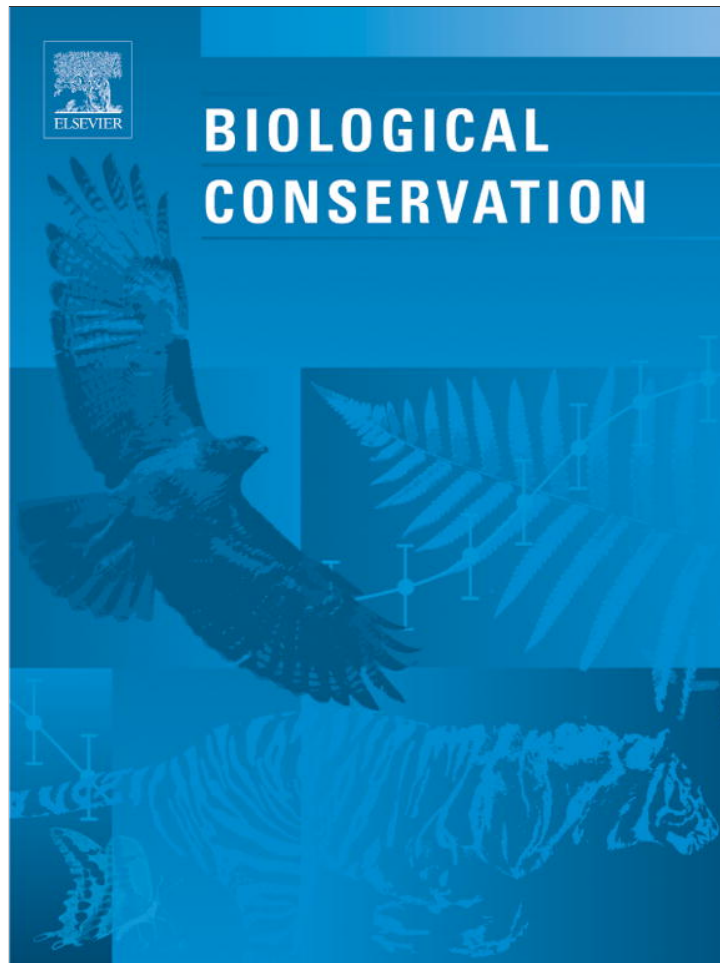


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Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

When is local the best paradigm? Breeding history influences conservation reintroduction survival and population trajectories in times of extreme climate events



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ARTICLE INFO

Article history:

Received 15 June 2012

Received in revised form 17 October 2012

Accepted 21 October 2012

Keywords:

Plant conservation

Reintroductions

Inbreeding

Outbreeding

Climate change

PVA

Demography

ABSTRACT

Creating self-sustaining populations resilient to stochastic events is the goal of conservation reintroductions. Concern about disrupting locally co-adapted gene complexes, outbreeding depression, and hybridization has led to a “local is best paradigm” for source selection, yet this policy constrains rare plant reintroduction efforts and may not always best conserve rare species. Using progeny from controlled crosses (control, selfed, near neighbor, far neighbor and between sites) with maternal plants from two sites, we tested survival and population trajectories of US endangered *Jacquemontia reclinata* reintroduced in 2004 and 2005 to three sites. By 2011, survival and recruitment was greatest for mixed-population progeny, was consistent across years, and became most apparent after extreme climate events (hurricanes, drought, and exceptional cold). Populations founded from mixed sources exhibited greater resilience to stochastic disturbances than those from a single source and had positive projected population growth at two of three sites. Recipient sites most proximal to maternal origin were not those with best survival. Maximizing reintroduced population persistence calls for re-examining paradigms, using decision trees and reintroduction guidelines to guide source selection choices. The local is best paradigm may be dooming many reintroductions to failure.

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1. Introduction

Concern about maintaining genetic integrity of wild populations has led many in the conservation community to recommend using local seed sources for restoration purposes so that local gene pools and adaptations to local conditions will be preserved and hybridization can be prevented (Vallee et al., 2004; McKay et al., 2005). Selection of appropriate source material for restorations is essential to achieve the goal of creating a sustainable population capable of evolving in the wild (Neale, 2012). Many rare species have small fragmented populations; individuals within may develop inbreeding depression, a condition that leads to reduced fitness (Frankham, 1995) and high risk of population extinction (Keller and Waller, 2002; Angeloni et al., 2011). Inbreeding depression is common across many populations (Angeloni et al., 2011) and spatial scales (Linhart and Grant, 1996). While mixing populations to increase gene flow would reverse the problem of inbreeding depression, concern that mixing may lead to disruption of locally co-adapted gene complexes and outbreeding depression has pre-

vented broad use of this practice (Hufford and Mazer, 2003; Frankham et al., 2011).

Determining whether it would be safe to mix populations for a restoration requires knowledge of population genetic structure and diversity (Hamrick et al., 1991; Keller and Waller, 2002). Using a decision tree can help predict the probability of outbreeding depression if similarities or differences in population taxonomy, chromosome ecology, and the length of time populations have been separated are known (Frankham et al., 2011). Estimates suggest the probability of outbreeding depression in populations separated in the last 500 years growing in similar environments would be small, but with few reintroduction projects examining genetic diversity directly, empirical evidence supporting or refuting theory regarding the impacts of mixing populations in restoration is sparse (Broadhurst et al., 2008; Frankham et al., 2011; Neale, 2012).

