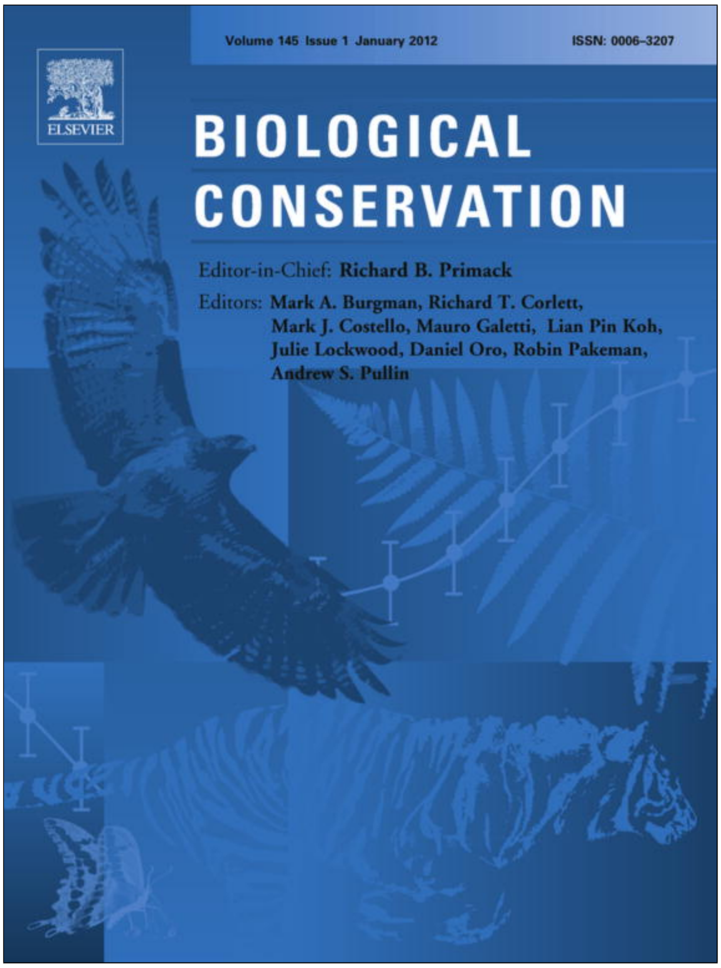
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Overcoming extreme weather challenges: Successful but variable assisted colonization of wild orchids in southwestern China

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ABSTRACT

Assisted colonization of endangered species to locations outside their native ranges in response to projected climate change has emerged as a potential, but highly controversial conservation tool. The debate has been largely philosophical and hypothetical as little biological data exist in the literature. In 2006, nearly 1000 endangered wild orchid plants belonging to 29 species were translocated to higher elevations in subtropical southwestern China in response to inundation threats from a hydropower project. We took advantage of this upward translocation to address one of the main biological concerns associated with assisted colonization, i.e. whether the target endangered species can survive in the novel environment that is projected to be suitable for them, sometime in the future. We assessed the impacts of two extreme weather events, translocation shock and herbivory, on survival of 20 of these species and 462 individuals that were translocated beyond their current range vs. within that range. A cold spell in 2008 on average caused 10% mortality, less than the mortality rate from herbivores. However, the cold spell was the only force that extirpated an out-of-range population. No mortality resulted from a drought event in 2010. The 5-year survival percentages were not different between low and wide elevation species (69.3% mean ± 36.3% standard deviation vs. 67.3% ± 30.9%). Orchids represent 10% of flowering plant diversity and are among the most endangered group of organisms due to a combination of their often specialized ecological requirements, habitat destruction, and overexploitation. The demonstrated ability to survive extreme environmental challenges indicates that assisted colonization may be a viable conservation tool for the many endangered orchids worldwide due to climate change and/or other reasons.

1. Introduction

Global warming is driving species migrations to higher latitudes and elevations (Chen et al., 2011; Parmesan and Yohe, 2003; Root et al., 2003). However, many species may not be able to keep pace with climate change due to their limited dispersal ability across already fragmented habitats (McLaughlin et al., 2002; Root et al., 2003; Thomas et al., 2004). These species are expected to experience habitat loss, population declines and elevated risks of extinction. Assisted colonization, a.k.a. managed relocation, assisted migration, refers to the movement of a species by humans beyond its native range, most notably to habitats at higher latitudes or higher elevations that are predicted to be suitable under future climatic conditions—has recently developed as a conservation concept (Hunter, 2007; McLachlan et al., 2007; Peters and Darling, 1985) and is rapidly gaining credence among conservation practitioners (Hoegh-Guldberg et al., 2008; Loss et al., 2011; Minteer and Collins, 2010; Richardson et al., 2009; Vitt et al., 2010). The pros and cons of assisted colonization have been debated intensely (Hewitt et al., 2011; Minteer and Collins, 2010; Ricciardi and Simberloff, 2009; Seddon, 2010). Some conservation biologists doubt the survival capability of endangered species subject to such action, while others worry about species becoming invasive in recipient community

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(Fox, 2007). Nevertheless, the measure has been attempted on only a few occasions (Stone, 2010a), and evaluated on even fewer taxa (Willis et al., 2009). As a consequence, the debate around assisted translocation as a viable conservation tool has been largely philosophical and hypothetical as little direct biological data exist in the literature.

