mixed mating system and the ability to produce seeds via autogamy, outcrossing or agamospermy without pollination (Koren et al., 1998). Presumably, self-pollination has prevailed in natural ginseng populations because of their low plant density. The occurrence of outcrossing, which is carried out by insect pollen transfer, cannot be excluded in natural environments, but this appears to be very rare and likely does not play a significant role in ginseng pollination. *P. ginseng* has also been shown to be a facultative apomict with a type of agamospermy resembling diplospory (Koren et al., 1998; Zhuravlev et al., 2008).

Studies on the genetic variability of *P. ginseng* using different molecular markers (allozymes, RAPD, ISSR) have detected very low levels of genetic polymorphism (Koren et al., 2003; Zhuravlev et al., 2008; Reunova et al., 2010a). Only 3 allozyme loci among 39 studied and only one of 74 RAPD loci were found to be polymorphic. These low levels (Table) do not differ significantly from estimates obtained with ISSR markers (P_{ISSR} = 9.3%, He_{ISSR} = 0.014, Reunova et al., 2010a). These data are also in agreement with the results of genetic studies on cultivated ginseng sampled from China and Korea (e.g., Kim & Choi, 2003). Thus, *P. ginseng* is characterized by a lower level of genetic variation than the average values found for rare endemic species (Table).

An analysis of population subdivisions based on allozymes and dominant DNA markers showed a low level of differentiation of natural *P. ginseng* populations and a decrease in the total genetic diversity in the Sikhote Alin population (Zhuravlev et al., 2008). The great majority (up to 95%) of the genetic variability in this species is concentrated within populations, whereas only 4.1% of the total variation was found to be distributed among 8 sub-populations (estimated by allozymes, Zhuravlev et al., 2008). Approximately 25% of the variation is distributed between populations (estimated with DNA markers, Reunova et al., 2010a). No correlation between geographic and genetic distances was found for the investigated populations using allozyme and DNA markers.

Extremely low levels of genetic variation are usually found in endemic or relic plant species with narrow ranges which can often be connected to a species' life history and/or evolutionary events such as selection or genetic drift. The low genetic diversity of *P. ginseng* populations indicates that this species has experienced a severe genetic bottleneck. In particular, the lack of variation in the Sikhote Alin population may be a result of a founder effect because of the lack of a refugium during the last Pleistocene-Holocene cooling. This hypothesis is supported by the results of an analysis of the genetic relationships of extant ginseng populations on the basis of allozymes and DNA markers (Zhuravlev et al., 2008; Zhuravlev et al, 2010; Reunova et al., 2010a). Without other available natural populations to analyze, we can only assume that the center of the genetic richness and, possibly, the center of the origin of ginseng was located southwest of its extant natural populations, potentially in a place where there is great industrial activity in modern China.

Another reason for the low genetic diversity found in *P. ginseng* may be adaptive selection that has occurred in response to climate cooling and during the expansion of the species northward from its southern refugia. Some peculiarities of ginseng biology (such as its underdeveloped embryos and aboveground germination) indicate that this species evolved during a warm climate as a representative of the ancient thermophilic flora. A number of *P. ginseng* traits, especially related to its mating system, indicate recent adaptations (Koren et al., 1998; Zhuravlev et al., 2008).

Past evolutionary events have resulted in extant ginseng populations being characterized by very low genetic variation. However, this low genetic diversity did not prevent the species from surviving across a wide territory until recently. Despite its weak competitiveness, *P. ginseng* possesses some degree of ecological flexibility, certain adaptations to unfavorable environments and the ability to ensure seed reproduction via different pathways. Among these properties, increased individual longevity may be the main mechanism underlying the long-term survival of the species under unstable conditions. Discoveries of 100-year-old ginseng plants are occasionally recorded, and cases of 300-year-old plants are well known

(Zhuravlev & Kolyada, 1996). In addition, the life spans of individual plants may lengthen in accordance with their ability to undergo long-term dormancy (in the form of so-called "dormant roots"). Because ginseng maintains a generative stage starting from an age of 3-5 years and lasting until death, annually producing up to 100 seeds per plant, a single individual can maintain a population's size for hundreds of years, even if only a small proportion of its offspring survives and reaches generative age. Moreover, the seeds of one generation can germinate over a period of several years because to mature, the underdeveloped embryo requires an alternation of warm and cold periods that can take from one to several years.

At the same time, limited opportunities for recombination (autogamy, agamospermy) can result in further reducing the genetic diversity of ginseng. Moreover, because all three extant ginseng populations occupy the northeastern margin of its former distribution area, their gene pools are not enriched by gene flow from extirpated central populations. With the continuing reduction of natural ginseng populations as a result of human activity, this species may become extinct in the wild very soon.

2.2 Japanese devil's-club, *Oplopanax elatus* (Nakai) Nakai

Oplopanax elatus is another member of the ancient family Araliaceae. This species is a deciduous shrub with a spiny stem approximately 1 m in height and large palmately compound leaves. The species' distribution area is quite limited. In Russia, *O. elatus* occurs in the southern Primorye, where its range is represented by several isolated populations associated with the main mountain peaks of the southern Sikhote Alin. Outside Russia, *O. elatus* grows on the northern Korean Peninsula (Kurentsova, 1968; Zhuravlev & Kolyada, 1996) and in Jilin Province in China (Xiang & Lowry, 2007) (Figure). *O. elatus* is a valuable medicinal plant; its effects are similar to those of ginseng, and it is authorized for medical use (Kurentsova, 1968; Zhuravlev & Kolyada, 1996; Schreter, 1975). This species is particularly vulnerable as a result of intensive harvesting and habitat disturbance due to fires and logging.