Increasing uncertainty of climate change is heightening the urgency of restoring rare species populations in a manner that will ensure the greatest success (Maschinski and Haskins, 2012). Common garden or reciprocal transplant experiments allow for in situ performance comparisons of populations (Hufford and Mazer, 2003) and these will become increasingly important tests of adaptation to changing climate (e.g., Marsico and Hellmann, 2009). As

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part of a landscape scale recovery effort for the US endangered *Jacquemontia reclinata* (Maschinski and Wright, 2006), we examined the influence of single-source versus mixed-population breeding history on plant survival and fitness in three locations along the southeastern coast of Florida, USA. We also tested whether distance of reintroduction site from maternal source influenced transplant survival. Further, we compared population growth during transition periods with and without extreme climate events and determined population viability of reintroduced populations with single-source versus mixed-population breeding histories.

2. Materials and methods

2.1. Background

J. reclinata (beach clustervine) is a perennial vine endemic to the South Florida coastal dune ecosystem. Mature plants produce multiple trailing stems from a central root. Plants may live 15 years or more in the wild and can achieve reproductive maturity within 1 year (S. Wright, *personal observation*). Its white flowers are visited by a wide array of generalist insects gathering nectar and pollen, including flies, wasps, bees, and butterflies, with greatest pollinator diversity in the largest plant populations (Pinto-Torres and Koptur, 2009). The capsular fruits produce one to four seeds; most seeds are dropped below the plants when the capsules open. Although many populations fruit prolifically, few seedlings establish in the wild (Maschinski et al., 2003). Large-scale natural disturbances (e.g., hurricanes), habitat fragmentation and alteration have restricted the species' range and contributed to its listing as federally endangered (USFWS, 1996; Lane et al., 2008). In 2011, approximately 730 wild individuals grew in ten sites in coastal strand and open maritime hammock, habitats that were once contiguous along the eastern coast of Florida USA (USFWS, 1996).

Prior to any reintroduction or augmentation, guidelines advise testing genetic structure of species with populations that have fewer than 50 individuals flowering and setting fruit, are highly fragmented and isolated, where no pollinators are present, or no viable seed is being set (Maschinski et al., 2012a). As *J. reclinata* has six of ten populations with fewer than 50 individuals and low recruitment growing in fragmented, isolated patches (Maschinski et al., 2003, 2011), we conducted genetic analysis on eight of the known wild populations to test population structure prior to initiating any reintroductions (Thornton et al., 2008). Random amplified polymorphic DNA markers indicated that the two largest populations used for maternal sources for this study, Crandon Park (2001 $n = 144$ plants in 700 m²) and South Beach (2001 $n = 245$ plants in 340 m²), were genetically similar (Nei's genetic distance = 0.05), and had greater genetic diversity ($I = 0.282$ and 0.360, respectively) than the small populations with <50 individuals ($I = 0.136$ –0.243). Because Crandon Park and South Beach were not significantly genetically differentiated, mixing sources was allowed by current guidelines (Maschinski et al., 2012a).

The source propagules for our reintroduction experiments were the F1 progeny of a controlled hand pollination experiment conducted by Pinto-Torres and Koptur (2009). Briefly, they collected seed from wild *J. reclinata* plants with known spatial location at Crandon Park (CR) and South Beach (SB) and germinated seeds at the Fairchild Tropical Botanic Garden nursery producing 65 reproductive maternal plants for crosses. Following protocols of Kearns and Inouye (1993), for each maternal source they produced six pollination treatments: control (bagged and unmanipulated), selfed, sibling (crossed with offspring from same parent), near neighbor (crossed with offspring of a wild parent from a patch <20 m away), far neighbor (crossed with offspring of a wild parent from a patch >20 m away), and between-site crosses with two maternal plant

origins (CR and SB separated by 71.4 km; Fig. 1). Measurements on seeds and seedlings resulting from the hand pollination trials determined that *J. reclinata* has a mixed mating system: flowers are able to set fruit with viable seeds with self pollen, but outcross pollen produces significantly greater fruit and seed set than self pollen (Pinto-Torres and Koptur, 2009). We maintained seedlings that resulted from the crosses in our nursery for 1 and 2 years until transplanting them to reintroduction sites. Not all hand pollination treatments from each maternal source lived to maturity, thus our experiments included eight maternal source X hand pollination treatments: CR-control, CR-self, CR-sibling, CR-far neighbor, SB-sibling, SB-far neighbor, and two between site crosses, CR × SB and SB × CR. We report results of pollination attempts, seeds set in 2002, and seedling survival in our nursery in 2003–2006 (Table 1). Full replication of treatments across the three reintroductions was limited by plant availability and space at recipient sites.