One of the main biological concerns in traditional endangered species reintroduction is whether the target endangered species can establish and survive (Falk et al., 2006; Godefroid et al., 2011; Maschinski and Haskins, 2012; Menges, 2008). Assisted colonization is similar to traditional species reintroduction from a practical point of view (Seddon 2010), the survival concerns can and will apply to the efficacy of assisted colonization as a species conservation tool. Such concern may be greater in the practice of assisted colonization because the target species will be moved to a novel environment, which is projected to be suitable for them some time in the future.

While most areas are getting warmer on average, they still experience extreme cold spells and other severe weather extremes. Severe weather events, though rare, function as stochastic forces regulating population dynamics (Altwegg et al., 2006; Parmesan et al., 2000) or define species distribution boundaries, as do severe freezes for many tropical and subtropical species (Holdridge, 1947; Holdridge et al., 1971). How extreme weather events, especially extreme cold and drought, which can pose stress different from the average warming trend, affect species that have been recently moved out of range, is critical in gauging the efficacy of assisted colonization as a species-focused conservation tool, but is unknown. One could draw inferences from studies on cases of reintroduction of endangered species within their historical ranges, as there are some parallels between assisted colonization and conventional reintroduction. However, few if any restoration projects have documented the impacts of rare, severe weather events on reintroduced populations (Maschinski and Haskins, 2012). Nevertheless, species under conventional reintroduction may be able to cope with these weather extremes as they have evolved with the stochastic weather regime within the native range, while this may not be the case for species under assisted colonization.

Concerns other than climate change have also triggered actions to move endangered populations outside historical ranges (Maschinski and Haskins, 2012; Ricciardi and Simberloff, 2009). This is the case with the many species of wild orchids in southwestern China. In 2006, in anticipation of the completion of the Longtan reservoir near the Yachang National Orchid Reserve in Guangxi, southwestern China, which is situated within a world orchid hotspot (Cribb et al., 2003), the reserve initiated a rescue program of rare and endangered plants. This program transplanted hundreds of orchids belonging to an estimated 29 species and 16 genera (unpublished data) from locations slated to be flooded at 350–400 m above sea level along a 20 km section of the Hongshui River. Because overexploitation is one of the leading causes of endangerment of orchid species in China, the orchids were moved to a forest site secured from poachers in the reserve that is approximately 1000 m above sea level (Appendix A). The recipient site is less than 30 km southeast from the source sites, but it is around 600 m higher in elevation and its mean annual temperature is approximately 3.6 °C cooler than the source sites (Huang et al., 2008). For many of the translocated species, such a move puts them beyond their natural elevational range. In this paper we took advantage of this assisted colonization "experiment" to assess the impacts of an extreme cold spell in 2008 and an extreme drought in 2010 on populations of wild orchid species that had been translocated beyond their range vs. those within ranges. In addition, we contrasted these impacts with those from herbivores and initial translocation stress, two other major mortality drivers.

2. Materials and methods

2.1. Study site

The Yachang Orchid Nature Reserve (hereafter refer to as the Yachang Reserve) is situated between 24°44′16″N and 24°53′58″N latitude, and 106°11′31″E–106°27′04″E longitude, in northwestern Guangxi, in the southeastern foothills of the Yunnan–Guizhou plateau (Fig. 1). It lives up to the reputation that Southwestern China, consisting of Yunnan, Guangxi and Guizhou Provinces, is a world orchid hotspot (Cribb et al., 2003). More than 140 species of orchids, some of which occur in extremely large, relatively undisturbed populations, can be found in this remote 220 km^2 state nature reserve (Liu et al., 2010).

The Yachang Reserve and adjacent forests range in elevations from 350 m above sea level at the Hongshui river banks in the northwest, to 1970 m above sea level at the highest point of the Panguwang Mountain in the southeast. The reserve consists of numerous hills of varying elevation, most of which are 1200 m above sea level or less and of limestone substrate. Terrain within the reserve and the surrounding area is complex, with rolling hills at some places and steep, near-vertical rock walls at others. Deep valleys cut by rivers or seasonal streams are common. Two major rivers, Hongshui in the north and Nanpanjiang (a tributary of the Hongshui) in the west, flow through or adjacent to the Yachang Reserve. The natural areas in the region support, from low to high elevation, tropical pine forests, mixed pine and evergreen broad leaved forests, subtropical evergreen, and mixed evergreen and deciduous broad-leaved forests.

The region has a typical subtropical monsoon climate with a mean rainfall of 1058 mm per year (Huang et al., 2008). Temperatures vary with elevation and season, from −3.6 °C at the highest point in the winter to 38 °C at the lower elevations in the summer. The local average annual temperature has increased significantly over the past 47 years (Fig. 2). The warming trend in southwestern China is forecasted to continue in this and the next centuries (Huang et al., 2005; Jiang et al., 2005; IPCC, 2007; Xu et al., 2009). There are pronounced seasonal variations in both rainfall and temperature (Corlett and Lafrankie, 1998; Huang et al., 2008), with nearly 60% of the rainfall occurring in the hot summer months and less than 10% in the cold winter months.