Oplopanax Miq. is a small genus that includes three species and demonstrates a classical Eastern Asian and North American disjunct distributional pattern. *O. horridus* occurs on the Pacific coast of the United States and Canada as well as around Lake Superior. *O. japonicus* is endemic to the Japanese Islands (Hokkaido, Honshu and Shikoku). This disjunct distribution pattern is observed for many plant genera and is explained by the existence of the land bridges between Eurasia and North America and between the Japanese Archipelago and the mainland during the Pliocene-Pleistocene. Based on the internal transcribed spacer sequences of nuclear ribosomal DNA (ITS rDNA), phylogenetic analysis confirmed the origin of the three *Oplopanax* species from a common East Asian ancestor. The closely related species *O. horridus* and *O. elatus* form a sister pair, and both are closely related to *O. japonicus* (Artyukova et al., 2005). An ancestral form that gave rise to *O. horridus* and *O. elatus* could have survived in the coastal zone during global cooling and the strengthening of climate continentality during the Early Pliocene and subsequently spread along the Pacific coast and across the Bering Bridge into North America.

In southern Primorye, *O. elatus* is mainly confined to the orotemperate belt in the altitudinal range of ca. 800 to 1,500 m above sea level and is a common species in the understory of fir-spruce forests (Kurentsova, 1968) occurring in moist, well-drained ecosystems. This species,

which is clearly representative of the thermophilic and hydrophilous Turgai flora, has found specific refugia in the understory of fir-spruce forests, which favors its growth. Only under these conditions does the species occur at lower altitudes in coniferous–deciduous forests. However, its growth in mixed forests is hindered not only by low humidity, but also by competition from shrubs and grasses, which are abundant in the understory of mixed forests in Primorye. In spruce forests, the shrub and herb layers are poorly developed, and *O. elatus* has an opportunity to achieve a wider distribution (Kurentsova, 1968). In these habitats, the species is usually very abundant and sustainable. However, it is unable to withstand competition from heliophilous species, which rapidly fill gaps after disturbances to primary stands, such as natural or artificial fires or logging.

O. elatus mostly reproduces vegetatively through lateral branches that form adventitious roots when in contact with the soil. This species grows clonally, and individual clones can include 20 or more shoots, which can remain connected by decumbent stems to the parental plant for extended periods of time (Kurentsova, 1968). The life span of a single shoot is up to 40 years, and the overall life span of an individual from germination to the death of all parts of the clone can reach 300 years (Zhuravlev & Kolyada, 1996). Propagation of *O. elatus* through seeds is impeded; the seed set on individual plants is high, but most seeds exhibit underdeveloped embryos. Delayed embryo development is an ancient feature of many Araliaceae. A small number of *Oplopanax* seeds germinate in the second year, and most of the seedlings die.

An analysis of genetic diversity using dominant molecular DNA markers (RAPD and ISSR) allowed the levels of intra- and interpopulation variability to be evaluated in three geographically isolated *O. elatus* populations (Reunova et al., 2010b). The level of genetic diversity in *O. elatus* is much less (Table) than that in *Kalopanax septemlobus* (*P* = 59.2%, *H*e = 0.119; Huh et al., 2005) or *Dendropanax arboreus* (*P* = 70.2%, *H*e = 0.253; Figueroa-Esquivel et al., 2010), which are Araliaceae species with more continuous ranges that have been studied using dominant markers.

The *O. elatus* sample from Mt. Litovka (Livadiiskii Range, southern Sikhote Alin) with the highest level of RAPD variability (*P* = 29.41%, *H*e = 0.110; Reunova et al., 2010b) is characterized by a level of genetic diversity similar to that detected based on allozyme data (*P* = 25.0%, *H*o = 0.131, *H*e = 0.113; Kholina et al., 2010). Allozyme analysis has shown a slight excess of heterozygotes in this population. This may be attributable in part to vegetative reproduction of pre-existing heterozygous genotypes and/or to selection favoring heterozygotes that are better able to adapt to new environments. The low polymorphism and allelic diversity in *O. elatus,* along with a rather high level of observed heterozygosity (*H*o), may be indirect evidence of the effect of genetic drift, which reduces allelic diversity and, consequently, the proportion of polymorphic loci. It seems likely that the source from which the studied *O. elatus* populations were established was heterozygous plants, especially if they were characterized by increased viability. In addition, an excess of heterozygotes and high values of *H*o may be explained by mutations that could have arisen in long-lived clones and been maintained by vegetative reproduction (similar to the serpentine endemic *Calystegia collina*; Wolf et al., 2000). Given the mainly vegetative mode of reproduction of *O. elatus* and the total life span of an individual accession lasting up to 300 years, accumulation of mutations maintained by vegetative reproduction cannot be ruled out.

Thus, based on different nuclear DNA marker data, the levels of genetic variation in the populations located near the northern edge of the *O. elatus* range appear to be comparable with the mean values reported for rare plant species (Table). In addition to its small distribution range and ecological specificity, the low level of genetic variation detected in *O. elatus* may be determined by the species' history. Reductions in polymorphism levels are caused by population bottlenecks resulting from dramatic decreases in population size. Bottleneck events have been proven to be the most probable reason for low polymorphism levels in relic Araliaceae species such as *P. ginseng* (Koren et al., 2003) and *Dendropanax morbifera* (Kim et al., 2006). As mentioned above, *O. elatus* inhabited deciduous Turgai forests. During periods of glaciation, broadleaved forests experienced dramatic range contractions and were forced to retreat southward, and the zone of high mountain vegetation was shifted to lower elevations. It has been suggested that coastal areas and the temporarily emerged continental shelves of the Sea of Japan connecting the Japanese Archipelago to the continent may have served as refugia for coniferous and broadleaved mixed forests (Sakaguchi et al., 2010). During its isolation in refugia and its subsequent expansion, *O. elatus* might have adapted to life in the understory of the fir-spruce forests. The possibility cannot be excluded that contractions in the species' population size following re-establishment from just a few founders could have happened more than once and may be occurring today, when these processes are associated with intense human activity (logging, fires and plant harvesting).