2.2. Experimental reintroductions

To increase the number of populations and to test how breeding history affected plant survival and recruitment, we reintroduced *J. reclinata* to three sites within its historical range along the eastern coast of south Florida (Fig. 1). We selected the reintroduction sites based upon a recipient site assessment and ranking system (Wright and Thornton, 2003; Maschinski et al., 2012b). Generally, the recipient sites featured good quality habitat with high native plant diversity similar to home sites, low invasive species cover, good land manager support, and ample spatial extent for population expansion. We use the term reintroduction to describe these experimental populations, which assumes that the species occurred historically at the sites, however at the time of reintroduction *J. reclinata* had been absent from all sites for at least 20 years. The timing of installation of plants into reintroduction sites varied due to logistics of site preparation by land managers. All plants were reproductive adults at the time of outplanting.

On July 24, 2004, at Haulover Beach, we planted 143 *J. reclinata* plants. Into twenty-four east to west oriented transects (15 m in length) we randomly placed at 3 m spacing one plant representing each of six hand pollination treatments (Table 2). Note one transect had only five plants. Spacing allowed for adequate plant growth and minimized intraspecific competition. The reintroduction area featured expansive restored dunes replenished with offshore substrate and planted with native coastal strand species.

Prior to the outplanting at Virginia Key, land managers removed invasive exotics *Casuarina equisetifolia* (Australian pine) and *Schinus terebinthifolius* (Brazilian pepper) to restore the open coastal strand area. Located 2.7 km from CR, Virginia Key is one of the last South Florida barrier islands remaining in a near natural state. It contains high plant diversity within beach dune, coastal strand, maritime hammock, and mangrove tidal swamp habitats. On April 7, 2005, we randomly planted 171 *J. reclinata* of four hand pollination treatments (Table 2) throughout suitable planting area. Planting areas were small patches that did not allow the transect design used at Haulover Beach.

Substrate re-nourished from offshore dredged sand characterizes the most northern reintroduction site, Delray Beach, a site restored from domination by the invasive exotic *Scaevola sericea* (beach naupaka) to a diverse planted native coastal strand community. Human-constructed dunes and walking paths shape the topography of the site and buffer the reintroduction from direct salty sea breeze. On February 16, 2005, along with native coastal dune plants, we randomly distributed 132 *J. reclinata* from six hand pollination treatments (Table 2) throughout suitable planting area. This reintroduction was integrated into a formal landscape that precluded use of transects.

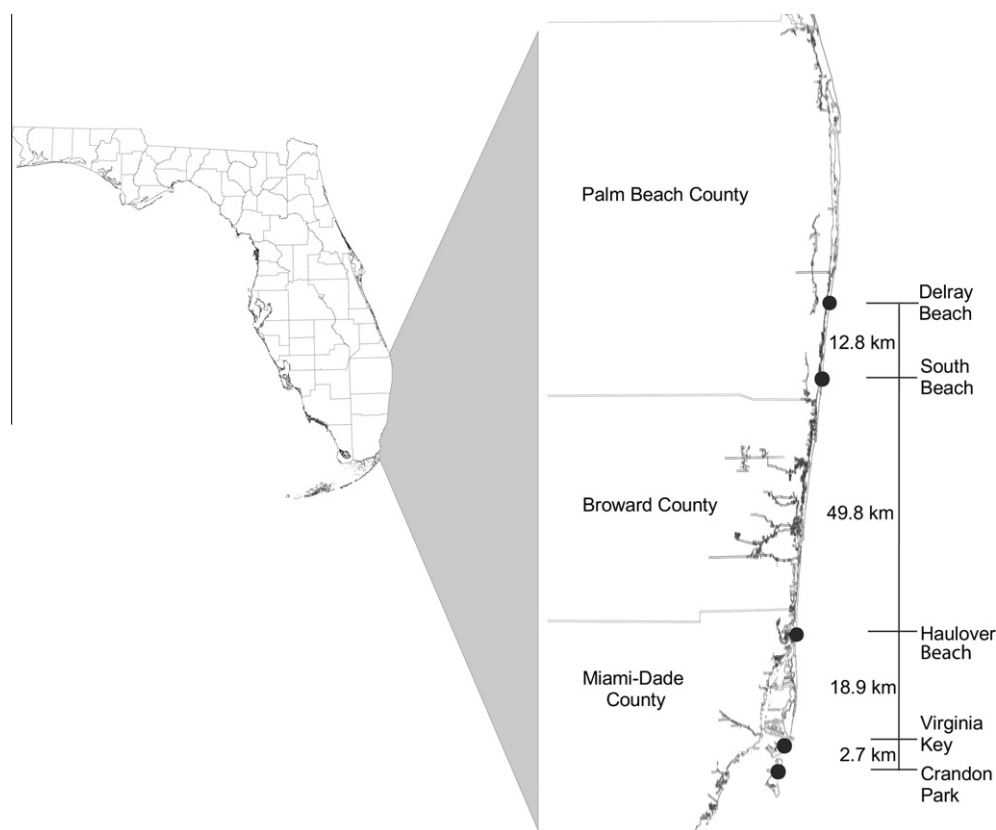


Fig. 1. Map of *Jacquemontia reclinata* populations indicating maternal source populations (Crandon and South Beach) for the experiment and the three reintroduction sites (Delray Beach, Haulover Beach, and Virginia Key). Map shows distances (km) between the sites.

