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Variation partitioning in canonical ordination reveals no effect of soil but an effect of co-occurring species on translocation success in *Iris atrofusca*

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Summary

1. Despite being expensive, complicated and less successful than the conservation of primary habitat, translocation is rapidly gaining importance as a conservation approach due to accelerated loss of natural environment. Finding the optimal abiotic and biotic conditions needed for successful translocation of plants can be difficult for species with limited information on prior distribution. Unfortunately, this is often the case with endangered plant species, including those urgently needing action.

2. We present a method of evaluating the relative importance of multiple environmental parameters in translocation success. This method is based on the application of variation partitioning in canonical ordination and it allows usage of not only multiple independent biotic and abiotic variables, but also multiple dependent variables for fitness estimates.

3. In this study, six soil parameters together with the abundance of 61 plant species and their total biomass were used to explain the variation in translocation success of *Iris atrofusca* plants among 22 microsites. The relative importance of each of the three factors was estimated using ordination techniques.

4. Soil characteristics and total biomass of other plants did not significantly affect the performance of translocated irises, but the species composition of the surrounding vegetation did have a significant effect. The abundance of relatively rare species was closely correlated with iris performance. It is likely that these species do not affect the irises directly but instead represent environmental conditions not measured in this study, which are necessary for the survival of irises.

5. *Synthesis and applications*. Variation partitioning appears to be a highly promising method for planning the translocation of plants and evaluating success due to its ability to estimate the unique contribution of each of two or more sets of environmental factors. It can be used to monitor success, and to identify the key contributory factors, in experimental translocations preceding actual introduction of plants in conservation programmes.

Key-words: canonical correspondence analysis, endangered plant species, habitat-suitability, niche space, redundancy analysis, soil characteristics, species abundance, variation partitioning

Introduction

Translocation of plants refers to their accidental or deliberate movement, within or beyond their natural range, by humans. The goal of translocations for conservation purposes is to establish new populations of rare and endangered species in order to increase the survival of the species as a whole (Heywood & Iriondo 2003). This practice may become more prevalent as human impact on the natural environment increases, even though it is more expensive, complicated and less successful than the conservation of primary habitat (e.g. Gordon 1996; Milton *et al.* 1999).

Currently, the evidence for the long-term success of translocations is limited (Maunder 1992; Seddon, Armstrong & Maloney 2007) and the reasons for success or failure can be difficult to determine (e.g. Morgan 1999). In the past, many translocation projects were performed without scientific rigour

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or hypothesis testing. Today, it is recognized that the factors determining success or failure of a translocation have to be studied using a scientifically based approach combining ecological theory and empirical tests (Sarrazin & Barbault 1996; Seddon, Armstrong & Maloney 2007; Menges 2008).

When plants are moved to a site outside the known native range (termed 'introduction'; IUCN 1987) one of the most important decisions is selecting the relocation site, and then the best microsites within the relocation site (e.g. Adamec & Lev 1999; Jusaitis 2005; Maschinski & Duquesnel 2006; Colas *et al.* 2008). By definition, the location where a population can be established has to be within the ecological niche of the species, i.e. the set of abiotic and biotic conditions under which the species can maintain populations without immigration (Grinnell 1917). However, determination of the species niche is not an easy task because the actual distribution of the species can be limited due to interspecific interactions (the difference between fundamental and realized niches, MacArthur 1972), as well as limited colonization ability and local extinction (Burkey 1995; Peterson, Soberón & Sánchez-Cordero 1999).

The method currently used for identifying the most suitable habitats for species is to search for a quantitative relationship between ecological and environmental features in the landscape and either (i) species occurrence in space prior to relocation or (ii) population establishment after relocation. Much progress has been made in the last two decades in the development of techniques predicting species distribution and then estimating potential site suitability for establishment (reviewed in Guisan & Zimmermann 2000; Stauffer 2002; Guisan & Thuiller 2005; Richards, Carstens & Lacey Knowlrs 2007; Elith & Leathwick 2009). These techniques generally involve the use of spatially explicit data through geographic information systems (GIS) and modelling a species' ecological niche. Particular examples include BIOCLIM (Busby 1991), HABITAT (Walker & Cocks 1991), DOMAIN (Carpenter, Gillison & Winter 1993), Genetic Algorithm for Rule-set Prediction (GARP) (Stockwell & Peters 1999) and Ecological-Niche Factor Analysis (ENFA) (Hirzel *et al.* 2002; Engler, Guisan & Rechsteiner 2004; Basille *et al.* 2008). These methods require detailed maps of species presence and environmental parameters, which limit the application of species distribution modelling to (i) large geographic scale of kilometres and (ii) species with documented and relatively wide distributions. Species that occupy only a limited number of locations including a patchy distribution at the fine geographic scale (tens or hundreds of metres) or where there is little information on prior distribution, require another approach. In these cases, an alternative approach is to analyse the success of an experimentally translocated population.

