The breeding system of *Ziziphus celata* Judd and D.W. Hall (Rhamnaceae), a rare endemic plant of the Lake Wales Ridge, Florida, USA: implications for recovery

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Abstract

Although the rarity of an endangered plant species can seldom be ascribed to its breeding system, knowledge of its breeding system may be critical to its recovery. The federally listed endangered *Ziziphus celata* (Florida ziziphus), a woody clonal shrub narrowly endemic to xeric upland habitats of the Lake Wales Ridge in central Florida, USA, is known from only five populations, four of which are sterile and perhaps unisexual. Altogether only 11 genotypes of Florida ziziphus have been identified by allozyme electrophoresis. We studied the breeding system of Florida ziziphus and found that it is an obligate outcrosser and that some genotypes are cross-incompatible. We have been able to demonstrate the cross-compatibility of only 11 of the 44 test crosses performed to date (25%), as measured by fruit yield. Cross-incompatibility is most likely due to shared self-incompatibility (S) alleles among the few remaining genotypes of these fragmented populations. The identification and translocation of compatible mating types to create reproducibly viable populations is essential for the recovery of Florida ziziphus. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Ziziphus celata; Rare plants; Reproductive biology; Restoration; Breeding system

1. Introduction

The development of recovery programs for rare and endangered plant species requires knowledge of breeding systems (Hamrick et al., 1991; DeMauro, 1993; Weller, 1994) as well as demography (Menges, 1991; Schemeske et al., 1994). Although the rarity of a plant species can seldom be attributed to its breeding system (Weller, 1994), the recovery of species made rare by anthropogenic means necessitates an understanding of the genetic and demographic consequences of its breeding system. Rarity may have several causes, not all anthropogenic (Rabinowitz, 1981; Fiedler and Ahouse, 1992). But for many endangered plants, rarity may be due to habitat loss, fragmentation or degradation and to the resulting genetic consequences via inbreeding depression, population bottlenecks and genetic drift.

The disruption of gene flow via pollen transfer and seed dispersal also contributes to the loss of genetic diversity within populations isolated by habitat fragmentation (Brown, 1992). In the case of self-incompatible species, the loss of genetic diversity among individuals in fragmented and isolated populations dooms them to extinction (Weller, 1994) without the translocation of cross-compatible genotypes to create viable (i.e. sexually reproducing) populations. In developing a recovery program for the federally listed endangered *Ziziphus celata*, we conducted a 3-year investigation of its breeding system.

*Florida ziziphus*, *Z. celata* Judd & D. Hall (Rhamnaceae), is a clonal xeromorphic shrub endemic to the Lake Wales Ridge of central Florida, USA, an area known for its high level of endemism and its many endangered species (Christman and Judd, 1990; USFWS, 1999). Today, only 15% of the xeric uplands of the Lake Wales Ridge remain, the rest having been lost to agricultural and residential development (Peroni and Abrahamson, 1985). There are only five known populations of Florida ziziphus, comprising 11 genotypes.
based on allozyme electrophoresis (Godt et al., 1997). At least four of the populations are sterile and perhaps uniclinal. Thus, the causes of endangerment of Florida ziziphus include habitat destruction and fragmentation, low genetic variability within and among populations, and sexual reproductive failure (USFWS, 1999; Weekley and Race, 1999).

Potential causes of reproductive failure in Florida ziziphus include self-incompatibility (within single-genotype populations) and/or cross-incompatibility among genotypes with shared S (self-incompatibility) alleles (Richards, 1986; Weller, 1994) or shared mating types based on floral phenology (Lyrene, 1983). These hypotheses are not mutually exclusive and other factors (e.g., pollinator limitation) could contribute to the failure of sexual reproduction in populations that flower profusely but do not set fruit. Our objectives were to elucidate the breeding system (including identification of floral visitors and the timing of anthesis), to determine the causes of reproductive failure, to identify cross-compatible genotypes, and to use this information to develop a recovery program for Florida ziziphus.