At all sites we recorded GPS locations and watered each plant with 1 quart of water at the time of the planting. The timing of the introduction at Haulover Beach during the rainy season reduced the need for supplemental watering, however at Virginia Key and Delray Beach land managers watered plants when needed until the rainy season started. We monitored plant survival and noted seedling establishment. We assumed the maternal parent of any seedling was its closest outplanted neighbor.

2.3. Analysis

We analyzed differences in survival (days alive since installation) using a general linear model, where hand pollination treatment (control, self, sibling, far neighbor or between site crosses) and maternal origin (CR or SB) were the fixed main effects and site was a random effect (SYSTAT, 2007). To determine whether there was an advantage to plants installed at sites closest to maternal origin, we analyzed maternal source and the distance from maternal source to recipient reintroduction sites and their interactions using general linear model (SYSTAT, 2007).

To help explain significant demographic trends, we gathered regional temperature and precipitation data from online sources. We report mean minimum soil temperature measured at a depth of –10 cm for January through April in 2005–2011 at Homestead, Florida using data from University of Florida Automated Weather Network (<http://fawn.ifas.ufl.edu/data/reports/>). In addition we report quarterly precipitation in Miami from 2004–2010 using data from Florida Climate Center, Florida State University, Center for Ocean-Atmospheric Prediction Studies (http://coaps.fsu.edu/climate_center/data/precip_miami.shtml).

We examined whether breeding history influenced survival in years with extreme climate events using a Kruskal–Wallis test on

population change during transitions with extreme events versus transitions where no extreme event occurred for mixed vs. single source crosses in all sites combined.

2.4. Population viability analysis

To understand the effect of breeding history on *J. reclinata* population viability, we developed three-stage composite models for each hand pollination treatment planted at the three sites based upon greenhouse and field measurements of experimental plants. Stages were seeds, non-reproductive seedlings, and reproductive adults. Using mean seed survival of Crandon sourced seeds collected from the wild population and buried to 5 cm in controlled experiments measured in 2003, 2006 and 2007 at Crandon Park (Pascarella et al., 2011), we estimated seed survival in the seed bank as 0.404. For each maternal origin X hand pollination treatment, we used mean percent germination and mean percentage seedlings surviving to adult stage measured in the greenhouse. To account for decreased germination rates in the field in comparison to the greenhouse, we multiplied each greenhouse seed germination value by 0.114, the field germination rate Pascarella et al. (2011) measured from seed bank trials at Crandon Park. Field measurements of average percent adult survival over the monitoring period at each site supplied the adult–adult vital rate. We determined reproductive value as number of seedlings observed at the reintroduction site in 2011 (where maternal plant was assumed to be the closest adult) per live adult observed in the previous monitoring period. For those treatments that had no recruitment, we used a conservative 0.001 estimate for the reproductive value.

For each breeding treatment we calculated population growth trajectories, extinction risk, and elasticities using the stochastic

Table 1
Comparison of total attempts, total seeds produced, and survival of seedlings in nursery 1, 3, and 4 years post-germination for six hand pollination treatments conducted on maternal plants from the two largest *Jacquemontia reclinata* populations. For further details see Pinto-Torres and Koptur (2009).

Maternal origin	Hand pollination treatment	Attempts	Failed attempts	% Fruit set/attempt	Total seeds 2002	Live seedlings May 2003	Total reintroduced by April 2005	Live seedlings in nursery July 2006	Total mortality	% Mortality
CR	Control	97	84	13	32	28	24	0	4	14
CR	Self	75	52	31	53	26	24	2	0	0
CR	Sib	81	43	47	109	93	70	22	1	1
CR	NN	15	9	40	14	9	0	0	9	100
CR	FN	117	44	62	205	145	98	45	2	1
CR	CR × SB	79	25	68	174	154	111	39	4	3
Total		464	257		587	455	327	108	20	
SB	Control	32	30	6	2	1	0	0	1	100
SB	Self	21	19	10	8	4	0	0	4	100
SB	Sib	18	9	50	29	20	15	0	5	25
SB	NN	17	10	41	20	11	0	0	11	100
SB	FN	16	5	69	42	26	22	0	4	15
SB	SB × CR	66	12	82	180	135	82	48	5	4
Total		170	85		281	197	119	48	30	

simulation program RAMAS GIS (Akçakaya and Root, 2005). We generated models with 1000 simulations over 50 years assuming exponential-type density dependence that would affect all vital rates. We generated standard deviation matrices assuming 4% of vital rates. Initial vectors had zero values for seed and seedling stages, but had the number of transplanted adults for the adult stage.

3. Results

Total seed set and seedling survival generally increased with crossing distance (Table 1). No SB-control, SB-self, SB- or CR-near neighbor progeny survived to be included in the reintroductions.

Mean plant survival was significantly lower at Virginia Key (789 ± 144 days alive) than at Delray Beach (1448 ± 322 days) or Haulover Beach (1639 ± 103 days; $F_{1,430} = 10.7, p = 0.001$). However, by 2011, the greatest recruitment occurred at Virginia Key, while the least occurred at Delray Beach (Table 2). Seedlings established at all reintroduction sites, but not adjacent to all hand pollination X maternal source treatment plants (Table 2).