2.2. Assisted translocation of endangered wild orchids

The Yachang Reserve had been subjected to logging and reforestation of different scales and intensity in the past four decades before the establishment of the nature reserve status in 2005. Some patches of forests, especially those on steep limestone hills, however, have escaped these man-made disturbances, and harbor a large number of wild orchid species and populations. The most recent environmental impacts have been from the completion of the 2nd largest hydropower project in China along the Hongshui river valley. In 2006, in anticipation of the completion of the Longtan reservoir, the portion of the hydropower project that is adjacent to the Yachang Reserve, the reserve initiated a rare and endangered plant rescue program. Besides a few tree species, the reserve translocated nearly 1000 orchid plants, mostly of reproductive sizes, belonging to 29 species and 16 genera. These plants were moved from locations slated for flooding along a section of the 20 km Nanpanjing river banks (all between 350 and 400 m above sea level) to a secured (from poachers) natural site at ~1000 m above sea level. The recipient site is less than 30 km away from, but ~600 m higher in elevation, and about 3.6 °C cooler on average than the source site. The recipient forest, which is composed of mixed broadleafed, evergreen and deciduous species, is less tropical in forest composition than the source sites, which are composed of

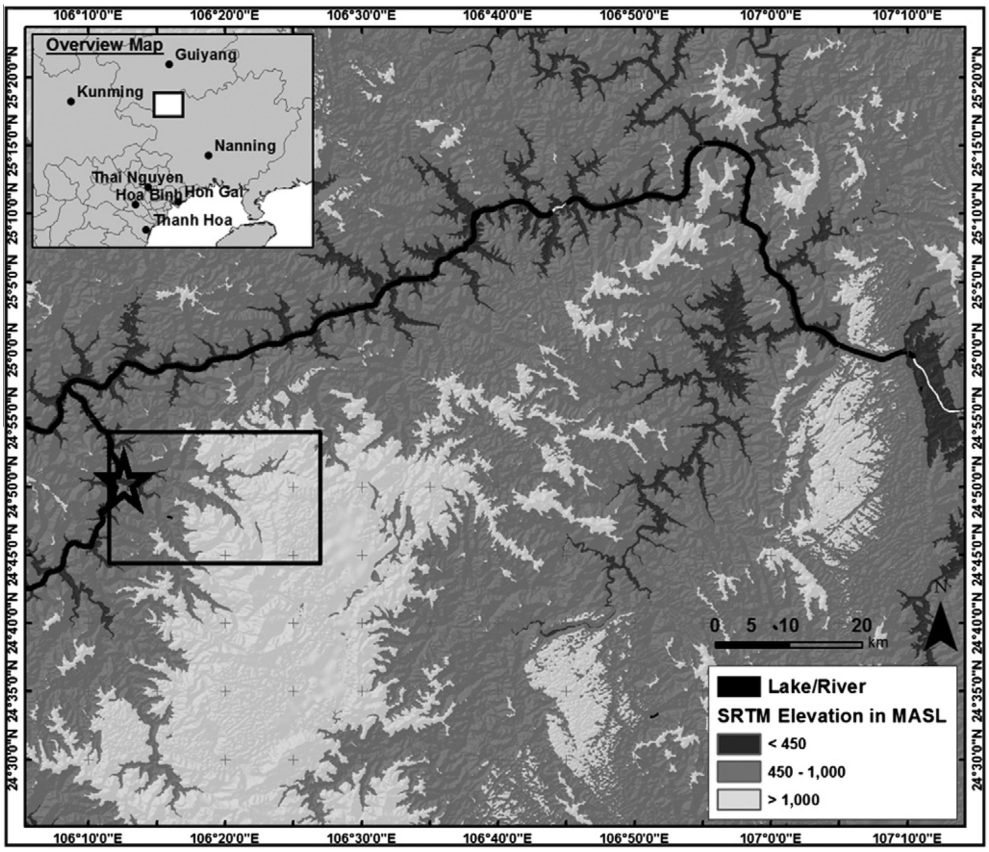

Fig. 1. Geographic location and elevation gradients of the Yachang National Orchid Nature Preserve (within the black box) and the adjacent Hongshui River area. Note that Nanning is the capital city of Guangxi Zhuang Autonomous Region, China. The star indicates the stretch of the Nanpanjing River (a tributary of the Hongshui) where the translocated orchids came from.

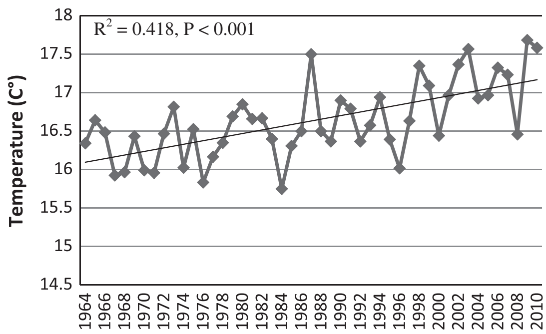

Fig. 2. Annual average temperature of the Yachang National Orchid Reserve in southwestern China from 1964 to 2010, based on a weather station at 1000 m above sea level and less than 30 km east of the reserve. The linear regression line shows the significant warming trend line ($Y = -29.704 + 0.023\,x$).

evergreen broad-leafed species (Appendix A). The source sites also harbor the tropical pine species (*Pinus yunnanensis* var. *tennifolia*) that is endemic to several valleys of the Nanpanjing and Hongshui rivers (Li and Wang 1981). However, the pine trees were rare, due to selective logging in the past.