2. Materials and methods

2.1. Species description and study sites

Florida ziziphus is a clonal, woody shrub to 2 m in height (Weekley and Race, 1999). Flowers are perfect and the fruit is a single-seeded drupe (Judd and Hall, 1984). Florida ziziphus begins flowering in late December/early January when plants are leafless except for the previous year’s extension growth (Weekley and Race, 1999). Generally, there is a second flowering flush in late January/early February after plants have refoliated; this second flush typically occurs on the previous year’s new growth. After opening, flowers remain open until abscission occurs in 3 or 4 days’ time. Fruits mature in late April/early May.

Florida ziziphus is known from only five sites in Polk and Highlands Counties, Florida, along the southernmost third of the Lake Wales Ridge (Fig. 1). The five populations occur on well-drained yellow sands (Table 1), which historically supported xeric upland ecosystems characterized as sandhill, turkey oak sandhill or oak-hickory scrub (Christman and Judd, 1990; Myers, 1990; Christman, 1995; Menges, 1999). Most of these sites have been converted to agriculture and three Florida ziziphus populations now occur in pastures largely denuded of native vegetation (Table 1). Only one population (P01; Fig. 1), at Lake Wales Ridge State Forest, is on publicly protected land. The populations vary in size from about a dozen ramets to several hundred ramets and occupy from 3 to 800 m² (Table 1).

Godt et al. (1997), using allogynous electrophoresis, found that each of the four Polk County populations comprises a single unique multilocus genotype and that the Highlands County population comprises seven additional genotypes (Table 1). All 11 genotypes are represented in an ex situ population in the Center for Plant Conservation National Collection at Bok Tower Gardens, Lake Wales, Florida. Our study was centered on the multi-genotype ex situ population and on two in situ single-genotype populations.

2.2. Breeding system and cross-compatibility of genotypes

To determine the breeding system of Florida ziziphus, we used a standard experimental protocol (e.g. Kearns and Inouye, 1993) to test for agamospermy (the ability to set viable seed without pollen), self-compatibility, autogamy (spontaneous selfing), crosses within single-genotype populations and crosses between genotypes (sensu Godt et al., 1997). It is necessary to test both for self-compatibility and autogamy to rule out the possibility that a self-compatible species fails to self due to the presence of spatial (herkogamous) or temporal (dichogamous) mechanisms that prevent the transfer of viable pollen to a receptive stigma. For the selfing treatment we used pollen from the same plant but not necessarily from the same flower. Application of this protocol resulted in five treatments and a control, requiring the bagging of treatment branches to exclude unwanted pollen transfers, emasculation of flowers and hand pollinations (Table 2). Altogether 2649 flowers were included in the six treatments of which 1675 were hand pollinations.

<table>
<thead>
<tr>
<th>Population*</th>
<th>Soil</th>
<th>Habitat</th>
<th>Size (m²)</th>
<th>No. Genotypes</th>
<th>No. Ramets</th>
</tr>
</thead>
<tbody>
<tr>
<td>P01</td>
<td>Tavares</td>
<td>Oak-hickory scrub; Turkey oak sandhill</td>
<td>800</td>
<td>1</td>
<td>52</td>
</tr>
<tr>
<td>P02</td>
<td>Tavares</td>
<td>Pasture</td>
<td>3</td>
<td>1</td>
<td>12</td>
</tr>
<tr>
<td>P03</td>
<td>Candler</td>
<td>Remnant sandhill</td>
<td>200</td>
<td>1</td>
<td>76</td>
</tr>
<tr>
<td>P04</td>
<td>Tavares</td>
<td>Pasture</td>
<td>500</td>
<td>1</td>
<td>287</td>
</tr>
<tr>
<td>H01-subp. 1</td>
<td>Astatula</td>
<td>Pasture</td>
<td>335</td>
<td>6</td>
<td>1097</td>
</tr>
<tr>
<td>H01-subp. 2</td>
<td>Astatula</td>
<td>Pasture</td>
<td>60</td>
<td>3</td>
<td>116</td>
</tr>
<tr>
<td>H01-subp. 3</td>
<td>Astatula</td>
<td>Pasture</td>
<td>20</td>
<td>2</td>
<td>207</td>
</tr>
</tbody>
</table>