Mean survival significantly depended upon distance between maternal and recipient sites ($F_{3,430} = 17.41, p = 0.0001$), but there was not a significant local advantage (Fig. 2). There were no significant interactions between hand pollination treatment and distance ($F_{2,430} = 0.827, p = 0.44$) nor treatment and maternal origin ($F_{3,430} = 1.292, p = 0.277$).

Plant survival (mean days alive since installation) was significantly greater with increased crossing distance. The between site crosses had significantly greater longevity than treatment groups of crosses between more proximate neighbors ($F_{1,430} = 7.96, p = 0.001$; Fig. 3) and no interactions were significant. This pattern of greatest longevity with greater outcrossing distance was consistent across maternal origins in all years of the study and became most apparent after extreme climate events (Table 2).

Significant mortality periods occurred between 2005–2006 and 2008–2011. Events occurring before 2006 that contributed to mortality were desiccation, competition, maintenance personnel excavating plants at Haulover Beach, burial by animals, and hurricane-related events. Four category two hurricanes created storm surge, heavy rains, and winds that impacted reintroduction sites. For example, in October 2005, Hurricane Wilma severely impacted Delray Beach burying 44 *J. reclinata* plants. We considered buried plants as dead in 2006 and 2007, but two of these resurfaced by 2011 (Table 2). Between 2008 and 2011 exceptional cold and drought occurred (Table 3).

Considering all sites combined, extreme climate events increased mortality. The mean proportion of adult transplants surviving was significantly greater during transition years in which there were no extreme climate events than in transition years with extreme events (Table 2). Mixed source populations had significantly less mortality than plants from single sources in transition years with extreme climate events, but did not significantly vary in transition years without an extreme event (Median percent mortality Single No Event = 0%, 95%CI = 0, 19; Mixed No Event = 4%, 95%CI = 1, 7; Single Yes Event = 33%, 95%CI = 25, 48; Mixed Yes Event = 27%, 95%CI = 17, 33; Kruskal–Wallis = 27.62, $p < 0.0001$).

Population trajectories greatly varied according to breeding history, maternal plant origin, and reintroduction site. Models predicted that populations founded with mixed-population transplants had positive population growth at two sites. At Haulover Beach, PVA models predicted population growth only for the CR × SB population ($\lambda = 1.030$; Table 4), while at Virginia Key, PVA models predicted positive population growth only for the SB × CR population ($\lambda = 1.036$). All other hand pollination treatment models predicted population declines within 50 years or less at any of the sites (Table 4).

Table 2

Planting date, hand pollination treatment and maternal source and number of plants installed for experimental reintroductions of *Jacquemontia reclinata* at three sites. Number of surviving plants from 2005 to 2011 is indicated. Years when monitoring was not conducted are indicated by – The number of seedling recruits observed in 2011 is specified. *Indicates that plants previously believed dead at Delray Beach were found alive in 2011. These plants had been buried in deep sand by storm surge deposition. Downward arrows indicate years of extreme climatic events. Note that we could not verify extreme cold temperatures at Delray Beach in 2010 from online sources.

Site	Date planted	Treatment	# Planted	Year monitored							Total recruits 2011
				2004	↓ 2005	2006	2007	2008	↓ 2009	↓ 2011	
Haulover Beach	23-July-04	Control	24	24	24	16	16	16	–	6	7
		CR-Self	24	24	24	11	11	11	–	8	7
		CR-Sib	24	24	24	17	17	17	–	9	8
		CR-FN	24	24	22	16	16	15	–	12	5
		CR × SB	24	24	23	22	22	20	–	14	20
		SB × CR	23	23	22	18	18	17	–	13	8
Virginia Key	7-April-05	CR-Sib	22	–	22	11	9	1	0	0	0
		CR-FN	52	–	52	25	21	17	15	10	31
		CR × SB	63	–	63	44	43	38	27	21	35
		SB × CR	34	–	34	21	21	19	18	16	30
Delray Beach	16-February-05	CR-Sib	24	–	24	10	10	–	–	11*	0
		CR-FN	22	–	22	11	11	–	–	11	1
		CR × SB-BS	24	–	24	16	14	–	–	13	0
		SB-Sib	15	–	15	10	7	–	–	5	0
		SB-FN	22	–	22	16	16	–	–	15	1
		SB × CR-BS	25	–	25	16	16	–	–	17*	1

Elasticity values indicated that the most important vital rate influencing the models was adult stasis followed with equal importance by reproductive value, seed–seedling, and seedling–adult vital rates. Treatment groups with the greatest recruitment coupled with high values in all these cells had highest population growth. At Delray Beach, the low recruitment observed in 2011 resulted in negative population growth models for all treatments despite the relatively high survival rates of adults in recent years (Tables 2 and 4).