As the environmental variables affecting performance of relocated organisms can be complex, they need to be identified and differentiated using multivariate statistical methods. One approach is to use stepwise multiple regression to develop a predictive equation for success of translocation in which independent variables will be ranked by their importance (Griffith *et al.* 1989). However, this approach requires a single dependent variable for translocation success, which can be binary (success vs. failure), ordinal (varying degrees of success) or continuous (e.g. population growth rate, percentage of survived plants or populations that became self-sustained). A requirement for a single variable summarizing the existing information on relocated plants/populations limits the application of this approach because many estimates of fitness are stage specific and vary in time. A potentially more efficient approach is one using not only multiple independent variables representing different environmental biotic and abiotic effects, but also multiple dependent variables for fitness estimates.

Canonical correspondence analysis (CCA) and redundancy analysis (RDA) are constrained multivariate ordination techniques widely used in ecology and vegetation science to extract the major gradients in response (dependent, usually biotic) variables attributed to the explanatory (independent, usually environmental) variables (e.g. Pivello, Shida & Meirelles 1999; Clarke, Latz & Albrecht 2005; Svenning & Skov 2005). A particular strength of CCA and RDA is their ability to remove the effect of undesirable variables (covariables) by regression-based covariance analysis prior to the analysis itself. This procedure is called partial canonical correspondence analysis (pCCA) or partial redundancy analysis (pRDA; ter Braak 1986). It is possible to measure the fraction of the variation in the dependent variables explained by each set of environmental variables alone as well as the fraction of the variation shared by the sets of variables by using CCA and pCCA (or RDA and pRDA) (Borcard, Legendre & Drapeau 1992; Noe & Zedler 2001; Volis *et al.* 2004).

High analytical power and the ability to efficiently reduce large data sets of both independent and dependent variables into only a few canonical axes make CCA and RDA attractive for finding a range of suitable environmental conditions for successful relocation. Specifically, CCA/RDA can help to find which environmental factors have the highest effect on individual performance and also the unique contribution of each of two or more sets of environmental factors to explaining the variation in individual performance. For example, species composition may significantly affect the performance of introduced plants (Elmendorf & Moore 2007). However, a hypothetical situation is possible when the vegetation effect may be indirect and reflecting other effects, such as differences in soil properties. Thus, both vegetation and soil will appear important for successful relocation, while in fact only the soil is important.

Iris atrofusca Baker is a highly endangered species in Israel (Shmida & Pollak 2007), with habitats in the Northern Negev being the most vulnerable throughout its distribution. Rapid destruction of the natural habitat of *I. atrofusca* due to land clearing and a lack of nature reserves containing populations of *I. atrofusca* in the Negev leave very limited conservation options for this species. Thus there is no alternative to translocation, i.e. introduction of the species into seemingly suitable protected areas with no record of prior occupancy. The habitat characteristics needed for success are not known for this species or similar endangered irises in Israel. For example, translocation of *Iris hermona* Dinsmore in the Golan Heights was unsuccessful, even though translocation was into a very similar habitat to the one that had been destroyed (Y. Sapir, unpublished data).

In order to investigate species habitat preferences for *I. atrofusca*, we set up a translocation experiment, using rhizomes rescued from a site under threat of destruction. We applied CCA/RDA for (i) partitioning the variation in performance of *I. atrofusca* into components due to vegetation composition, total plant biomass and soil properties and their shared effects and (ii) for determining the environmental factor(s) directly affecting species introduction success.

Materials and methods

The study area was Lahav North Nature Reserve which is 1·15 km^2 in size and located in the semi-arid climatic zone of Israel (ca. 300 mm annual rainfall; Shachak *et al.* 2008). The reserve is typified by low hills less than 500 m above sea level, with plant formation typical for the transitional zone between Mediterranean and desert vegetation (known as batha), dominated by *Sarcopoterium spinosum* (L.) Spach, *Phlomis brachyodon* (Boiss.) Zohary, *Asphodelus ramosus* L. and *Gundelia tournefortii* L. (Tsoar & Ramon 2002; Fig. 1). There are no records of *I. atrofusca* ever occupying this site. However, it is within the discontinuous distribution range of *I. atrofusca*, with the nearest population found 9 km south-west of the Reserve at the Dudaim forest.

Rhizomes rescued in spring 2006 in the nearby Goral Hills region (road-building strip for new railroad tracks) were planted in autumn 2006 in sets of 62 rhizomes in each of 22 microhabitats in Lahav North Nature Reserve (Fig. 1). Each set comprised the following size classes (number in parentheses): <5 g (14), 5–10 g (10), 10–20 g (23), 20–30 g (10), 30–40 g (3) and >40 g (2). In spring 2007, 2008 and 2009 we counted the number of plants that emerged, flowered and set fruit at each site, making a total of nine performance variables (Fig. 2).