* The Polk County populations are designated P01–P04. The Highlands County site (H01) has three sub-populations.
Fig. 1. Distribution of five known populations of *Ziziphus celata* on the Lake Wales Ridge in Polk and Highlands Counties, Florida. Field data was collected by Carl Weekley using a Trimble Pro-XL Global Positioning System. The map was created at the Archbold Biological Station Geographic Information System Laboratory and prepared by Roberta L. Pickert (31 March 2000).
We excluded pollinators by enclosing treatment branches in 25×30 cm DelnetR (PQ218) heat-sealed, non-woven pollination bags (Applied Extrusion Technologies, Inc. Delnet Nonwoven Fabrics. Middleton, DE). Color-coded tape indicating treatment was used to anchor the sealed end of the bag. The open end of the bag was secured with a twist tie so that we could access the flowers for emasculation and pollen transfer.

We performed hand-pollinations using newly opened flowers from bagged pollen source branches. Flowers in transit between sites were transported in an ice chest in labeled petri dishes to keep them fresh. We gently swiped pollen donor anthers across the stigmatic surface of the pollen recipient, using magnifying optivisors to observe the deposition of pollen grains.

Application of the full experimental protocol in the first year of this study (1997) resulted in a characterization of the breeding system. Hand-pollinated test crosses carried out in subsequent years (1998–1999) focused on the identification of additional compatible genotypes (sensu Godt et al., 1997). With 10 available genotypes (sensu Godt et al., 1997) there were 45 possible one-way crosses (or 90 crosses, counting reciprocals). We used the same methods for hand pollinations as were used for the breeding system experiments, with one minor exception. If pollen was not available from bagged pollen source branches, we used unbagged flowers that had opened but in which the petals, which initially enclose the anthers, had not yet reflexed. By peeling back the clasping petals we were able to obtain fresh pollen.

2.3. Identification of floral visitors and timing of floral events

We identified floral visitors that were known to us (e.g. honeybees and butterflies) and collected unknown insects for identification by Mark Deyrup at the Archbold Biological Station Invertebrate Lab.

We determined the timing of anthesis by recording the number of tagged flowers with exposed anthers at four time periods (0800, 1100, 1400 and 1700 h) over several days. Open flowers were removed to avoid duplicate sampling.

To determine the timing and duration of stigma receptivity, we compared the results of hand-pollinated crosses performed at three times post flower opening: <4, 4–8, and 12–24 h. We also performed hand pollinations on emasculated and non-emasculated flowers to determine if emasculation had any effect on fruit set. To test for pollinator limitation and the efficacy of hand pollination, we compared fruit yields of hand-pollinated crosses vs. open-pollinated controls.

2.4. Statistical analysis

Because most treatments resulted in large numbers of zeros for fruit yield, the data were non-normal and could not be transformed to normality. We therefore relied on the non-parametric Mann-Whitney and Kruskal–Wallis tests, using SPSS 9.0 (SPSS, 1999). Since sample sizes in the multiple-comparison tests were greater than 10, we used the chi-square approximation of the Kruskal–Wallis H statistic (Sokal and Rolf, 1995), which is the test statistic produced by the SPSS procedure.

3. Results

3.1. Breeding system and cross-compatibility of genotypes

In 1997, experimental treatments for agamospermy, self-compatibility, autogamy, within (single-genotype) population crosses, and open pollinated controls within single-genotype populations yielded no fruit. However, some between-genotype (sensu Godt et al., 1997) crosses were fertile and open-pollinated controls within the multi-genotype ex situ population also yielded fruit.

Twelve of 829 hand-pollinated between-genotype crosses produced mature fruits (1.4%; Table 3). Open-pollinated plants not included in the treatments in the ex situ population produced ~2600 fruits. In addition, 35 parthenocarpic (seedless) fruits were obtained from open-pollinated flowers not included in the treatments.

We tested 44 of the 90 (49%) possible two-way crosses available to us. Of these, only one quarter (11 of 44) yielded fruit (Table 4). We obtained 68 fruits from 2641 hand-pollinated crosses (2.6%; Table 3). Annual per genotype fruit yields ranged from less than 2% to greater than 30% for the compatible crosses (Table 4).