4. Discussion

As rare species populations become increasingly fragmented, habitat restoration and reintroduction will become more important components of biodiversity preservation. Building new populations that are functional, self-sustaining, and resilient to stochastic events will require knowing whether to reinstate gene flow between fragmented populations or preserve local adaptation. And this is especially critical with more extreme and variable climatic events. The ability to persist through extreme climatic events will be critical to a species ability to shift range in response to a changing climate (Early and Sax, 2011). In our study, mixed-population *J. reclinata* progeny proved to have higher survival than control, selfed or far neighbor progeny, despite site-specific circumstances such as hurricane impacts. It is noteworthy that the mixed population advantage became more apparent after periods of extreme environmental stress from hurricanes, drought, and cold temperatures. Mixed-population founders had greatest numbers of next generation recruits, they showed greater resilience to climatic events, and had greater recovery by 2011 than the single source founders. Extreme drought and temperatures have been documented to be correlated with decreased production, survival, and germination of seeds (Torang et al., 2010), changes in community composition, diversity, and ecotone boundaries (Jimenez et al., 2011), but to our knowledge ours is the first study documenting that mixing rare populations aids persistence in the face of extreme climatic events. Thus mixing populations is warranted to restore *J. reclinata*, while using single population sources or “local is best paradigm” for reintroductions will decrease the likelihood of population persistence.

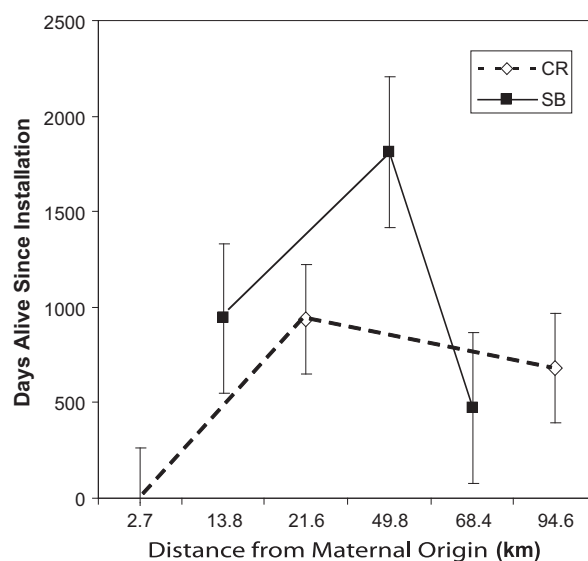


Fig. 2. Influence of distance from maternal origin to recipient site on survival of *Jacquemontia reclinata*. Patterns for offspring from Crandon Park (CR) and South Beach (SB) maternal plants are indicated.

Evidence that only mixed source populations showed positive population growth at two sites suggests that hybrid vigor overcame negative effects of inbreeding depression. While there is no evidence of outbreeding depression detected within the study period, some data are consistent with inbreeding depression in the two source populations: no SB-self, SB-control, or CR or SB near neighbor individuals reached adult stage in the nursery and no CR-sib individuals survived more than 3 years at VK. There is stronger evidence of inbreeding depression in the SB source population, which is larger and occupies less than half the area of CR.

Others have reported that mixing populations, particularly if they are closely related and have inbreeding depression, resulted in heterosis (Rogers and Montalvo, 2004). Short-term studies have provided evidence that rare plant reintroductions have had greater success from mixed sources than from single sources (Vergeer

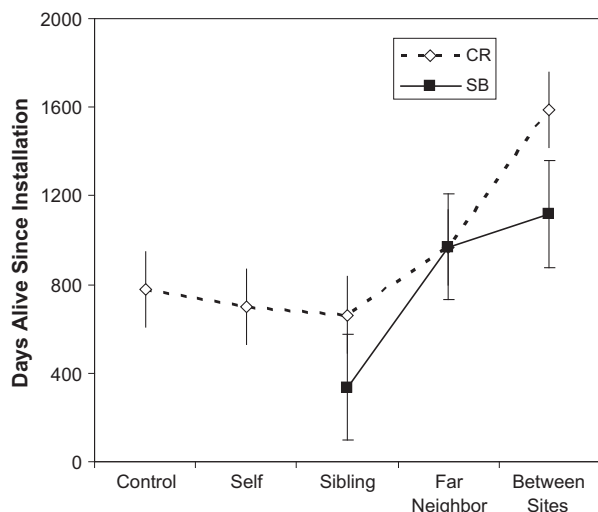


Fig. 3. Mean survival of offspring from Crandon Park (CR) and South Beach (SB) maternal plants generated from five hand pollination treatments and reintroduced to three sites. Mean days alive since installation \pm 1 SE are indicated.

Table 3

(A) Mean minimum soil temperature ($^{\circ}$ C) measured at a depth of 10 cm below the soil surface from 2004 through 2011. Freezing temperatures occurred in January through April at Homestead, Florida indicating that 2010 was an exceptionally cold winter (University of Florida Automated Weather Network: <http://fawn.ifas.ufl.edu/data/reports/>). (B) Monthly precipitation in Miami during from 2004 to 2010, the years the reintroduced plants have been in the wild, indicate that the winter of 2008–2009 was an exceptionally dry winter (Florida Climate Center, Florida State University, Center for Ocean-Atmospheric Prediction Studies: http://coaps.fsu.edu/climate_center/data/precip_miami.shtml). na = indicates data were unavailable. Bold values indicate extreme climate events.