In addition, in the second year (spring 2008) the plant community at each site was sampled using random quadrats of either 1 m^2 (one per site) or 0·125 m^2 (two per site). Quadrat size was chosen according to the vegetation density and homogeneity of the site. All plants from a quadrat were harvested, brought to the laboratory, identified to species level, counted and dried to constant weight to determine the total plant biomass at each site. The vegetation data set had, therefore, two parts: the number of individuals per species (Table S1, Supporting information) and total plant biomass (Table S2, Supporting information) per 1 m^2 per site (when 0·125 m^2 quadrats were used, the data were standardized per 1 m^2). In total, 75 plant species were found across the sites. During the same year (spring 2008), soil samples were taken at each site and analysed for six soil characteristics (Tables 1 and S3, Supporting information).

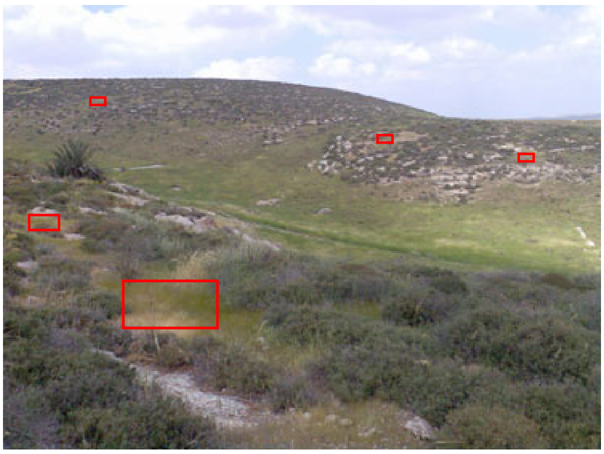

Fig. 1. Example of five relocation sites within the Lahav North Nature Reserve.

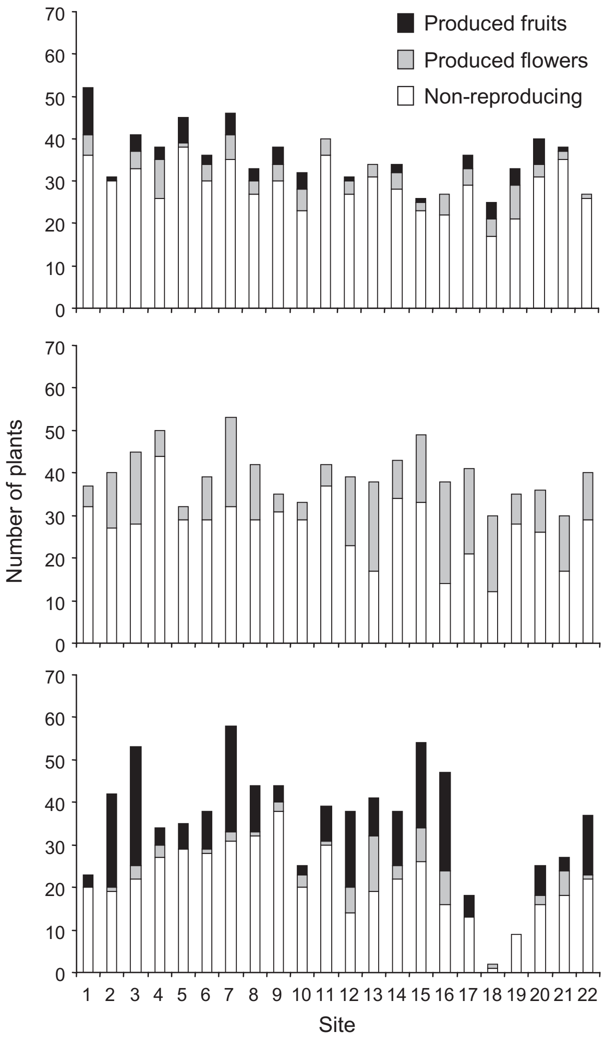

Fig. 2. Survival and reproduction of *I. atrofusca* (number of plants) 1, 2 and 3 years after experimental introduction at Lahav North Reserve in the 22 sites (from top to bottom). 62 rhizomes of Goral origin with equal representation of different size classes were introduced at each site in fall of 2006, counting was done in spring of 2007, 2008 and 2009.

Therefore, we had four multivariate data sets: species abundance (75 variables), biomass (one variable), soil (six variables) and iris performance (nine variables) data for each of 22 sites.