An analysis of the clonal structure of the population from Mt. Litovka indicated that in a sample of 29 accessions, there were a total of 22 multilocus genotypes. Only four of these genotypes were found more than once (from two to four times). The genotypic diversity (G/N) was determined to be 0.76, indicating that 76% of the individuals exhibited unique genotypes. Simpson's diversity index, D, is equal to 0.97, whereas the mean D value for 21 species of clonal plants has been 0.62 (Ellstrand & Roose, 1987). The existence of a great number of different genotypes along with low genetic variation has been reported for a number of species (Watkinson & Powell, 1993; Xie et al., 2005 and references therein). This phenomenon may be explained by the sporadic seed propagation in these species. In general, even a small number of individuals resulting from sexual reproduction is sufficient to make a population genotypically variable. Our findings imply that in the population of *O. elatus*, sexual reproduction succeeds periodically and results in the maintenance of a certain level of genotypic diversity. In addition, it has been suggested that events such as a presumptive origin from heterozygous founders, the accumulation of mutations and the retention of the changes via vegetative reproduction could promote the high level of genotypic variation observed.

The rarity of *O. elatus* is largely a result of this species' ecological specificity, dependence on humidity and low competitive ability. Anthropogenic influences (plant harvesting and habitat destruction) threaten the existence of this species. The flexibility of its reproductive system, combining different modes of reproduction, allows this species to renew heterozygous genotypes by clonal growth and to contribute additional variability resources through sporadic seed reproduction. At the same time, some features of the species' biology (the long life span of a single clone, overlapping generations and the ability to cross-pollinate) also help to maintain a certain level of polymorphism. The existing level of genetic diversity can be crucial to preventing the negative consequences associated with a small number of isolated populations and genetic drift.

2.3 Manchurian birthwort, *Aristolochia manshuriensis* Komarov

Manchurian birthwort, *Aristolochia manshuriensis* Kom., is a relic woody liana that belongs to the ancient angiosperm family Aristolochiaceae. This species is endemic to the Manchurian floristic region (Kitagawa, 1979) and occurs in the montane mixed forests of China and Korea (Figure). In the southern part of the Russian Far East, the species reaches the northern boundary of its range. *A. manshuriensis* prefers specific habitats in river floodplains at a certain altitude above sea level, along chutes and in steep slope foots, especially those with northern slope aspects, avoiding sunlit habitats associated with soil overheating. All Russian *A. manshuriensis* populations are located in the valleys of just three rivers and their tributaries. These populations are fragmented and separated by ridges. Within populations, plants grow at an uneven density, forming patches separated by 0.5–4 km from each other. The growth and expansion of natural *A. manshuriensis* populations are suppressed, and their natural regeneration is very poor (Kurentsova, 1968). At least three of four extant *A. manshuriensis* populations are now located in disturbed habitats and are experiencing strong anthropogenic pressure.

A. manshuriensis exhibits no means of vegetative reproduction, possesses a poor rooting ability and requires a long period of root formation (Shulgina, 1955). Seed reproduction in this species is usually successful, but spontaneous fruit set of only 2% has been documented. The seed set on a fruit is rather high because all mature fruits contain approximately 100 fully viable seeds. A histological analysis showed normal development of flower structures, a high level of pollen-grain fertility (97%) and a large number of pollen grains in the anthers of this species (Nakonechnaya et al., 2005).

Its seeds are adapted to spread by water and by wind (Nechaev & Nakonechnaya, 2009). These seeds are characterized by underdeveloped embryos, but seed germination is usually successful after winter dormancy or brief artificial stratification (Adams et al., 2005). Under favorable conditions, seedlings develop to the generative stage over 10-12 years, reaching a height of 15 m or more (with support) by this age. A long life span for a single *A. manshuriensis* plant is estimated to be more than 40 years. Under unfavorable conditions, plants can be kept in a virgin state for many years without flowering.

Similar to most Aristolochiaceae species, *A. manshuriensis* is an evolutionarily outcrossing plant exhibiting special adaptations of its flower structures (gynostemium) to ensure cross-pollination by insects. Autogamy and geitonogamy are possible, but pollinators are required to perform self-pollination as well as cross-pollination (Nakonechnaya et al, 2008). This species is characterized by long-term and abundant blossoming as well as a long life span of individual flowers, which increases the possibility of cross- and self-pollination. However, the presence of suitable insect pollinators during *A. manshuriensis* blooming is a precondition for successful seed reproduction in this plant. The flower structure of *A. manshuriensis* is matched to insect pollinators with a certain body size and thorax structure to allow the transfer of a sufficient number of pollen grains to the stigma. Among the visitors to *A. manshuriensis* flowers, flies of the genus *Pegoplata* (Anthomyiidae) are the only possible pollinators (Nakonechnaya et al., 2008). These flies have many other substrates available for breeding and larval feeding, which may be a cause of their rare visitations to *A. manshuriensis* flowers and, as a result, the rare fertilization and low fruit set of this species. Given that many Aristolochiaceae species are associated with specific insect pollinators (Nakonechnaya et al., 2008 and references therein), it may be assumed specific pollinators of

marginal populations of *A. manshuriensis* have been lost as a result of shifts in the areas occupied by flora and fauna during the Pleistocene cooling. However, the high seed productivity of each mature fruit indicates the high potential fecundity of the species.

The mean level of genetic variability in *A. manshuriensis* is rather moderate based on allozymes (Nakonechnaya et al., 2007) and RAPDs (Table). The relatively high level of heterozygosity in *A. manshuriensis* populations compared with the average values for rare endemic species (Table) may be explained by outcrossing. Indeed, an excess of heterozygotes has been revealed within *A. manshuriensis* populations, despite their small population sizes, and no inbreeding has been found at the species level (Koren et al., 2009).

The relatively low level of population differentiation identified with molecular markers may be indicative of gene flow among populations in the present or recent past. Another possible reason for the low differentiation observed may be the greater degree of habitat integrity and the closer connections between populations that existed in the past (Koren et al., 2009). This explanation is supported by the low mean genetic distances between populations (D_N = 0.0096) and the value of gene flow between populations (Nm = 3.96) calculated based on G_{ST}, which shows that the isolation of the populations studied is incomplete.