	2004	2005	2006	2007	2008	2009	2010	2011
A. Minimum Temperature of Soil at – 10 cm								
January	12.7	12.7	10.3	12.4	10.2	8.2	0.0	11.8
February	15.7	13.3	9.8	8.0	11.5	7.7	0.0	14.4
March	18.6	14.6	13.8	16.2	13.1	11.6	0.0	15.2
April	17.9	na	18.7	14.5	14.7	15.3	0.0	21.6
B. Total Precipitation (cm)								
January	2.52	1.92	0.32	0.54	1.25	0.34	0.89	6.48
February	3.08	0.62	3.47	2.13	4.11	0.12	4.69	0.58
March	1.5	3.97	1.1	2.7	5.24	1.78	2.81	2.87
April	4	3.27	0.23	5.33	3.78	1.17	8.95	6.73
May	2.45	7.47	8.62	5.28	1.71	7.53	3.42	0.13
June	6.79	17.6	7.05	15.22	9.63	11.64	7.2	16.94
July	6.74	5	7.32	9.03	8.93	6.17	7.36	14.50
August	10.09	9.27	12.95	4.44	9.99	7.91	8.75	28.14
September	10.88	9.91	16.73	8.22	7.87	6.83	15.89	11.40
October	5.54	5.48	1.64	9.63	6.51	2.62	1.58	39.45
November	0.34	2.7	1.63	0.66	0.97	2.97	2.35	3.96
December	0.51	1	3.11	0.79	0.28	3.01	1.21	na

et al., 2005; Godefroid et al., 2011). Heterosis may improve fitness and provide an opportunity for range expansion (Rogers and Montalvo, 2004). In contrast, inbred individuals often show reduced fitness and less resilience to stress than outcrossed individuals (Keller and Waller, 2002).

Local germplasm did not always yield the greatest reintroduction survival. Broadhurst et al. (2008) admonish that the “local is best paradigm” may lead to significant restoration failure in many taxa precisely because of inbreeding depression and these failures may erode confidence in restoration programs in general. Our findings support this argument especially because our two mixed populations were not genetically differentiated and showed signs of inbreeding depression. Maintaining small inbred populations of endangered species in isolation is not only ill-advised, it may doom

restoration efforts to failure. Using single source material will increase the probability of inbreeding in small introduced populations (Vergeer et al., 2004). However, genetics are not the only consideration. In our study, proximity to maternal origin was less important than site identity. Optimal recipient site distance from maternal source may be geographic, but it is also likely to be related to ecologic similarity (Maschinski et al., 2012b). This finding has implications for managed relocation or assisted colonization practice. We suggest that when selecting recipient sites for reintroductions, whether they be within current range or outside of range, pollination syndrome, maternal distance from recipient site, and similarity to maternal site ecology should be considered.

Reintroductions are opportunities to improve the evolutionary potential of degraded wild populations that may suffer from inbreeding or outbreeding depression (Neale, 2012). Any decision to mix populations for restoration will require first knowing some ecological, demographic and genetic information, as all interact to ensure the persistence of a species (Keller and Waller, 2002). It is noteworthy that gathering uncontested information takes time and resources that are not always available to conservationists. Our ecological and genetic studies of *J. reclinata* began in 2000 (Thornton et al., 2008; Pinto-Torres and Koptur, 2009) and the reintroduced populations only reached the demographic benchmark of next generation recruitment 5 years after installation. Indeed decades may be required before a population viability analysis would be possible to demonstrate that the populations were sustainable if conditions remained constant (Maschinski, 2006). The consequences of mixing populations may influence different life stages and generations differently (Fenster and Galloway, 2000), therefore long-term monitoring is essential to test theory.

Few reintroduction studies have been established long enough to satisfy the data requirements needed to build PVA models (Albrecht et al., 2011; Knight, 2012; Monks et al., 2012) and few may have had the benefit of agency support for the foundational research we enjoyed. This is not a shortcoming of reintroduction practice; it is a reality of the time required to research fundamental biology and establish populations with next generation recruitment. Time lags for population establishment will vary across sites. We have observed good recruitment at two sites, but not at the third. Our PVA models predicted negative population growth for the Delray Beach population, the site with low recruitment, regardless of transplant breeding history. Because this site has vigorous, healthy, fecund plants, we expect the population will likely recruit next generation offspring if and when conditions become optimal for seed germination and establishment (e.g., Venable, 2007) however, sufficient recruitment has not yet occurred to provide data for the models. The population growth metric (λ) allowed us to compare growth rates across breeding treatments during the time-frame included in the models (Crone et al., 2011), however more time will be needed to assess whether future generations of these mixed populations are as sustainable as the PVA models predict. Future population sizes will greatly depend upon environmental stochasticity and whether hybrid advantage breaks down.