DATA ANALYSIS

The effects of the three sets of environmental variables (species abundance, biomass and soil) on variation in plant performance were examined with ordination techniques, using CANOCO (ver. 4.02; ter Braak & Smilauer 2002). Since a relationship between each of the three factors and performance of relocated iris plants may be caused by partial redundancy with the other factors, we applied the method of variation partitioning (Borcard, Legendre & Drapeau 1992). We estimated the following components of variation: 'pure' effects of abundance, biomass and soil (i.e. variation that can be explained by

Table 1. Qualitative soil characteristics, their description and categorization

Soil characteristics	Description	Categories
Depth	Depth of soil profile to parent or subjacent material	< 20 cm; 20–40 cm; 40–60 cm; > 60 cm
Humus	Humus of root-inhabited horizon, according to Munsell Soil Colour Charts	Low (10 YR 4/4, 5/3, 5/4); intermediate (10 YR 4/3, 5/2); high (10YR 3/3, 4/2; 7·5YR 4/2)
Presence of Bk horizon	The subsoil layer (horizon B) with large accumulation of carbonates (k)	Absent; low (Bk fragmentary, weak or unstable sub-angular structure); intermediate (Bk visible, moderate sub-angular structure); high (Bk clear, sub-angular to cubic or angular structure)
Alluvium	Depth of crumb or granular structure	Absent; low (< 40 cm); high (< 60 cm)
Stoniness	Rock fragments by volume (%)	Low (< 15%); intermediate (15–30%); high (30–60%)
Parent material	Type of parent material	El – eluvium of lime rocks or limestone; L – mainly loessial sediments; D – diluvium, talus sediments

each of the three factors and is not shared by the other factors); variation that is shared by two factors, either 'abundance & biomass', 'abundance & soil' or 'biomass & soil'; variation that is shared by three factors, 'abundance & biomass & soil'; and variation explained by no factor, which is the unexplained variation in iris performance.

Performance data was represented by nine variables: number of plants that survived, flowered and produced fruit in 2007, 2008 and 2009 (Fig. 2). No plants set fruit in 2008 because all flowers were consumed by insects that year. To justify usage of more than one performance variable, Pearson product–moment correlation coefficients, and their significance after sequential Bonferroni adjustment, were used to assess the correlation among those variables.

Soil data comprised a single matrix with six independent variables, including one categorical (parent material) and five ordinal variables (Table S3, Supporting information). Plant abundance data included abundance per 1 m^2 of 75 plant species (Table S1, Supporting information), belonging to the following life forms: annual forbs (39), annual grasses (14), perennial forbs (9), geophytes (8), perennial grasses (3) and annual/perennial forbs (not identified to the species level) (2). However, prior to the analysis 14 species which occurred only once in the vegetation dataset were excluded (Boeken & Shachak 1994), leaving 61 variables of species abundance for the analysis. Plant abundance data was log-transformed and biomass data was represented as the total plant biomass per 1 m^2 at each site (Table S2, Supporting information).

In order to reduce the number of independent variables, both species abundance and soil data sets were reduced using either Principal Components Analysis (PCA) or Correspondence Analysis (CA), and the values of the first several axes were used as the derived variables (Fig. 3). The choice between PCA and CA was made according to ter Braak & Smilauer (2002), assuming either a unimodal model (CA) or linear model (PCA) for the relationships of independent variables with the ordination axes. The number of derived axes for the sites scores, to be used in the variation partitioning analyses, was chosen to represent as much variation as possible in the original data, but not to exceed the number of dependent variables (which is equal to nine).

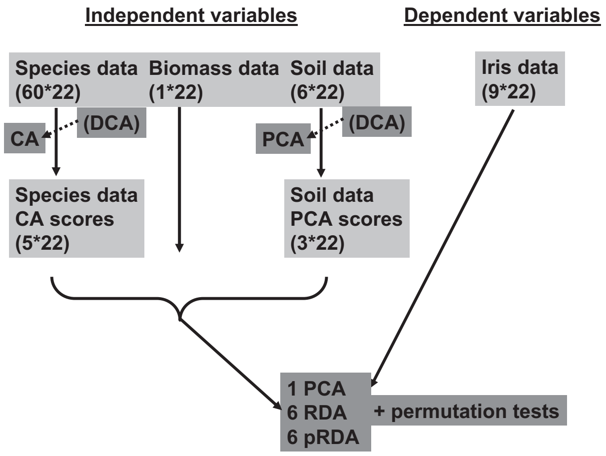

Fig. 3. Conceptual diagram of the multivariate statistical procedure used to estimate the proportions of variation in performance of translocated iris due to environmental variation in vegetation composition (abundance), total plant biomass and soil characters. DCA was conducted to determine the gradient length in species and soil data, in order to choose between PCA and CA for these variables. Then the three independent sets of variables were used in 12 combinations (see Table 2), as constraining variables and/or covariables in RDA, while the dependent variable was always the iris performance data. A permutation test was done in each analysis to assess the significance of the effects.