2.3. Planting and monitoring

We planted the rescued plants in the recipient site based on the species' habits, i.e. we planted ground orchids (with soils from source sites surrounding the root tissues) in soil on the forest floor, lithophytic orchids on rocks or in crevices with limited soil, and epiphytic orchids on tree trunks. Forest canopy cover was also taken into considerations qualitatively. Most transplants were carried out from March to October 2006. We mapped and labeled the translocated plants and were able to monitor 20 of the 29 species, a total of 462 individuals from the start of this assisted colonization "experiment" in 2006 through May 2011 (Table 1). Specifically, we surveyed these plants for survival six times: in December 2006, December 2007, March 2008 (immediately following the extreme cold event, see below), November 2008, May 2010 (following the extreme drought), and in May 2011. We were also able to record whether each of the translocated species had flowered, largely due to a concurrent flowering phenology study from late 2006 to December 2008, which included fourteen of the 20 species (Liu et al. unpublished data). We obtained flowering information of the other six species from more casual observations. We did not quantify flowering events via, for example, counting the number of individuals that were flowering.

2.4. Recent extreme weather events

In January and February of 2008, nearly 2 years after the translocations, a large scale, extreme cold spell struck southern China (Zhou et al., 2011). In the Yachang region, the average temperature of January and February of 2008 (5.4 °C) was the second lowest recorded since 1964, when the weather station was established (Fig. 3a). Nevertheless, damage to the canopy at the recipient site was minimal. In early 2010, a severe drought hit southwestern China (Stone, 2010b). In the Yachang region, the rainfall during the dry season (October–April) of 2010 (172 mm) was the lowest in recorded history (Fig 3b). These two extreme weather events provided rare opportunities to examine impacts of extreme weathers on the assisted upward translocated orchid populations.

Table 1
Species, number of individuals of the 20 wild orchids that were moved from 350 to 400 m above sea level upward to ~1000 m above sea level in the Yachang National Orchid Nature Reserve in southwestern China and their mortality information from 2006 to 2011. No mortality resulted from the extreme drought in 2011 so it is not included. Species are listed from low to high vertical distribution range. **Bold** indicates low elevation species. [1] Narrow endemic species are those whose current range include only Guangxi, Guizhou, Yunnan and northern Vietnam or fewer areas because these areas are adjacent to one another and share similar limestone landscape and climatic characteristics; while tropical China and Asia include subtropical regions. *Rare species found in fewer than 3 locations within the Yachang Reserve, each with fewer than 100 reproducing plants. "e" indicates epiphytic, "l" lithophytic, and "g" ground orchid. Data on *Cymbidium bicolor* subsp. *obtusum* and *C. aloifolium* were merged because the two species were indistinguishable vegetatively, and have similar vertical distribution ranges.

Species	Local vertical distribution range	World-wide distribution[1]	Assisted migration date	No. plants transplanted	Mortality due to			No. plants alive in 2011
					Transplant	Extreme cold in 2008	Herbivory	
Cleisostoma nangongense*[*,e]	350–500	Narrow endemic	4/21/2006	17	7 (41.2%)	0	0	10 (58.8%)
Cleisostoma paniculatum[e]	350–500	Tropical China	4/30/2006	3	0	0	0	3 (100%)
Robiquetia succisa[e]	350–500	Tropical Asia	9/9/2006	36	0	0	27 (75%)	9 (25%)
Vandopsis gigantea[e]	350–500	Tropical Asia	12/14/2006	38	4 (10.5%)	34 (89.5%)	0	0 (0%)
Dendrobium lindleyi[e]	350–600	Tropical Asia	8/21/2006	26	0	0	0	26 (100%)
Liparis viridiflora[g]	350–600	Tropical Asia	5/17/2006	2	0	0	0	2 (100%)
Cymbidium bicolor subsp. ***obtusum*** [1] and ***C. aloifolium*** [1]	350–700	Tropical Asia	9/11/2006	91	5 (5.5%)	6 (6.6%)	0	80 (87.9%)
Cheirostylis chinensis[e]	350–800	Tropical Asia	9/11/2006	5	0	0	0	5 (100%)
Cymbidium tracyanum[e]	600–850	Tropical Asia	5/19/2006	31	0	0	7 (22.6%)	24 (77.1%)
Acanthephippium sylhetense[g]	350–900	Tropical Asia	9/11/2006	4	0	3 (75%)	0	1 (25%)
Calanthe argenteo-striata[g]	350–900	Tropical China	5/19/2006	31	2 (6.5%)	0	0	29 (93.5%)
Dendrobium williamsonii[*,e]	400–900	Tropical Asia	8/30/2006	6	4 (66.7%)	0	0	2 (33.3%)
Phaius flavus[g]	350–900	Tropical Asia and Japan	5/17/2006	1	0	0	0	1 (100%)
Eria corneri[l]	350–1000	Tropical Asia	5/17/2006	30	10 (33.3%)	0	0	20 (66.7%)
Paphiopedilum dianthum[*l]	400–1100	Narrow endemic	12/16/2006	21	0	0	0	21 (100%)
Paphiopedilum hirsutissimum [l]	400–1100	Tropical Asia	12/16/2006	30	8 (26.7%)	0	0	22 (73.3%)
Paphiopedilum micranthum[*,l]	350–1000	Narrow endemic	5/17/2006	2	0	0	0	2 (100%)
Luisia teres[e]	350–1200	Tropical Asia	5/17/2006	5	3 (60%)	0	0	2 (40%)
Cymbidium tortisepalum var. *longibracteatum*[*g]	350–1600	Tropical China	10/15/2006	83	0	0	63(75.9%)	20 (24.1%)
Total				462	43 (9.3%)	43(9.3%)	97(21.6%)	279(60.4%)