Ten of the 11 successful crosses involved a single genotype from the ex situ population, either as a pollen donor or as a pollen recipient.

<table>
<thead>
<tr>
<th>Bagging</th>
<th>Self-compatibility</th>
<th>Autogamy</th>
<th>Within-genotype</th>
<th>Between-genotype</th>
<th>Control</th>
</tr>
</thead>
<tbody>
<tr>
<td>267</td>
<td>452</td>
<td>352</td>
<td>394</td>
<td>829</td>
<td>355</td>
</tr>
</tbody>
</table>
We found no significant differences in fruit yield among hand-pollinated crosses performed within 4 h of flower opening compared to those performed later the same day or on the following day (chi-square approximation of Kruskal–Wallis $H = 0.744$, $d.f. = 2$, $P = 0.689$). Tests for the effects of emasculation and non-emasculation on stigma receptivity resulted in no significant difference in fruit yield (Mann–Whitney $U = 17.5$, $P = 0.934$).

In comparing percent fruit yield for hand-pollinated crosses vs. open-pollinated controls, we found no significant differences either overall (Mann–Whitney $U = 847.5$, $P = 0.481$) or among the treatments (chi-square approximation of Kruskal–Wallis $H = 2.645$, $d.f. = 4$, $P = 0.619$). These among treatment comparisons were based only on the ex situ population, since the open-pollinated controls at the single-genotype sites predictably yielded no fruit.

### 3.2. Floral visitors and timing of floral events

Insect visitors to Florida ziziphus flowers were diverse and abundant, especially on sunny days. Floral visitors included flower flies (*Cepostylum nigrum* and *Allograpta* sp. *Syrophidae*), a muscid fly (*Coenosopos prima* *Musciidae*), a bee fly (*Villa* sp. *Bombyllidae*), bees (*Apis mellifera* *Colletidae* sp. *Colletidae*), a parasitoid wasp (*Tiphia floridana* ssp. *flavulina* *Tiphidae*), blowflies (*Calliphoridae*) and the zebra longwing (*Heliconius charitonius Tuckeri* *Helidonidae*) and Gulf fritillary (*Agraulis vanilla nigror* *Helidonidae*) butterflies.

Florida ziziphus flowers opened throughout the day. Two to three hours after budbreak, reflexing petals exposed pollen-bearing anthers. Anthesis also occurred throughout the day, generally peaking around noon. The pace of flower opening and pollen presentation was accelerated on warmer days. In 1997, flowers ($n > 30$) on five of seven genotypes showed peak anthesis between 1100 and 1400 h, with a third to a half of the flowers presenting pollen within that interval (Fig. 2). The two outliers reached peak anthesis between 1400 and 1700 h. Similar results were obtained in other years.

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### Table 3

<table>
<thead>
<tr>
<th>Year</th>
<th>No. H01 genotypes</th>
<th>No. other genotypes</th>
<th>No. flowers hand-pollinated</th>
<th>No. fruit (% yield)</th>
<th>No. open-pollinated fruits</th>
</tr>
</thead>
<tbody>
<tr>
<td>1997</td>
<td>6</td>
<td>1</td>
<td>829</td>
<td>12 (1.4%)</td>
<td>~2600</td>
</tr>
<tr>
<td>1998</td>
<td>5</td>
<td>2</td>
<td>482</td>
<td>0 (0.0%)</td>
<td>~2500</td>
</tr>
<tr>
<td>1999</td>
<td>6</td>
<td>3</td>
<td>1330</td>
<td>56 (4.2%)</td>
<td>~8000</td>
</tr>
<tr>
<td>Total</td>
<td>7</td>
<td>3</td>
<td>2641</td>
<td>68 (2.6%)</td>
<td>~13,100</td>
</tr>
</tbody>
</table>

* Not all genotypes were crossed in any one year, but over three years all available genotypes were used. Overall fruit yield percentage is based on mean yield of three years.

b In ex situ H01 population at Bok Tower Gardens.