With climate change models predicting more variable and more extreme events (Allan and Soden, 2008; Bender et al., 2010; Durack et al., 2012), initiating reintroductions with the highest probability of survival will best ensure conservation of biodiversity. We call for a re-examination of the “local is best paradigm” as the default policy for reintroductions. In the absence of the luxury of ample time and finances to decide which source material is appropriate for a reintroduction we advise using decision trees (Frankham et al., 2011) and reintroduction guidelines (Maschinski et al., 2012a) and paying close attention to ecology, life history, habitat specialization, and dispersal mechanisms of target species. For example, selfing, gravity-dispersed, herbaceous annuals with habitat spe-

Table 4

Matrices generated for each hand pollination X maternal origin treatment at three reintroduction sites. Lambda values for each are indicated. NA indicates hand pollination X maternal origin treatment was not installed at the reintroduction site.

Haulover Beach					Virginia Key					Delray Beach				
	Seeds	Seedlings	Adults	Lambda		Seeds	Seedlings	Adults	Lambda		Seeds	Seedlings	Adults	Lambda
Control				0.896	Control				NA	Control				NA
Seeds	0.404	0	0.437		Seeds	NA		NA		Seeds	NA		NA	
Seedlings	0.103	0	0		Seedlings	NA				Seedlings	NA			
Adults	0	0.857	0.808		Adults		NA	NA		Adults		NA	NA	
CR-Self				0.941	CR-Self				NA	CR-Self				NA
Seeds	0.404	0	0.637		Seeds	NA		NA		Seeds	NA		NA	
Seedlings	0.086	0	0		Seedlings	NA				Seedlings	NA			
Adults	0	0.96	0.837		Adults		NA	NA		Adults		NA	NA	
CR-Sib				0.926	CR-Sib				0.453	CR-Sib				0.806
Seeds	0.404	0	0.471		Seeds	0.404	0	0.001		Seeds	0.404	0	0.001	
Seedlings	0.098	0	0		Seedlings	0.098	0	0		Seedlings	0.098	0		
Adults	0	0.813	0.848		Adults	0	0.813	0.286		Adults	0	0.813	0.806	
CR-FN				0.924	CR-FN				0.961	CR-FN				0.850
Seeds	0.404	0	0.333		Seeds	0.404	0	1.824		Seeds	0.404	0	0.091	
Seedlings	0.08	0	0		Seedlings	0.08	0	0		Seedlings	0.08	0		
Adults	0	0.86	0.876		Adults	0	0.860	0.727		Adults	0	0.860	0.833	
CR × SB				1.030	CR × SB				0.991	CR × SB				0.823
Seeds	0.404	0	1.0004		Seeds	0.404	0	0.921		Seeds	0.404	0	0.001	
Seedlings	0.09	0	0		Seedlings	0.09	0	0		Seedlings	0.09	0		
Adults	0	0.895	0.905		Adults	0	0.895	0.863		Adults	0	0.895	0.823	
SB × CR				0.923	SB × CR				1.036	SB × CR				0.889
Seeds	0.404	0	0.471		Seeds	0.404	0	1.578		Seeds	0.404	0	0.063	
Seedlings	0.08	0	0		Seedlings	0.08	0	0		Seedlings	0.08	0		
Adults	0	0.795	0.86		Adults	0	0.795	0.882		Adults	0	0.795	0.880	
SB-Sib				NA	SB-Sib				NA	SB-Sib				0.694
Seeds	NA		NA		Seeds	NA		NA		Seeds	0.404	0	0.001	
Seedlings	NA				Seedlings	NA				Seedlings	0.086	0		
Adults		NA	NA		Adults		NA	NA		Adults	0	0.85	0.694	
SB-FN				NA	SB-FN				NA	SB-FN				0.897
Seeds	NA		NA		Seeds	NA		NA		Seeds	0.404	0	0.063	
Seedlings	NA				Seedlings	NA				Seedlings	0.084	0		
Adults		NA	NA		Adults		NA	NA		Adults	0	0.731	0.888	

cialization have been shown to be more prone to maladaptation when populations are mixed, whereas wind-pollinated and seed-dispersed species would be more suitable for population mixing (Broadhurst et al., 2008). For rare species with few remaining individuals, great care is warranted and our ultimate goal is creating populations with the greatest genetic potential possible, but we concur with Frankham et al. (2011) that conservationists are being overly concerned about outbreeding depression, assuming local adaptation, when the central focus should be maximizing genetic diversity and trusting in natural selection.

Acknowledgements

We thank our funding agencies: US Fish and Wildlife Service, Florida Department of Agriculture and Consumer Services Division of Plant Industry, and Miami-Dade Environmentally Endangered Lands and Natural Areas Management Departments. Many hands helped with logistics and implementation of this research. For logistical and field help special thanks to Rob Barron, Juan Fernandez, Joe Maguire, Steve Forman, Phil Gonsiska, Bob Petzinger, Jennifer Possley, Julissa Roncal, Jim Schurer, Mary Rose, Kristie Wendelberger, Palmetto Senior High School students: Jackie Hatler, Alix Hallen, Alyssa Crittenden, Naomi Harris, Rayne Zhu, Rachel Harris, Gina He, Sam Pawliger, and Wendy Liu. Matthew Albrecht, Tom Whitham, Eric von Wettberg, Eric Menges, Kay Havens, and anonymous reviewers gave helpful comments on earlier versions of this manuscript.

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