Within two of the most disturbed populations, a statistically significant subdivision is shown with both allozyme and RAPD markers. Moreover, an effect of a genetic bottleneck is revealed in three populations that have undergone strong anthropogenic pressure (Koren et al., 2009). These findings indicate a reduction in gene flow between subpopulations in recent years as result of the intensive disturbance of their habitats.

Thus, the relic populations of *A. manshuriensis* exhibit moderate levels of genetic diversity. The low level of differentiation between the populations is probably connected with the evolutionary history of the species and the interaction of various factors, such as migration and selection. Despite the fact that all of the extant *A. manshuriensis* populations in the Russian part of the range are isolated from one another by ridges, they all grow in the valleys of rivers with their headwaters in the Borisovskoe Plateau and may have a common origin. It is likely that fragmentation of the *A. manshuriensis* populations occurred recently during the increase of human activities and the forest destruction that took place in the 20th century (Koren et al., 2009). The ongoing degradation of natural populations seems not to be associated with depletion of the gene pool and inbreeding depression. Because of the small size and fragmentation of these populations and their isolation from each other and from the species distribution center, genetic drift makes a significant contribution to the decrease in this species' genetic variability. In addition, anthropogenic influences, such as fires and uncontrolled harvesting of plants for their medicinal value (Bulgakov & Zhuravlev, 1989), also play a role in the contraction of the *A. manshuriensis* population size. Seed reproduction through outcrossing seems to be the only means for Manchurian birthwort to maintain a sufficient level of genetic variation. The preference of this species for specific ecotopes, its poor potential to undergo vegetative reproduction and its rare fertilization as well as its weak competitive ability in the virgin stage do not allow it to expand beyond the boundaries of its existing stands.

2.4 Russian arborvitae (Siberian Cypress, Russian Cypress), *Microbiota decussata* Komarov

The perennial evergreen decumbent coniferous shrub *Microbiota decussata* Kom. (Cupressaceae) is known from the southern part of the Russian Far East, where it occurs on

some mountain peaks in the Sikhote Alin Mountains. The species is strongly restricted in its distribution, with its natural range stretching from 43˚ 00′ N to 48˚ 50′ N, from the subalpine zone of southeastern Primorsky Territory to the mountains in the Anyuy River basin in Khabarovsk Territory (Figure).

M. decussata is the sole species in the genus *Microbiota*, which is the only Cupressaceae genus endemic to the Sikhote Alin Mountains, and it is considered to represent one of the plant species that existed in this mountain system before the mountain-valley glaciers developed (Shlotgauer, 2011). The Sikhote Alin palynofloras contain pollen of Cupressaceae (Pavlyutkin et al., 2005 and references therein), but the cupressaceous pollen grains could not be distinguished beyond the family level. The fossil species *Cupressinoxylon microbiotoides* Blokhina from the Eocene/Oligocene deposits of Yuri Island of the Kurils is considered to have represented a putative species of the genus *Microbiota* (Blokhina, 1988). Of the extant Cupressaceae species, *M. decussata* is most closely related to *Platycladus orientalis* based on morphological data. The only fossil record of *M. decussata* was found in the Pavlovka lignite field (the southern Primorye) dated to the Pliocene or the late Eocene through late Oligocene (Pavlyutkin et al., 2005 and reference therein). In the Pavlovka deposits, wood of *M. decussata* was found together with fossilized wood of *P. orientalis* (Bondarenko, 2006). The presence of both species in the Pavlovka lignite field indicates their co-occurrence in the Oligocene/Pliocene plant associations of Sikhote Alin. Currently, *Platycladus orientalis* is a common tree in China and is widely cultivated elsewhere in Asia, eastward to Korea and Japan, southward to northern India and westward to northern Iran, whereas *M. decussata* is not found outside Russia. Its range is restricted to the Sikhote Alin, where the species exhibits a strongly disjointed distribution (Figure). Phylogenetic studies based on ITS rDNA and chloroplast markers (Gadek et al., 2000; Little et al., 2004) have confirmed the genetic affinity of the two taxa, which are placed in a sister clade to *Calocedrus*.

The heliophilous Russian arborvitae shrubs inhabit steep stony slopes and scree fields at altitudes from ca. 300 to 1,700 m above sea level (mainly at or above the timberline) under climatic conditions that impede the growth of forest vegetation. The xerophytic species *M. decussata* is a poor soil-tolerant plant that is resistant to a wide range of temperatures. As it grows under very harsh climatic and edaphic conditions, *M. decussata* is a pioneer in the colonization of cold stone deserts and participates in soil formation processes (Urusov, 1979). This low shrub with creeper and ascending branches often forms dense (crown density of 1.0) monodominant stands (Kurentzova, 1968; Krestov & Verkholat, 2003). In the southern part of its range, populations of *M. decussata* are more sustainable than those of another subalpine shrub, *Pinus pumila*. At the northern boundaries of its range, in the Anyuy and Chor River basins, the viability of *M. decussata* populations appears to be lower as a result of competitive inhibition by boreal species. Under these circumstances, fruiting of Russian arborvitae is rarely observed (Melnikova & Machinov, 2004), and the species is replaced by *P. pumila* (Kurentzova, 1968; Urusov, 1988).

M. decussata is an anemophilous monoecious plant that propagates sexually and by layering. The plant begins bearing fruits at 14–17 years, and the maximum life span of individuals has been determined to be approximately 250–300 years. The female cones of this species contain only a single 2 mm long naked seed. The seeds are able to disperse over a very short distance, dropping near the parent plant, though sporadic dispersal by animals cannot be ruled out. The seeds retain germination capacity for a long period but germinate almost

exclusively after fires (Urusov, 1979). Outside the area occupied by their parent population, seedlings and juvenile plants are extremely rare (Kurentzova, 1968). *M. decussata* grows very slowly (3–7 cm a year) and can extend into new free habitats through the slow creeping of stems (up to 3–5 m in length) that produce roots at their nodes (Urusov, 1988).