2.5. Data analysis

We summarized plant mortality over the 5-year period for each orchid species and attributed drivers of the mortality as stress of transplanting, the extreme cold spell in 2008, the extreme drought, and insect/mammal herbivory. Plants that died from stress after the initial transplant did so within the first year after (recorded during surveys in December 2006 and 2007), well before the extreme cold event, and without any signs of herbivory. Plants affected by the extreme cold event showed severe leaf burn and died soon thereafter. Finally, mortality attributed to herbivore damage was associated with obvious signs of mammal and insect feeding.

We also defined the natural elevational range of each orchid species within the Yachang Reserve and adjacent areas from plot sampling on 17 hills, arbitrarily selected throughout the Yachang Reserve and adjacent areas. On each selected hill, three 30 m × 20 m plots at the bottom, middle, and top of the hill were established and surveyed. This elevational range data was supplemented by observations during numerous haphazard foot patrols of all hills within the reserve from 2006 to 2010. We then compared plant mortality associated with the four drivers (transplanting stress, extreme cold, drought, and herbivores) between low elevation species, i.e. species whose vertical distribution ranges are below 900 m above sea level, lower than the elevation of the assisted migration recipient site (~1000 m above sea level) and wide elevation species, i.e. whose ranges span beyond 900 m above sea level (Table 1).

The differences in mortality due to transplant stress, herbivore, and cold between low and wide elevation species were examined using nonparametric Mann–Whitney *U* Tests. Fisher Exact Significance was used for these tests. Drought was not included in the statistical analysis because it caused zero mortality (see Results). The differences in percentage survival from 2006 to 2011 (arcsine square root transformed) between the low and wide elevation groups were examined using ANOVA, with initial population size as a covariate. Survival differences between epiphytic and ground orchids are also tested using ANOVA.

3. Results

Among the 20 species monitored, 14 were low elevation species with their vertical distribution ranges restricted to below 900 m above sea level, and six were wide elevation species with their vertical distribution ranges extending beyond 900 m above sea level (Table 1). The 2008 extreme cold spell led to mortality in four of 20 species, one of which (*Vandopsis gigantean*, Table 1) was extirpated by the event. Of all species pooled, around 9.3% of the plants died due to the direct impact of the extreme cold, but this mortality occurred only in low elevation orchid species (Fig. 4C). However, the percentage of mortality due to cold was not statistically different between the low and the wide elevation species (Mann–Whitney $U = 1.644$, $P = 0.517$), due to the large variance in the variable. In contrast, no direct mortality was recorded from the 2010 extreme drought (Table 1). Plants that died within the first year of planting, due to the stress of transplantation, represented 9.3% of total plants (Table 1). About 21.0% of the plants died due to herbivory by insects and/or small mammals. Mortality due to transplant stress (Mann–Whitney $U = 0.224$, $P = 1$) or herbivory (Mann–Whitney $U = 0.005$, $P = 1$), were not different statistically between the low and wide elevation species. (Fig. 4A and B).

Of all species pooled, 60.4% of individual plants survived the 5-years period following transplanting (Table 1). Initial translocation population sizes ranged from 1 to 83 individuals among

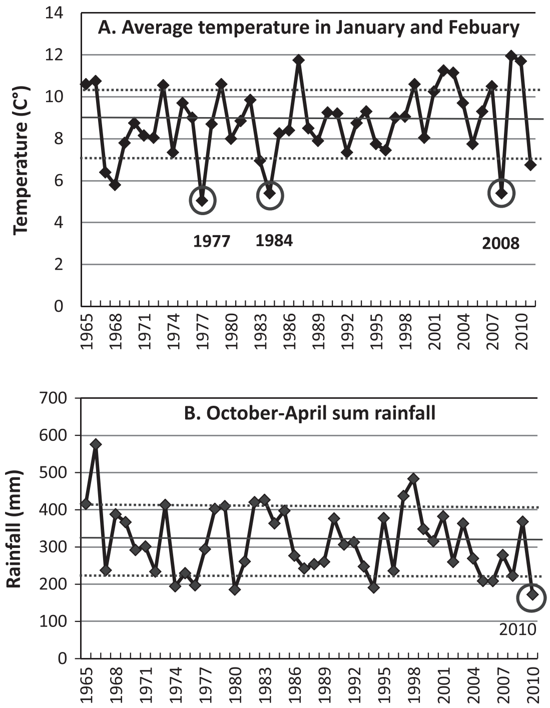

Fig. 3. Climatic graphs of the Yachang National Orchid Reserve in southwestern China for 1964–2010: Temperatures, highlighting the extreme cold spell in January and February of 2008 (A); and total rainfall from October–April, highlighting the severe drought in 2010 (B). The Solid lines indicate the average temperature of rainfall over the 46 years period, while the dash lines indicate one standard deviation.

species (Table 1), but it was not a significant factor affecting survival percentages in 2011($F = 1.004$, $P = 0.331$). Final survival percentages were not different between low and wide elevation species (Fig. D; 69.3% mean ± 36.3% standard deviation vs. 67.3% ± 30.9%), nor between ground and epiphytic orchids (68.5% ± 40.23 vs. 68.7% ± 33.9%).