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### Table 4

Results of 44 of 90 possible crosses between genotypes (sensu Godt et al., 1997) of *Ziziphus celata* carried out between 1997 and 1999*

<table>
<thead>
<tr>
<th>H01-G1</th>
<th>H01-G2</th>
<th>H01-G3</th>
<th>H01-G4</th>
<th>H01-G5</th>
<th>H01-G6</th>
<th>H01-G7</th>
<th>P02</th>
<th>P03</th>
<th>P04</th>
</tr>
</thead>
<tbody>
<tr>
<td>H01-G1</td>
<td>–</td>
<td>0 (0/13)</td>
<td>6.1 (3/49)</td>
<td>0 (0/90)</td>
<td>0 (0/19)</td>
<td>0 (0/27)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>H01-G2</td>
<td>–</td>
<td>0 (0/46)</td>
<td>0 (0/12)</td>
<td>8.7 (9/103)</td>
<td>0 (0/30)</td>
<td>0 (0/40)</td>
<td>0 (0/63)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>H01-G3</td>
<td>12.5 (1/8)</td>
<td>0 (0/49)</td>
<td>–</td>
<td>11.5 (10/87)</td>
<td>11.8 (6/51)</td>
<td>–</td>
<td>29.2 (7/24)</td>
<td>0 (0/29)</td>
<td>0 (0/10)</td>
</tr>
<tr>
<td>H01-G4</td>
<td>32.4 (23/71)</td>
<td>11.5 (10/87)</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>H01-G5</td>
<td>0 (0/48)</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>H01-G6</td>
<td>–</td>
<td>0 (0/15)</td>
<td>0 (0/28)</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>H01-G7</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>P02</td>
<td>0 (0/10)</td>
<td>0 (0/218)</td>
<td>0 (0/77)</td>
<td>0.8 (1/132)</td>
<td>0 (0/8)</td>
<td>0 (0/29)</td>
<td>0 (0/14)</td>
<td>0 (0/63)</td>
<td>–</td>
</tr>
<tr>
<td>P03</td>
<td>0 (0/70)</td>
<td>0 (0/218)</td>
<td>0 (0/77)</td>
<td>0.8 (1/132)</td>
<td>0 (0/8)</td>
<td>0 (0/29)</td>
<td>0 (0/14)</td>
<td>0 (0/63)</td>
<td>–</td>
</tr>
<tr>
<td>P04</td>
<td>0 (0/26)</td>
<td>0 (0/35)</td>
<td>0 (0/13)</td>
<td>1.1 (1/89)</td>
<td>0 (0/32)</td>
<td>0 (0/27)</td>
<td>0 (0/53)</td>
<td>0 (0/45)</td>
<td>0 (0/247)</td>
</tr>
</tbody>
</table>

* Columns are pollen donor genotypes, rows are pollen recipient genotypes. The first number in each cell is the percent fruit yield based on the mean of all test crosses for that genotype; the second number (a ratio) shows number of fruit obtained over number of flowers in each test cross.
4. Discussion

4.1. Breeding system, cross-incompatibility and causes of reproductive failure

This study demonstrates that Florida ziziphus is an obligate outcrosser and that many genotypes are cross-incompatible. At least three-quarters (33 of 44) of the hand-pollinated crosses resulted in no fruit and the true number of incompatible crosses may be even higher given that Florida ziziphus often produces seedless (parthenocarpic) fruits or apparently normal “seeds” with aborted embryos (Weekley and Race, unpublished data).

The floral morphology of Florida ziziphus suggests a generalist insect-vectored pollination syndrome (Faegri and van der Pijl, 1979; Bertin, 1989). The diverse suite of floral visitors observed during this study is consistent with the floral morphology of Florida ziziphus, as is regular and substantial fruit production in the open-pollinated multi-genotype ex situ population at Bok Tower Gardens. Although specific pollinators were not identified, Florida ziziphus is undoubtedly insect-pollinated. Since hand-pollinated crosses failed to increase fruit yield compared to open-pollinated crosses, there is no evidence to suggest that Florida ziziphus is pollinator-limited.