M. decussata exhibits a high level of nuclear genome variation (Table), despite the restricted and fragmented range and geographical isolation of its populations (Artyukova & Kozyrenko, 2009). The gene diversity within populations from the southern and middle parts of the range of this species is slightly higher than that in the northern population from the Chor River basin, which is in close proximity to its northern range limits. The lower level of gene diversity in the northern population might be caused by severe temperature conditions interfering with sexual reproduction; thus, species dispersal occurs mainly by layering. The highest level of genetic diversity is found in the population from the central Sikhote Alin. The lack of population-specific RAPD markers and the similar high levels of diversity retained in the populations could be caused by a common gene pool and ancient polymorphism. The genetic differences among all pairs of populations (separated by 10–400 km) fit an isolation-by-distance model. Overall, based on RAPD markers, the level of nuclear genome variation in endemic *M. decussata* (Table) is comparable with that found in some other Cupressaceae species with fragmented or restricted ranges (e.g., Hwang et al., 2001; Allnutt et al., 2003; Hao et al., 2006).

Based on sequence data from noncoding cpDNA regions, a considerable level of haplotype diversity and a low level of nucleotide diversity have been revealed in *M. decussata,* which is similar to what has been found in some other woody species, including two species of Cupressaceae, *Cunninghamia konishii* and *C. lanceolata* (Hwang et al., 2003). A common haplotype for all populations has not been found, though three haplotypes of the central Sikhote Alin population are also present in southern and/or northern populations. The large number of unique, closely related haplotypes within each population may suggest that the distribution area of *M. decussata* was fragmented a long time ago by the extirpation of populations in the adjacent territory.

In contrast to nuclear DNA, there is no significant isolation-by-distance effect observed in the plastid genome in this species, but cpDNA data related to differentiation show a nonrandom geographical distribution of haplotypes. Differentiation in *M. decussata* appears to be associated with historical events and the complex mountain topography of its range. The results of nested clade analysis and coalescent simulation data provide evidence of species expansion (Artyukova et al., 2009). The presence of the same substitutions and shared haplotypes in populations from opposite ends of the range indicate that ancestral populations of this species might have formerly exhibited a contiguous distribution range. The highest gene diversity in both genomes and the presence of shared haplotypes in the population from the central Sikhote Alin, which coincides in position with the assumed site of this species' origin at the watershed of the ancient Ussuri and Partizanskaya River basins (Urusov, 1979), may indicate its ancient origin. The fossil data (see above) confirm the occurrence of *M. decussata* in the Oligocene/Pliocene plant associations of Sikhote Alin near the southern limits of the current species range.

Unique species life-history traits have ensured the survival and range expansion of *M. decussata*, while most Arcto-Tertiary species, including species of Cupressaceae, either

shifted their ranges south (e.g., *Platycladus orientalis*) or vanished (e.g., putative common ancestor of *M. decussata* and *P. orientalis*). The long-term persistence of *M. decussata* in the territory that has been ice-free during glaciations as well as traits such as a long life span and pre-reproductive phase, the long-term survival of its seeds in soil seed banks and spreading by layering, seem to enable the retention of historically established levels of gene diversity in fragments of the ancestral populations of this species. Climatic and landscape changes at the Pleistocene–Holocene boundary caused the timberline to rise, and *M. decussata*, like most contemporary montane plants, retreated toward higher elevations. The enrichment of plant communities of the Sikhote Alin Mountains with cool temperate and boreal species also resulted in the shifting of *M. decussata* stands to ecotopes with severe climatic and soil conditions (e.g., steep, stony slopes and scree fields) and in the splitting of the large ancestral population, forming its disjunct present-day distribution.

The modern populations of *M. decussata* have the ability to survive the ongoing climate changes and global warming because of the physiological and ecological range of tolerance and life history traits of this species. Upward shifts of the timberline forcing *M. decussata* to migrate up to mountain summits with taluses (Urusov, 1988; Krestov & Verkholat, 2003) may lead to further contraction of its remnant populations on mountains at middle elevations. However, because this species can survive under harsh environmental conditions (e.g., poor soil, high solar radiation, extreme winds), which are unsuitable for other species, it could survive on the highest mountain peaks.

2.5 *Oxytropis chankaensis* Jurtzev

Oxytropis chankaensis Jurtz. (synonym *O. hailarensis* subsp. *chankaensis* (Jurtzev) Kitag.) is a perennial herb with a narrow habitat range that is restricted to the west shore of Khanka Lake (Kharkevich & Kachura, 1981; Pavlova, 1989; Yurtsev, 1964), which is the largest lake in Northeast Asia (Figure). *O. chankaensis* plants occur only in sandy habitats on a narrow strip along the Khanka Lake shoreline, forming separate populations numbering approximately 80 to 500 individuals (Kholina & Kholin, 2006). The genus *Oxytropis* DC is comprised of approximately 450 species occurring predominantly in the mountains of Asia. The high ecotopic diversity and the mosaic of conditions in mountain ecosystems lead to the occurrence of neighbouring populations of *Oxytropis* species with different ecological requirements and contribute to the enhanced speciation and interspecific hybridization in the genus. These processes explain the current controversy within the taxonomy of this genus (Malyshev, 2007, 2008).

A legume species originally found on the shoreline of Khanka Lake was first described as a distinct endemic species, *Oxytropis chankaensis*, based on the observation of definite morphological differences compared with its congeners (Yurtsev, 1964). In the International Legume Database (ILDIS), *O. chankaensis* is considered to be a subspecies of *O. hailarensis* Kitag., the species that occurs in China and Mongolia (Bisby et al., 2009). In the Flora of China (Zhu et al., 2010), both species are regarded as synonyms of *O. oxyphylla* (Pall) DC, a type species of section *Baicalia,* subgenus *Oxytropis* (Malyshev, 2007). However, *O. chankaensis* and *O. oxyphylla* are clearly distinguished by morphological features and by their ploidy levels: *O. oxyphylla* is diploid (2n = 16; Zhu et al., 2010), whereas *O. chankaensis* is tetraploid (2n = 32; Probatova et al., 2008a). Phylogenetic analyses of the ITS rDNA and

three noncoding regions of chloroplast DNA strongly confirm that *O. chankaensis* and *O. oxyphylla* are distinct species (Artyukova et al., 2011a).