Variation partitioning

Technically, variation partitioning is done by CCA, pCCA, and CA (Borcard, Legendre & Drapeau 1992) or by RDA, pRDA, and PCA. The RDA/pRDA/PCA was chosen in our case, since we assumed a linear, and not a unimodal, relationship between the environmental gradients and iris performance. The PCA estimated the total amount of variation (sum of all eigenvalues) in the dependent variables. Several RDA and pRDA were conducted (Fig. 3), with different combinations of one, two or three variables as the constraining variables and/or covariables. The sum of all canonical eigenvalues in these analyses was used to partition the variation into components. When variables from different data sets were used together either as constraining variables or covariables, both datasets were simply combined. For example, the dataset 'abundance + biomass' (A + B; see Table 2) is a dataset of six variables (5 + 1). Calculation of variation components is described below.

Significance of effects

Statistical significance of each environmental effect was determined by a Monte Carlo permutation test with 999

Table 2. Pearson product–moment correlations among nine performance traits

	T 2007	T 2008	T 2009	FL 2007	FL 2008	FL 2009	FR 2007
T 2008	0·10						
T 2009	0·09	0·65*					
FL 2007	0·59	0·05	−0·34				
FL 2008	−0·37	0·26	0·25	−0·33			
FL 2009	−0·21	0·55	0·80*	−0·45	0·65*		
FR 2007	0·70*	−0·14	−0·31	0·85*	−0·38	−0·44	
FR 2009	−0·12	0·61	0·80*	−0·37	0·56	0·95*	−0·32

T – total; FL – flowered; FR – set fruits. *Significance ($P < 0{\cdot}05$) after sequential Bonferroni adjustment.

permutations in the relevant ordination analysis. The environmental variables explaining most of the variation in dependent variables were selected using the forward selection procedure in CANOCO, with a cut off point of $P = 0{\cdot}10$ (default).

Results

PERFORMANCE DATA

There were no strong and consistent correlations among the three performance traits in the same year and across years (Table 3). Only seven out of 28 trait correlations were significant.

VEGETATION AND SOIL DATA

Species abundance and soil data sets were reduced using CA and PCA, respectively (Fig. 3). Based on the gradient length in DCA, PCA was chosen for the soil data and CA for the (log-transformed) species data (1·6 and 4·4 SD, respectively). For plant abundance data, the first five CA axes were used, summarizing 61·2% of the original data matrix variation. For soil data, the eigenvalues of the first three principal components were 0·54, 0·17 and 0·16. The eigenvalues of the remaining axes did not exceed 0·06 and therefore only the first three PCs were retained, summarizing 86·8% of the variation. Overall, after data reduction through CA and PCA, we had four data sets: abundance (five variables), biomass (one variable), soil (three variables) and iris performance (nine variables; Fig. 2).

The derived soil variables (principal components) can be interpreted based on the contribution of original soil variables (Table 2). The first principal component (PC1) is positively associated with soil permeability and water accumulation as indicated by its positive correlation with soil depth and diluvium, and negative correlation with eluvium. Thus the sites having high scores for PC1 are those allowing accumulation of water runoff, such as terrace slopes and valleys. The second principal component (PC2) is negatively correlated with soil depth indicating conditions of high runoff and shallow soil. The third principal component (PC3) is positively correlated with loess soil and high humus content indicating high soil fertility.

Among the 22 relocation sites of the Lahav Nature Reserve, five grasses out of 61 species were the most abundant (per 1 m^2): *Stipa capensis* Thunb., *Carex pachystylis* J. Gay, *Brachypodium distachyum* (L.) P. Beauv., *Avena sterilis* L. and *Hordeum spontaneum* K. Koch., comprising 53, 23, 12, 5 and 2%, respectively, of the total number of plants in the 22 sites. These five species together comprised 94% of plant abundance, while the abundance of each of the remaining 56 species was less than 1%. *S. capensis* was the most abundant species (53%), with over 15 000 plants, and an average density of 997 plants m^{-2} where it was recorded. However, the most common species across sites was *A. sterilis*, which was found at 17 of the 22 sites. It is followed by *S. capensis* and *H. spontaneum*, found in 16 and 11 sites, respectively; while the remaining 58 species were found in 8 sites or fewer. The other two abundant species mentioned above, *C. pachystylis* and *B. distachyum*, were found at just 3 and 6 sites, respectively.

Table 3. Contribution of soil characteristics to the first three axes derived by PCA on soil data (total variation explained: 86·8%)

	Principal components		
Soil characteristics	1	2	3
Depth of soil	0·73	−0·61	0·18
Humus	−0·03	0·07	0·85
Presence of Bk horizon	0·82	0·54	0·12
Alluvium	0·64	0·02	−0·66
Stoniness	0·85	−0·27	0·02
EL	−0·89	0·07	−0·18
D	0·83	−0·13	0·01
L	0·14	0·14	0·43
Variation explained (%)	54·1	16·8	15·9

El – eluvium of lime rocks or lime stones; L – mainly loessial sediments; D – diluvium, talus sediments.