All 20 translocated species flowered at least once 1 year after the translocations.

4. Discussion

4.1. Survival patterns of within vs. out of range translocations

4.1.1. Extreme cold event

Our study indicated that out of range translocated species were the only group suffering mortality and extinction from the extreme cold spell. The sole species that was extirpated by the cold event, *V. gigantea*, had a relatively large initial population size, with 38 reproductive individuals transplanted, all but four of these perished due to the cold spell. The other four plants died due to transplant shock. Extreme cold is known to be a major stochastic force in subtropical regions that can cause high mortality in tropical-origin, native or introduced species (Ross et al., 2009; Quinlan, 2010; Mazzotti et al., 2011). *V. gigantea* is an epiphytic, tropical orchid, whose distribution does not extend north of the Yachang region (Chen et al., 2009). Populations under northward or upward out of range translocations may resemble populations that are living along the species' range boundaries in that they are more likely to be subject to stressful, harmful or lethal weather events (Hoffman and Parsons, 1997). It is likely that the translocation destination, being 600 m higher, is out of the climate envelope of *V. gigantea*. In addition, tropical, especially epiphytic species may be more vulnerable to threats from extreme cold events than non-tropical and ground species during assisted or natural poleward or upward colonizations because they lack certain adaptations (e.g. plant dormancy), and are not buffered by soil in cold air temperatures.

Nevertheless, it is remarkable that all other low elevation species, also of tropical origin, most of which are epiphytic and lithophytic species, survived the extreme cold with little or no mortality. With all species pooled, about 1/4 of the mortality over the 5-year period was caused by the extreme cold event. While reports on mortality caused by extreme weather are common, few have compared it to other mortality sources over long terms (but see Altwegg et al., 2006). Altwegg and colleagues (2006) reported that 50% of the adult mortality of a temperate bird species (*Tyto alba*) can be attributed to harsh winters over a 65 year period, well within the species' distribution range.

4.1.2. Drought

Even more remarkable is that no direct mortality due to the drought was recorded. This is also true for natural orchid populations at the same site (Liu, unpublished data). For example, both *Paphiopedilum dianthum* and *P. hirsutissimum* have natural resident populations near the translocated populations. No adults or juveniles from these two natural populations died following the drought, even though the drought was the most severe over the 46 years of recorded history. These studied orchid species, most of which being epiphytic or lithophytic, are probably well adapted to periodic extreme dry conditions. For example, many orchids in both groups, have succulent leaves or stems. However, the plants in these resident populations did reduce their numbers of stems and produced fewer flowers per plant as consequences of the same drought (Liu, unpublished data). Impacts of the drought on the growth and reproduction of the transplanted populations were not known as these parameters were not quantified.

Extreme weather events, both drought and extreme cold, could cause local population extinctions, as reported for the Edith's Checkerspot butterfly (*Euphydryas editha*; Ehrlich et al. 1980; Singer and Thomas 1996; Thomas et al. 1996). However, the two extreme weather events did not impose equal impacts on translocated populations in our study.

4.1.3. Herbivory

Herbivory by insects and mammals led to higher mortality than either the extreme cold spell or initial transplant stress. Both within and out of range translocation groups had species suffering from mortality due to herbivore damages. It is expected that plants introduced within their current natural range should suffer from herbivore damage because herbivores on resident populations might easily move to the new populations. In contrast, out of range translocated species may sustain lower levels of herbivore damage, as often seen in populations introduced from out of range areas for horticultural purposes. In fact, relief from herbivore pressure for introduced species is a well-studied phenomenon as it relates to the species invasiveness in the recipient communities (the enemy release hypothesis) (Keane and Crawley, 2002). However, such relief from herbivores could only be true if the species has specialist herbivores that are absent in the introduced range. No damage due to specialist herbivores was observed for any of the translocated orchids. *Robiquetia succisa* and *Cymbidium tracyanum*, two out of range introductions were eaten by generalist rodents, and occurred throughout the monitoring period (75%, 27 out of 36 plants). On the other hand, only one species of the within range introduction, *Cymbidium tortisepalum* var. *longibracteatum*, experienced mortality due to herbivory, all of which occurred after the extreme drought, presumably due to scarcity of other food plants.