O. chankaensis is the only representative of section *Baicalia* in Primorye (Pavlova, 1989). It is an outcrossing species that is pollinated by bumblebees, like most *Oxytropis* species (Yurtsev & Zhukova, 1968), with pollen potentially being dispersed over long distances. *O. chankaensis* is characterized by a long flowering period (from the third week of May until mid-August) and a high number of flowers per plant (up to 400, an average of 40 inflorescences with 4–14 flowers per plant) as well as high pollen fertility (95.7 ± 1.4%), which contribute to successful pollination and fertilization. The plants of this species exhibit high fecundity, with fruits containing up to 20 seeds, and an individual plant produces approximately 4,000 seeds (Kholina et al., 2003). The first fruits mature by the end of May, and fruiting lasts until September. Mature spherical pods can be dispersed by wind and water over long distances beyond the limits of local populations, while some seeds from dehiscent pods are gravity-dispersed over only a short distance from the maternal plant to form the soil seed bank. During the vegetative season, seedlings emerge from the seeds of the first fruits, and some of the seeds begin to germinate in the following year, after a winter dormancy period.

Ontogenic features of *O. chankaensis* (Kholina & Kholin, 2006), such as its long life span, overlapping generations, the multiplicity of its development, its early transition to the generative state and the long period of the generative state, are the most important characteristics of this species for maintaining its population numbers and preserving genetic heterogeneity. The juvenile and immature stages are the most vulnerable stages of the species' life cycle.

The characteristics of the reproductive biology of *O. chankaensis*, such as the normal structure and function of the reproductive organs, the high fertility of pollen, the considerable duration of the flowering period and the long life of the flower, result in reliable pollination and high seed production. This species is characterized by a combination of different modes of dissemination, hardseededness and long-term maintenance of germination (over 10 years). Seed dispersal over short and long distances by wind and water promotes intraspecific genetic structure and the homogenization of populations through gene exchange. The longevity of the seeds leads to their accumulation in the seed bank in the soil, and these seeds replenish the gene pool of a population when they germinate. The high fecundity of *O. chankaensis,* together with mechanisms that support recombination (the predominance of cross-pollination) and the exchange of genes (via pollen and seeds), provides reliable renewal of this species *in vivo*.

An allozyme analysis showed that *O. chankaensis* is an autotetraploid that arose through the fusion of nonreduced gametes in the course of multiple crosses between genetically different plants (Kholina et al., 2004). The recurrent polyploidy events in the evolutionary history of this species are confirmed by the presence of several chloroplast DNA haplotypes in each population (Artyukova et al., 2011b). In addition, the levels of genetic diversity in *O. chankaensis* populations revealed using allozymes (Kholina et al., 2009) and RAPDs are high compared with the average values for rare endemic species (Table).

The most striking feature of the *O chankaensis* plastid genome, which is maternally inherited in Fabaceae, is the unexpectedly high cpDNA haplotype diversity (Table) for a species with

an extremely narrow geographic range. At the same time, its nucleotide diversity is low. Most (≥90%) of the genetic variability of nuclear markers and of the chloroplast markers is distributed within populations. Unlike most angiosperms (Petit et al., 2005), the level of cpDNA subdivision in this species does not differ from the levels of differentiation of the nuclear genome based on RAPD markers (Table). In addition, correlation between geographic and genetic distances is absent for the plastid and nuclear genomes. The low population partitioning (cohesive genetic system) and lack of phylogeographic patterning may be attributed to both recent fragmentation of a once continuous population and extensive (past/modern) gene flow via pollen and seeds, which prevents the accumulation of genetic differences.

Despite the slight divergence observed, each population possesses a unique part of the species gene pool. The biological traits and reproductive features of this species as well as the existence of tetrasomic inheritance and recurrent tetraploidy events in its evolutionary history contribute significantly to the maintenance of genetic diversity.

Thus, the narrowly endemic species *O. chankaensis* exhibits adaptive mechanisms that enable it not only to successfully renew its populations in the coastal zone, which are exposed to frequent flooding and other adverse factors, but also to maintain the high level of recombination responsible for the survival of the species in a changing environment. Apparently, the rarity of this species is a result of its high habitat specificity; it lives only on the sandy shores of a large lake where there is intense insolation and high air humidity. Fluctuations in its population size as a result of lake-level oscillations can result in reduced numbers at some localities, but in these cases, the species' high productivity and reserves of genetic variability, which enable adaptive responses of species, help to restore the populations. The threat of total destruction of the species is raised by human-induced habitat destruction.

2.6 *Iris mandshurica* Maximowicz and *I. vorobievii* N.S. Pavlova

Iris L. is a Northern Hemisphere genus of flowering plants composed of approximately 280 valid species. As they are mostly open land plants, *Iris* species are adapted for living in a wide range of habitats from cold and montane regions to grassy slopes, steppe meadowlands, arid and marsh areas and riverbanks, though there are no truly sylvestral plants among this group. Irises are outcrossing species exhibiting flowers with specialized structures to insure cross-pollination; their fruits (dry capsule) contain numerous seeds that can disperse through a variety of mechanisms, such as barochory, autochory, anemochory, hydrochory, myrmecochory and zoochory. In addition, these perennial plants reproduce asexually through bulbs or rhizomes that form dense or loose colonies (tufts) and grow in size over 20 years. Many *Iris* species inhabiting Russia are at the border of their geographical ranges and occur in small, isolated populations. In the southern part of the Russian Far East, there are 11 *Iris* species, mainly belonging to the subgenus *Limniris,* section *Limniris* (Pavlova, 1987). Only two species, *Iris mandshurica* Maxim. and *I. vorobievii* N.S. Pavlova, are representatives of a small section of dwarf irises, *Psammiris,* of the subgenus *Iris.* Psammirises usually have yellow flowers with a yellow beard in the center of the outer three perianth segments ("falls") and seeds with a white appendage (loosely called aril) indicative of possible dispersal by ants.