VARIATION PARTITIONING

We used 12 ordination analyses (Table 4, lines 2–13) to calculate the explained variation (%). Variation in the iris data alone, in the unconstrained analysis (PCA), is scaled to equal unity in CANOCO (line 1); therefore the sum of eigenvalues in the constrained analyses (RDA and pRDA) is a measure of variation in the response data (performance of relocated plants) accounted for by the constraining data (lines 2–13). From the sums of eigenvalues in the 12 ordination analyses (Table 4) we calculated the proportions of variation in iris performance data explained by each respective factor, shown in a Venn diagram (Fig. 4). Each rectangle area represents the proportion of variation explained by species abundance, biomass and soil data (*a*, *b* and *s*, respectively). The area of overlap between rectangles represents the two- or three-factor shared effects (*ab*, *as*, *bs* and *abs*).

Species abundance explained the largest proportion of the iris performance data (47·4%), and after removal of the component shared with biomass and soil it still explained 40·0%.

Table 4. Results of ordination analyses, including the multivariate method, variable(s) and covariable(s) used, the component of variation explained, its value and significance

	Statistical analysis	Constraining variable*	Covariable*	Component of variation	Sum of all canonical eigenvalues	Significance of all canonical axes (*P*-value)
1	(PCA)	–	–		(1)	
2	RDA	A	–	*a* + *as* + *ab* + *abs*	0·474	0·013
3	RDA	B	–	*b* + *ab* + *bs* + *abs*	0·070	0·221
4	RDA	S	–	*s* + *as* + *bs* + *abs*	0·194	0·219
5	RDA	A + B	–	*a* + *b* + *ab* + *as* + *bs* + *abs*	0·509	0·035
6	RDA	A + S	–	*a* + *s* + *as* + *ab* + *bs* + *abs*	0·598	0·015
7	RDA	B + S	–	*b* + *s* + *bs* + *ab* + *as* + *abs*	0·232	0·285
8	pRDA	A	B + S	*a*	0·400	0·029
9	pRDA	B	A + S	*b*	0·035	0·325
10	pRDA	S	A + B	*s*	0·124	0·250
11	pRDA	A + B	S	*a* + *b* + *ab*	0·439	0·036
12	pRDA	A + S	B	*a* + *s* + *as*	0·563	0·028
13	pRDA	B + S	A	*b* + *s* + *bs*	0·159	0·281

*Species abundance data were the first five axes of CA on the log-transformed species abundance matrix. Biomass data were the original total biomass values. Soil data were the first three axes from the PCA on the soil characters matrix. Iris data (response variable) were the original values in the nine-parameter matrix.
Explanatory variable/*component of variation*; A/*a* – species abundance; B/*b* – biomass; S/*s* – soil.

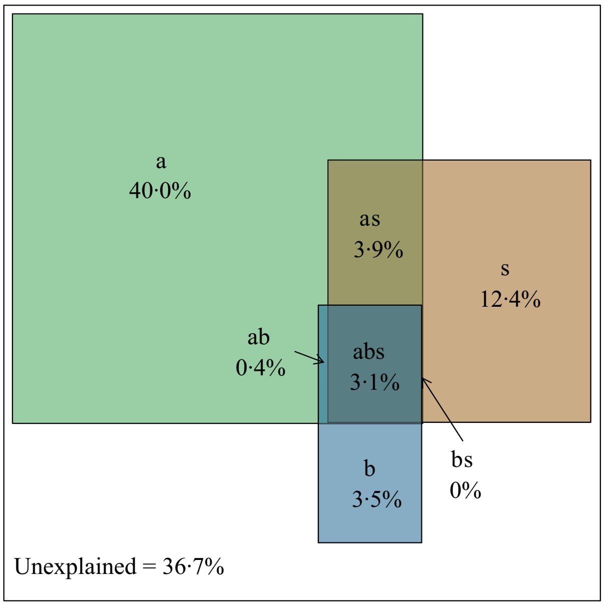

Fig. 4. Venn diagram of variation partitioning of iris performance. Each area represents variation in iris performance data explained by the following independent variables: *a* – species abundance; *b* – biomass; *s* – soil; *ab*, *as*, *bs*, *abs* – two- and three-factor shared effects.

Soil data explained 19·4% of the variation and 12·4% after accounting for abundance and biomass. Biomass of vegetation in each site explained 7·0% of the variation and 3·5% when other effects were removed. The shared effects were small in magnitude. Together species abundance and soil, species abundance and biomass, and biomass and soil explained 3·9, 0·4 and 0% of the variation, respectively. The shared effect of all three factors together (species abundance, biomass and soil) comprised 3·1%. The remaining 36·7% of iris performance variation were not explained by any of the variables.