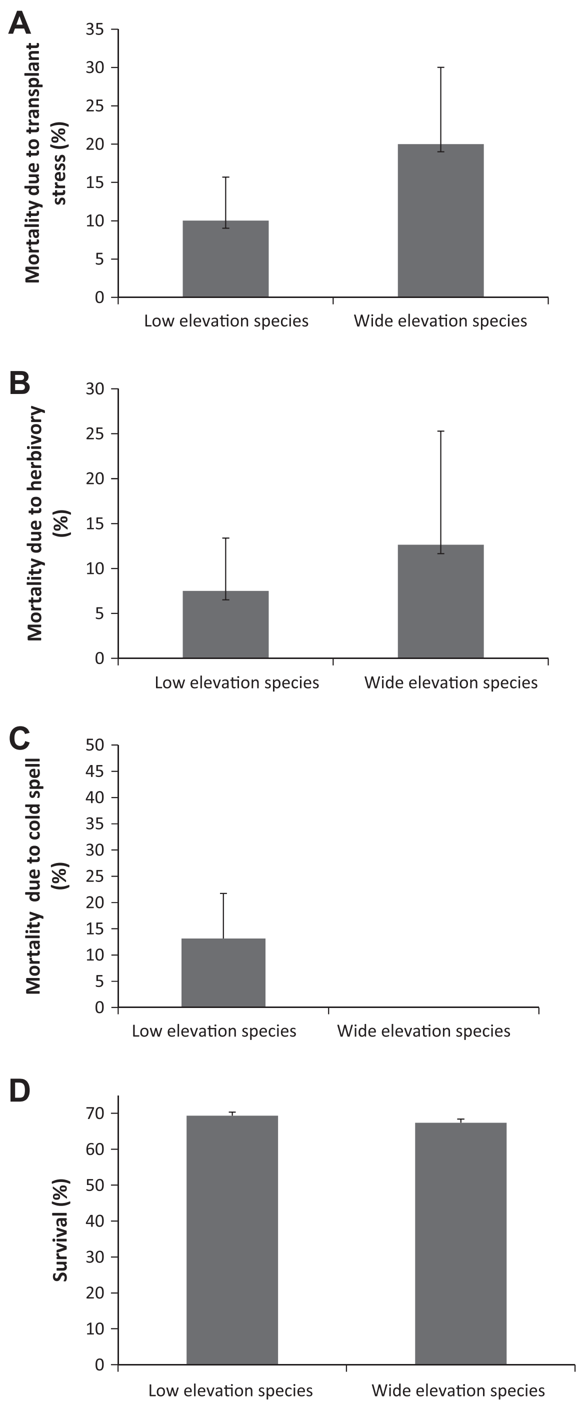

Fig. 4. Mortality rates due to transplanting stress (A), herbivory (B) and cold spell (C), and survival till 2011 (D) of plants of 20 wild orchid species that were transplanted to habitats at higher elevations in southwestern China. Error bars are standard errors. Species were grouped based on their local vertical distribution patterns. Low elevation species ($N = 14$) are those whose natural distribution ranges do not extend above 900 m above sea level while wide-ranging species ($N = 6$) are those that do. Note that no plant died due to the cold spell in wide-ranging species.

4.1.4. Transplant shock and other potential mortality factors

It is not unusual that plants experience mortality within the first year of transplanting due to the inability to acclimatize (Maschinski and Haskins, 2012). In our study, mortality due to transplant shock was low overall (10%) compared to other orchid reintroduction attempts (Maschinski and Haskins, 2012; Yam et al., 2010). The low mortality rate due to transplant shock can probably be attributed to the use of mostly reproductive size plants. In general, transplanting larger plants results in greater success than transplanting smaller plants (Godefroid et al., 2011; Maschinski and Haskins, 2012; Menges, 2008; Yam et al., 2010). The likelihood that the transplants had acquired the required mycorrhizal fungi in roots before transplantation may have promoted success (Dixon et al., 2003). In addition, mortality due to translocation shock was not different between the low and wide elevation species, likely due to the large variation among species (ranging from 0% to 67%), and/or to the existence of genetically based clinal variation along elevation gradient in the wide elevation species.

Competition with resident plants in the new location can also lead to plant mortality (Maschinski and Haskins, 2012). However, competition in our case is not a factor because being epiphytic or lithophytic, or limestone specialists, the monitored transplants were mostly free from competition with other plants.

4.2. What the survival data can and cannot tell us about the assisted colonization processes

In this study, recruitment and biotic interactions of the transplants, critical success criteria for reintroduction of rare species (Pavlik, 1996), were not assessed. For species with short generations, it is relatively easy to assess the success of the translocation. For long-lived species such as most orchids, evaluating success is more complicated and should be done on various surrogate variables at different time frames (Maschinski and Haskins, 2012; Menges, 2008). Distinguishing conditions that allow adult plants to persist, i.e. the persistence niche (sensu Holt 2009), from conditions that allow seed set, seed germination and seedling growth, i.e. the recruitment niche, allows us a better understanding of the processes that lead to the long term success or failure of natural or assisted colonization into new ranges, as also advocated by Hewitt et al. (2011).