The sterility of within-genotype crosses lends support to the Godt et al. (1997) hypothesis that the four single-genotype populations are self-incompatible clones. Godt et al. (1997) further hypothesized that these unilocular populations arose either through agamospermy (the asexual production of viable seeds) or through vegetative growth and fragmentation. Since we found no evidence to support the agamospermy hypothesis, it appears that the four single-genotype populations are remnants of single genets that became fragmented over time.

Although sexual reproductive failure within single-genotype populations of Florida ziziphus is adequately explained by clonal self-incompatibility (Godt et al., 1997), cross-incompatibility between genotypes must be due to other mechanisms.

Some members of the genus Ziziphus [Z. spina-crista (Galil and Zeroni, 1967), Z. jujuba (Lyrene, 1983), and Z. mucronata subsp. mucronata (Zietsman and Botha, 1992)] have distinct early and late flowering types, based on time of anthesis. These species are protandrous (anthesis precedes stigma receptivity) and flowers on an individual plant all open and present pollen at the same time. Each mating type is self-incompatible and sexual reproduction only occurs with crosses between individuals of the contrasting type (Lyrene, 1983). However, in Florida ziziphus, there is overlap between sexual functions and pollen presentation occurs throughout the day, rather than at discrete periods. Thus, our results rule out the possibility that cross-incompatibility between genotypes is due to shared mating type based on floral phenology.

Small populations of a self-incompatible species may fail to reproduce sexually due to the loss of diversity in S alleles (Richards, 1986; Weller, 1994). Genotypes sharing the same S allele are cross-incompatible. Populations comprising a single S-allele genotype (or a few incompatible S-allele genotypes) are condemned to self-sterility and extirpation. Cross-incompatibility between genotypes of Florida ziziphus is probably due to the reduction in the number of S alleles in its small and fragmented populations, so that surviving genotypes share the same few S alleles. However, we can not entirely rule out the possibility that other mechanisms (e.g. pollen sterility) play a role in the sexual reproductive failure of some genotypes.

4.2. Implications for recovery of Florida ziziphus

Rare species are no more likely to be obligate outcrossers than common species (Weller, 1994). However, the loss and fragmentation of habitat, resulting in a reduction of genetic diversity via inbreeding depression or other mechanisms, ultimately constitutes an insurmountable hurdle for non-selfing species. Isolated, genetically depauperate populations of obligate outcrossers are doomed to extinction without the translocation of compatible genotypes.

The historical distribution, range and abundance of Florida ziziphus are unknown. Its current rarity may be due to long- or short-term causes, anthropogenic or otherwise. Florida ziziphus may always have been rare.

It was apparently overlooked by such observant field botanists as J. K. Small (1869–1938) and R. M. Harper (1878–1966), both of whom did extensive work in the Central Lakes District of Florida (which includes the Lake Wales Ridge) prior to the wholesale destruction of Florida ziziphus’s presumed habitat, which began in the 1950s. Whatever its historical distribution and abundance, the destruction and fragmentation of habitat which has taken place over the last few decades have resulted in remnant, genetically depauperate and largely self-sterile populations persisting on degraded sites (e.g. three of five populations are in pastures).

Fragmented populations of self-incompatible species are obviously at a disadvantage compared to selfing species, especially if self-incompatible populations are far enough apart that pollen exchange and seed dispersal among them becomes unlikely. Depending on the vitality of a given genotype, isolated non-breeding populations may persist through vegetative growth for a protracted time but these populations are not viable over the long term.

Development of a recovery program for Florida ziziphus without an understanding of its breeding system would be impossible. We now know that the creation of viable populations necessitates the translocation of cross-compatible genotypes. Cross-compatibility of genotypes
must be experimentally established since ostensibly distinct genotypes may share S alleles.

Our recovery program for Florida ziziphus has two components: (1) the introduction of cross-compatible genotypes to the single-genotype populations; and (2) the establishment of new populations (comprising several cross-compatible genotypes) in appropriate habitat on protected land. Both genetically enhanced populations and experimentally created populations must be closely monitored for sexual reproductive success. Demographic data on enhanced and created populations will be used to model the long-term viability of individual populations and of the species.

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