Psammirises are mainly Asian species, and only *Iris arenaria*, which is considered a synonym of *I. humilis*, is widely distributed in southern Europe (Alexeeva, 2008). *I. mandshurica* and *I. vorobievii*, which are found in the south of Primorye, are very similar to *I. humilis*, but they differ from each other and from *I. humilis* in some morphological features (Pavlova, 1987; 2006; Alexeeva & Mironova, 2007; Bezdeleva et al., 2010) and in their chromosome numbers (Probatova et al., 2008b; Shu, 2000). The distinctiveness of these species has also been confirmed by the use of molecular DNA markers (Kozyrenko et al., 2009).

In Russia, small and disjunct populations of *I. mandshurica* occur rarely (Figure, arrows) on dry grassy slopes, stone hills and in the steppe meadow. *I. vorobievii* is found in the only locality in the extreme south of Primorye (Figure, arrow), where it grows on open grassy slopes of hills and in the meadows of fluvial terraces as low-density, isolated patches (Pavlova, 2006; Alekseeva, 2008). Outside Russia, *I. mandshurica* mainly occurs at altitudes of ca. 400–800 m in northeast China (Heilongjiang, Jilin and Liaoning Provinces) and in northern Korea (Figure; Shu, 2000), whereas there are no available data on the range of *I. vorobievii*, though the occurrence of the species in adjacent regions in China and Korea (Figure, strips) cannot be ruled out.

Like all *Iris* species, *I. mandshurica* and *I. vorobievii* reproduce sexually and asexually through rhizomes. The seeds of both species are gravity-dispersed to only a short distance from a maternal plant, though secondary dispersal by ants cannot be excluded entirely. *I. mandshurica* exhibits a thick, shortened rhizome growing almost horizontally and forming loose turf. The vertical, stout rhizome of *I. vorobievii* is very short (1 cm in length) and presents only a few lateral buds; the rhizome grows at one end while the old part of it dies, and the rhizome does not reach great lengths (Bezdeleva et al., 2010). These features indicate that the species is a short-lived perennial (Alexeeva, 2008), living no more than 5–7 years. In contrast to most *Iris* species, *I. vorobievii* is difficult to cultivate.

Both psammirises studied exhibit similar levels of nuclear and plastid DNA diversity (Table). Based on RAPD markers, the genetic diversity in populations of *I. mandshurica* and *I. vorobievii* corresponds with that in natural populations of the rare and endangered European steppe plant *Iris aphylla* (P = 30.6%, He = 0.097; Wróblewska & Bzosko, 2006) but is lower than that in the widespread species *I. humilis* (P = 48.1%, He = 0.168; Kozyrenko et al., 2009). Notably, the genetic diversity value in *I. humilis* is in accord with the average value for plants with mixed breeding systems (He = 0.18; Nybom, 2004), whereas in *I. mandshurica* and *I. vorobievii*, these values are significantly lower (Table). This may indicate the prevalence of vegetative propagation over propagation through seeds in the populations studied.

I. mandshurica and *I. vorobievii* show considerable levels of haplotype diversity, along with low levels of nucleotide diversity in the chloroplast genome, which is transmitted through seeds in *Iris* species (Cruzan et al., 1993). Low nucleotide diversity and high levels of cpDNA haplotype diversity have been found in some widespread (e.g., *I. humilis*, Kozyrenko et al., 2009) and endemic perennial herb species (e.g., *Aconitum gimnandrum*, Wang et al., 2009; and *Oxytropis chankaensis*, Artyukova et al., 2011b). However, for most angiosperms, including *Iris* species (e.g., Cornman & Arnold, 2007), populations are often fixed for single cpDNA haplotypes, and polymorphic populations possessing different haplotypes occur in potential contact zones of different maternal lines or at sites of long-

term persistence. In contrast, the populations of *I. vorobievii* and *I. mandshurica* contain 13 and 6 haplotypes, respectively, which may result from historical gene flow, retention of ancestral polymorphisms that accumulated over a long period in more continuous ancient populations, or a putative origin from several founders. Based on cpDNA haplotypes, demographic event analyses show that populations of both species have undergone bottleneck events and expansion in the past (Kozyrenko et al., 2009).

Apparently, the main reason for the rarity of *I. mandshurica* and especially of *I. vorobievii* is the scarcity of suitable habitats for these psammirises in Primorye. As *I. vorobievii* and *I. mandshurica* represent components of steppe vegetation and grow in specific edaphic conditions, they are members of several steppe communities that are likely remnants of previously more widespread steppe vegetation (Krestov & Verkholat, 2003). The contractions of such relic communities result from climate and natural community changes (natural succession) and, in recent years, from anthropogenic habitat destruction. Their isolation from the main part of the species' ranges, limited seed dispersal and poor vegetative reproduction make these psammirises particularly vulnerable and may lead the species to extinction.

3. Conclusion

It is usually assumed that a certain level of genetic diversity is necessary for the long-term prosperity of a species. Indeed, different genotypes confer different levels of resistance to various environmental stresses, and consequently, the greater the diversity of the genotypes in a population, the more effective its ability to withstand unfavorable conditions will be. Therefore, the existence of a low level of genetic diversity is often considered to represent a crucial stage for the survival of a species or even a sign of its extinction. However, despite several attempts to determine the average levels of genetic variation in different categories of plants (e.g., Gitzendanner & Soltis, 2000; Nybom, 2004), it is still unknown what level of polymorphism should be considered critical for the existence of a certain species. Thus, some rare endemic species exhibit higher levels of genetic diversity than the average values found for this category of plants, such as *Oxytropis chankaensis* (Table). At the same time, very low levels, or even an absence of genetic variability has been found in other narrowly endemic plants (e.g., *Bensoniella oregona*, Soltis et al., 1992). It is impossible to predict the fate of a species on the basis of its genetic diversity alone. Here, we have attempted to address some species existing under extreme conditions in the context of a variety of environmental, biological, evolutionary and other influences.