The orchids' ability to overcome extreme weather challenges and to flower in the translocation site indicates that the new location is likely to be within the persistence niche of these orchids. Evidence is mixed, however, regarding whether the translocation is within the orchids' recruitment niches. Casual observations had indicated that at least two of the translocated species, *Cymbidium bicolor* and *Calanthe argenteo-striata*, both out-of-range translocations, set fruits almost annually. Other species might have set fruit but escaped our notice, as fruit set was not a specific observation target during the study period. In addition, lack of fruit set in the translocated populations within a short to medium time frame (<5 years) may not indicate that the site does not offer conditions for the species to do so. The percentage of fruit set per flower can be very low in natural populations at the same site (Shi et al. 2009; Hong Liu, unpublished data). Finally, no seedlings were observed within 0.5 m around any translocation plants during the 2011 survey. To decide whether the translocation site is within the recruitment niches of these orchids, quantification of fruit set through extensive field observations and experiments on seed germination and seedling growth are needed.

4.3. Implications for future assisted colonization of orchids and other endangered plants

Out of range introduction for rare species conservation has been seem as the last resort (Falk et al., 1996; IUCN, 1998; Maunder, 1992; Vallee et al., 2004) or not a viable option at all (Davidson and Simkanin, 2008; Ricciardi and Simberloff, 2009) by conservation researchers and practitioners. Those that embrace the measures recommended very small steps (Maschinski and Haskins,

Table 2
Vegetation and climatic characters of assisted migration source and recipient sites at the Yachang National Orchid Nature Preserve in southwestern China. Climate data were based on (Huang et al. 2008).

Site type	Plant community type	Common canopy species	Common understory species	Temperature (°C)			Annual rainfall (mm)
				Annual average	January average	July average	
Source (350–400 m ASL)	Evergreen broad-leafed forest	*Bombax malabaricum*	*Bauhinia apertilobata*	20.4	11.7	27.4	940.8
		Burretiodendron esquirolii	*Callicarpa macrophylla*				
		Ficus microcarpa	*Cipadessa cinerascens*				
		Ficus oligodon	*Clerodendrumjaponicum*				
		Pinus yunnanensis var *tennufolia*	*Dalbergia hancei*				
		Pterocarya stenoptera	*Dischidia chinensis*				
			Hoya lyi				
			Piper hancei				
			Pterolobium punctatum				
			Rachelospermum jasminoides				
			Rhapis filiformis				
			Vitis pentagona				
Recipient (1000 m ASL)	Mixed evergreen-deciduous broad-leaved forest	*Carpinus purpurinervis*		16.8	8.1	23.3	997.5
		Cyclobalanopsis glauca					
		Lysidice rhodostegia					
		Platycarya longipes					
		Quercus pbillyraeoides	*Myrsine africana*				
			Rapanea neriifolia				
			Raphiolepis indica				
			Smilax china				

2012). These may be wise rules, considering potential species niche limitations (Colwell and Rangel, 2009) and extreme weather challenges. Relatively short distance (35 and 65 km) but out of range translocation of two species of butterflies were reported to be successful with population persistence and expansion in temperate Scotland over 6 years following introduction (Willis et al., 2009). However, multiple, sequentially northerly translocations may be needed, given such a short distance move at each attempt, to meet the demands based on the projected magnitude of climatic change within the next century. This scenario may not be possible because of the associated large monetary demands and logistic challenges. It cost nearly 10 million RMB (equivalent of $1.5 million USD) to implement the transplant project reported here, a fund solicited successfully by the Guangxi Forestry Bureau to the hydropower construction company. The level of funding for wild plant rescue is unlikely to be duplicated in China, or other parts of the world in the future. Nevertheless, as demonstrated in this paper, conservation practitioners may have little choice where they can relocate species. In the case presented here, there were no secured locations at lower elevations that could receive such massive amounts of translocations of poachable plants.

Should there be no logistical constraints, then ideally one should first establish the niche for each of the threatened species, preferably through carefully designed experiments, rather than inferences from current distribution range. The latter does not always correspond to the potential niches (Angert, 2009; Hutchinson, 1957). In addition, for some species, the recruitment niche may be completely nested within their persistence niche (Holt, 2009). However, for species with complex life history such as orchids, this may not be the case. For example, mycorrhizal fungi that are needed for seed germination and seedling growth may be different from those needed for adult growth and flowering. Regardless, it will be necessary to learn whether a new release site is within the recruitment niche as well as the persistence niche to decide whether assisted colonization may be a viable conservation tool for an endangered species. Optimal translocation sites can perhaps be decided through detailed studies of the species' biology (Maschinski and Haskins, 2012).

Finally, although rare and difficult to predict, extreme weather exerts substantial influence on population dynamics (Altwegg et al., 2006) and species boundaries (Zimmermann et al., 2009). When choosing release sites, accounting for potential impacts of extreme weather events, such as incorporating the coldest or the driest conditions seen in an area into the experiments determine niche limits, will increase the chance of long term success.

Several lines of work have shown that orchids as a group had much lower than expected naturalization rate among the flowering plants (Daehler, 1998; Pemberton and Liu 2009; Pyšek, 1998), and among the orchids naturalized, few impose notable ecological impacts. Many studied orchids show dependency on specific pollinators, and nearly all orchids are dependent on specialist or generalist mycorrhizal fungi for germination (Otero et al., 2004). Together with other specific abiotic requirements, these two biotic dependencies explain the low naturalization rate and low level of invasiveness of orchids. Species with high and or multiple biotic and abiotic dependencies, represented here by orchids, but not restricted to orchids, will probably have low risk of having high negative impacts in the new ranges.

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Appendix A

(See Table 2).

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