The RDA and pRDA revealed, using Monte Carlo permutation tests, that only the effect of species abundance on iris performance was significant (Table 4). This effect was significant when confounding effects of other variables were not removed (lines 2, 5, 6, 11, 12; Table 2), as well as when these effects were fractioned out (line 8). The effects of total plant biomass and soil on iris performance were not significant (Table 4).

A relationship between iris performance variables, experimental relocation sites and species composition/abundance (summarized in two CA axes) can be seen on ordination (RDA) triplot (Fig. 5). The triplot shows a substantial variation among different performance measures/years of observation, and that population at site 7 had consistently higher performance than other populations across performance measures and years of observation. Vegetation (species composition/abundance) was associated with iris performance two and three years after introduction, but not in the following introduction year.

Forward selection of significance testing has further shown that only one of the abundance variables had a significant effect – the second CA axis summarizing species abundance data ($P = 0{\cdot}001$; $P > 0{\cdot}05$ for the other four axes). This means that abundance of species with the highest contribution to Axis 2 of the CA is most correlated with iris performance. Thus, the species with the highest absolute values on Axis 2 are the most important (Fig. 6). Among these species, two abundant species *B. distachyum* and *C. pachystylis* were associated with poor iris performance. Other species with high absolute scores were relatively rare, and they did not belong to particular life forms (Fig. 5). For example, the five species with the highest scores (two negative and three positive) were: an annual grass, *Avena barbata* Pott ex Link; a geophyte, *Ornithogalum narbonense* L.; and three annual forbs, *Crupina crupinastrum* (Moris) Vis., *Hedypnois rhagadioloides* (L.)

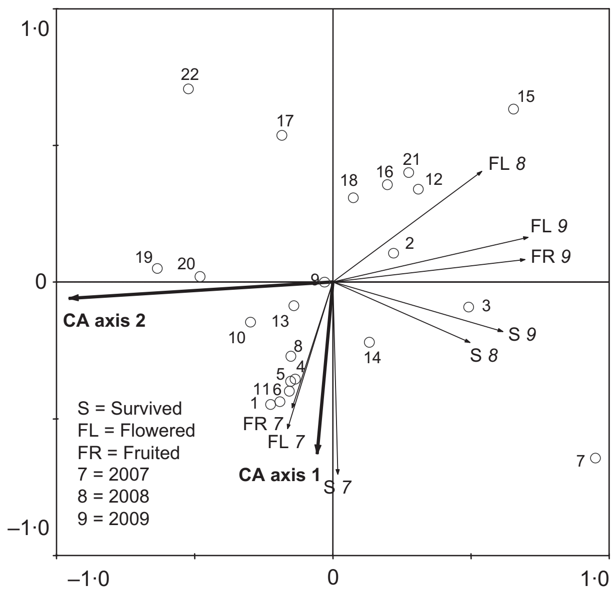

Fig. 5. Ordination (RDA) triplot showing variation in iris performance (arrows) among the experimental relocation sites (dots), and effect of species composition/abundance summarized in two CA axes. Note that only CA Axis 2 had a significant effect on iris performance.

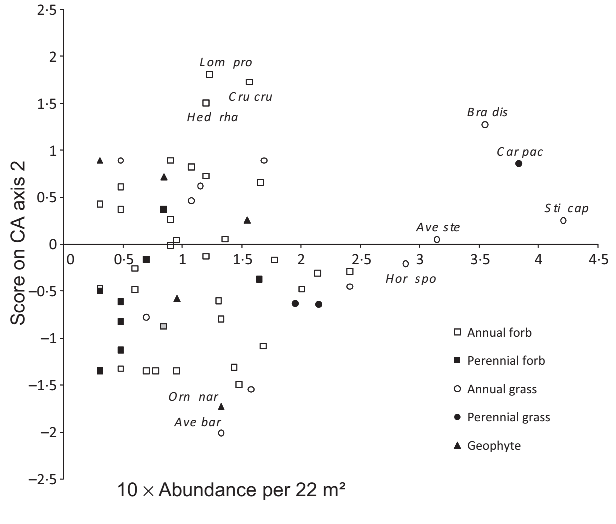

Fig. 6. Species scores on CA Axis 2 as a function of log-transformed abundance per 22 m^2 (in all sites combined). Species are marked according to their life form. The CA Axis 2 (*Y* axis) was the only CA axis having significant effect on iris performance. This means that abundance of species with the highest absolute scores on this axis correlates with iris success.

F. W. Schmidt and *Lomelosia prolifera* (L.) Greuter & Burdet. Conversely, the importance of three of the five most common species was low, as suggested by their low scores on Axis 2 of the CA (Fig. 5).