All of the species described above are represented by small, fragmented, marginal populations. Each of these species is characterized by a particular level of genetic diversity, ranging from very low (*Panax ginseng*) to high (*Oxytropis chankaensis*). Despite these differences, all of these plants exhibit weak competitiveness, and none of them can be considered prosperous. These species are not dominant in their respective plant communities, and they inhabit specific (often quite narrow) ecological niches where their existence is maintained more or less successfully for a long period. Without the effects of human activity, these species could probably exist in this state indefinitely. What are the mechanisms that ensure the long-term existence of these species in small, isolated populations at the limit of their climatic and environmental tolerance?

For ginseng, longevity appears to be most important factor for its survival. Indeed, a lifetime of up to several hundred years is unusual for an herbaceous plant that is incapable of vegetative reproduction. Ginseng maintains the ability to produce seeds throughout its life span, and it appears that as a result of apomixes, its seed production is not particularly dependent on environmental conditions or the availability of pollinators. A large number of fully viable seeds and an extended period of embryo maturation allow revival of populations of this species, even from a small number of individuals over the course of many years.

Similar to ginseng, *Aristolochia manshuriensis* only exhibits seed-based reproduction. The life span of this species is not as long as that of other woody plants and is near the average for woody vines. This species has a very poor ability to reproduce vegetatively, and there are major limitations on its seed reproduction as a result of adaptation to pollination only by certain insects. Though adaptation to specific pollinators prevents inbreeding, pollination decreases if pollinators are absent, and the resulting fruit development is low. In this case, high seed production (a large number of seeds per one fertilization event) and adaptability to seed transfer by wind and water seems to be of primary importance for the survival of the species. Even a single successful fertilization every several years could guarantee population restoration if conditions are suitable for seed germination. Under unfavorable conditions, plantlets of this species can exist in a juvenile state for a long time, which allows a population to survive until the re-establishment of suitable conditions.

The ability for vegetative propagation is a pathway for the survival of some species (*Oplopanax elatus*, irises and *Microbiota decussata*). This pathway also allows for the rehabilitation of a species, even after a significant reduction in its population, and it effectively allows clonal colonies to reoccupy their habitats, where suitable conditions for the species are associated with an absence of competitors. The flexibility of the reproductive system of *O. elatus*, combined with its different modes of reproduction allows it to renew heterozygous genotypes by clonal growth and to contribute additional variability resources through sporadic seed reproduction. At the same time, some features of the biology of this species (the long life of a single clone, overlapping generations and the ability to cross-pollinate) also help to maintain a certain level of polymorphism.

For *I. mandshurica* and *I. vorobievii,* vegetative reproduction (even if poor) seems to be the only way to survive under unfavorable conditions. Rare reproduction through seeds allows for the maintenance of a certain level of genetic diversity in its populations. However, the spread of both species beyond the borders of their existing populations is unlikely as a result of the scarcity of suitable habitats. Poor vegetative reproduction and limited seed dispersal as well as isolation from the main part of the species range (*I. mandshurica)* or its occurrence in a single locality (*I. vorobievii)* make populations of both species vulnerable. In the case of *I. vorobievii*, this vulnerability may lead to rapid species extinction.

The pattern of genetic diversity and the structure of populations in the endemic species *M. decussata* are congruent with the leading edge model of colonization. It could be proposed that extant southern populations represent the putative species range center. Populations that expanded southward during dry and cool periods at the Oligocene/Miocene boundary have become completely extirpated following climate changes in the Quaternary. The distribution area of *M. decussata* became fragmented quite some time ago through the displacement of the species toward mountain peaks and the extinction of stands in the

adjoining territories. The remnant *M. decussata* populations have the potential for survival under ongoing climate changes and global warming because of this species' physiological and ecological range of tolerance, reproduction by layering and other life history traits.

In the case of endemic or rare species, one must distinguish between relics left by the extinction of related populations and newly evolved taxa. All relics that survived the repeated periods of Pleistocene climate cooling have apparently experienced a severe genetic bottleneck, not only as a result of genetic drift associated with the reduction of populations, but also because of selection acting in a rapidly changing climate. Because of this selection, the fittest individuals have survived. Among the representatives of the ancient tropical floras (*P. ginseng, O. elatus, A. manshuriensis*) only a small number of genotypes are likely to have possessed such fitness. By acquiring a mechanism for survival in harsh environments, these species have lost much of their genetic diversity.

In the case of the narrowly endemic species *O. chankaensis*, the situation is different. This species possesses adaptive mechanisms that enable it not only to successfully renew its populations in the coastal zone, which are exposed to frequent flooding and other adverse factors, but also to maintain the high level of recombination responsible for the survival of the species in a changing environment. This is a relatively young species, and its biological characteristics may promote its prosperity and wide distribution; the only obstacle to this is its high habitat specificity; it only inhabits the sandy shore of a large lake where there is intense insolation and high air humidity. However, there are no such habitats nearby, and the small number of plants in some populations makes this species vulnerable.

The patterns observed for various rare species often do not fully correspond to the general idea of survival at the edge of their range. Plant species exhibit tremendous variation in life history traits that may help them survive in harsh or changeable environments. The cause of a plant's rarity depends on the effects of different historical, biological and genetic factors. In all cases, different compensatory mechanisms, such as increased longevity and fertility, the formation of soil seed banks and vegetative reproduction, are involved. The adaptations of these species are not always successful because the historically established balance between reproduction and dispersal can be disturbed. However, in the absence of destructive human activities, many rare species could exist for an indefinite time.

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