Discussion

Analysis of performance variables suggests that (i) survival, probability of flowering and fruit set, are largely independent from each other in relocated *I. atrofusca* plants and (ii) inter-annual climatic variation differentially affects plants across sites. This means that no single performance trait measured in a given year can be used for comparisons between sites. Instead, multi-year data on a suite of performance traits are needed for reliable inferences about relocation success across sites.

The RDA performed on a set of environmental (explanatory) and plant performance (response) variables allowed precise partitioning of effects of species abundance, total plant biomass and soil properties. Species abundance and soil effects on iris performance were largely independent and not correlated among sites, and only the effect of the former was significant. The effect of total plant biomass was also non-significant, and explained only a small portion of variation in iris performance. Therefore, relocation success for this species could be influenced either directly by interaction with plant community composition; or indirectly by some unmeasured environmental (biotic or abiotic) factors of which plant abundance is an indicator. Although the first explanation may apply to a few species (e.g. *B. distachyum* and *C. pachystylis*), the second explanation seems more likely for two reasons. First, the effect of total biomass was very small, suggesting that the competitive effect of vegetation on the relocated irises is low. Secondly, the abundance of several rare plant species was most strongly correlated with iris performance while abundance of the common species, except for *B. distachyum* and *C. pachystylis*, did not correlate with iris performance (Fig. 6). It is likely that these rare species do not affect the irises directly but are indicators of environmental conditions, other than the soil characters measured, which are important for iris success. It is known that environmental conditions vary greatly on a small scale in water-limited systems, due to resources redistribution creating landscape heterogeneity (Boeken & Shachak 1994; Boeken *et al.* 1995; Shachak, Sachs & Moshe 1998; Shachak *et al.* 2008). This pattern was studied in several sites in Israel, including an area (Lehavim) only 4 km southwest of our study area (Shachak *et al.* 2008). In general, both physical environment (rock-soil ratio, topography) and biological landscape modulation (shrub mounds, biological soil crust, animal diggings) were found to affect runoff redistribution, thus creating water and nutrient enriched or impoverished patches, which in turn affects vegetation community composition. If the performance of iris plants is affected by the patch characteristics as well, plant species indicative of the preferred patches can be identified and used for selection of the introduction sites.

Species of the section Oncocyclus in the genus *Iris* are well adapted to aridity and are mostly found in the semi-arid habitats of the Middle East (Avishai 1977). In Israel, these species occupy open low-herbaceous or shrub communities (Sapir *et al.* 2002). There is evidence that they suffer from light competition with shrubs, such as *Sarcopoterium spinosum*, as succession progresses in herbaceous plant communities (Segal 2006). However, the relocation sites in our study area were always chosen to be herbaceous vegetation patches, even where the overall *Sarcopoterium spinosum* cover was high (Fig. 1). Therefore, competition with shrubs as a factor negatively affecting relocation success can be ruled out. Competition with herbaceous vegetation is also unlikely, as indicated by the relatively small effect of the most abundant plant species on iris performance and by the very low amount of variation in iris performance explained by variation in plant biomass. As for the negative effects of *B. distachyum* and *C. pachystylis* on iris plants, this may be due to allelopathy. For example, litter of *Brachypodium retusum* negatively affected seedling growth of an endangered shrub *Cistus heterophyllus* (Navarro-Cano 2008).

The results of this study have demonstrated the usefulness of CCA/RDA for understanding the causes of relocation success or failure. The many biotic and abiotic factors affecting individual performance are often complex and/or highly inter-correlated, therefore elucidating the primary environmental effect(s) on relocated plants is challenging. Counter intuitively, the effect of soil was less important than plant abundance/composition. The effect of the total biomass, indicative of intensity of competition for resources, was negligible; only the effect of composition/abundance of surrounding relocated plants vegetation was significant and explained more than 40% of variation in performance of iris plants. Counter intuitively again, abundances of rare rather than common species, correlated with iris performance.

These findings show that CCA/RDA can help with the choice of future translocation microsites, the most important decisions in translocation, according to the knowledge gained about the ecological niche of the species. On the other hand, we have seen that even in relocations of perennial plants, it is difficult to ascertain what environmental factors determine success.

To conclude, variation partitioning can be used to monitor success and to identify the key factors in experimental translocations preceding actual introduction of plants in conservation programmes. The (partial) ordination techniques, due to their ability to integrate multiple datasets and reduce the list of possible effects, can be a useful tool for improving our knowledge of the ecological requirements of endangered species.

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Supporting information

Additional Supporting Information may be found in the online version of this article.

Table S1. Abundance and life form of 75 plant species per 1 m^2 for 22 sites

Table S2. Total plant biomass (dry weight) per 1 m^2 for 22 sites

Table S3. Soil characteristics measured at the 22 sites. See 'Materials and methods' section for explanation of sampling methods and abbreviations

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