Host-plant-based restoration as a potential tool to improve conservation status of odonate specialists

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Abstract. 1. Several species worldwide show rapid range retraction due to habitat degradation, and some of them have restricted distribution and specific resource needs. Such cases deserve particular attention and need urgent conservation actions to avoid extinction, and one way is to facilitate colonisation of new habitats by resource supplementation.

2. Here, we investigate the changes in range distribution, during the last decade (2007–2016), of an endangered endemic damselfly, *Calopteryx exul* Selys, and assess the importance of its favourite host-plant (*Potamogeton nodosus*) in colonisation and population dynamics in the last existing population of Algeria.

3. We first used dynamic occupancy models to assess range distribution dynamics and we found that both occupancy and colonisation probabilities of the species were positively dependent on the occurrence of *P. nodosus*. There was also evidence that extinction probability increased with habitat disturbance but decreased with the occurrence of *P. nodosus*. Our experimental restoration showed that the augmentation of patches of *P. nodosus* increased the total number of individuals, the number of reproductive events and philopatry.

4. Our study highlights the importance of insect–plant relationship in the establishment of effective restoration plans because of their implication in colonisation and extinction processes and population dynamics.

5. Since most insect species from different orders and ecosystems are ecologically dependent on plants, our restoration approach may benefit a large range of threatened species and improve their conservation status.

Key words. *Calopteryx exul*, conservation, insect–plant relationship, IUCN, North Africa, odonate.

Introduction

Among the most critical current environmental issues is the rapid loss of biodiversity in different biotopes (Ceballos *et al.*, 2010; Barnosky *et al.*, 2011). The intensification of urbanisation, industrialisation and agriculture is the major cause of the high extinction rate (Smith *et al.*, 1999), which threatens ecosystem functioning and human well-being (Mace *et al.*, 2012). The extinction rates are expected to be highest in insects (Dunn, 2005), since they represent the mostly highly diversified group on earth (Wilson, 1992). In freshwater ecosystems, 60% of animal diversity is composed of aquatic insects (Dijkstra *et al.*, 2014). Yet, freshwater habitats have been under constant human pressure (Meybeck, 2003; Vorosmarty *et al.*, 2010) because of the growing demands for water, energy and food (Ward, 1998). For instance, estimations have suggested that a minimum of 10 000–20 000 aquatic insect species are extinct or at risk of extinction (Strayer & Dudgeon, 2010). Despite that, there has been a marked lack of applied conservation research that addresses important

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ecological processes that improve the conservation status of aquatic insects in the wild.

Colonisation of new habitats is an important ecological process that allows species to expand their distribution and avoid extinction (Thomas *et al.*, 2001). Some species have good dispersal capacity and can colonise new habitats, but others do not travel long distances and thus cannot shift their range (Pöyry *et al.*, 2009). Even with high dispersal capacity, colonisation processes may be altered by the lack of suitable habitats due to drastic habitat fragmentation (Fahrig, 2003). Therefore, understanding the factors that control colonisation processes is important for restoration of wild populations of threatened species (Brooker *et al.*, 1999).

Insects, like any other animal groups, need an array of resources to establish a viable population in a new habitat. Plants represent an important resource that insects exploit for food, shelter and reproduction (Jolivet, 1998). Although some insects use many plant species to meet their biological and ecological needs, many species are specialists and rely on only a few plant species (Jonsen & Fahrig, 1997). These cases occur in odonate (dragonflies and damselflies) species that oviposit endophytically in a restricted number of host-plants (Corbet, 1999). Many of these species show alarming decline in the range of their distribution (Matushkina & Lambret, 2011; Andersen *et al.*, 2016), and their conservation requires the consideration of host-plants as a vital resource for long-term persistence.

Calopteryx exul is an endangered damselfly endemic to the Maghreb (Morocco, Algeria and Tunisia). The species has a very patchy distribution (Boudot, 2010), and shows a marked preference to lay eggs in *Potamogeton nodosus* (R. Khelifa, unpublished data). In Algeria, the Seybouse (meta-)population is the only one confirmed to be in existence. The species was thought to be extinct because it had not been observed for a century (since Martin, 1910). In 2007, the species was recorded in the Seybouse watershed (Khelifa *et al.*, 2011) and has been surveyed regularly since then (Khelifa *et al.*, 2016a). Estimation of the size of five subpopulations in the Seybouse River recorded 2200 individuals, which nearly corresponds to a fourth of the estimated global population and the largest number ever estimated for the species (Khelifa *et al.*, 2016a). Due to increasing anthropogenic pressure, several subpopulations have recently become extinct (see results). The species needs an urgent restoration plan to improve the conservation status through an increase in the local range and population size (Khelifa *et al.*, 2016b).

In this study, we aim to assess three questions related to species conservation status, ecology and restoration: (i) how did the range of the species change over the last decade? (ii) what are the main environmental factors that determine occupancy, colonisation, extinction and detection of the species? (iii) how can we increase the range and population size of the species? The first question is assessed by analysing long-term changes in the number of subpopulations and range using detection/non-detection data that were collected from 2007 to 2016 in the Seybouse watershed. The second question is answered by using dynamic occupancy models (DOM) to estimate the effect of some environmental factors (including the occurrence of *Potamogeton nodosus*) on four parameters: occupancy, colonisation, extinction and detection (MacKenzie *et al.*, 2003). Studies have shown that DOM are powerful for assessing the dynamics of species range (Kéry *et al.*, 2013). The third question is addressed by combining field restoration experiments with capture-mark-recapture of adults to estimate changes in site occupancy, population size and philopatry to reproductive sites. Based on the three questions, we propose a conservation plan that will likely expand the range of the species and increase the size of populations.

Materials and methods

Study area, study species and data collection

The study was conducted in Seybouse watershed (6471 km²), one of the largest watershed in Algeria. It is situated in Northeast Algeria and flows into the Mediterranean Sea about 80 km from the Algero-Tunisian border (Fig. S1). The main watercourses of the watershed are two rivers (Bouhamdane and Cherf) that meet at Medjez Amar village (36°26′36.05″N, 7°18′39.66″E) to form the Seybouse River (225 km long). The bank vegetation is dominated by *Typha angustifolia*, *Tamarix gallica*, *Phragmites australis* and *Paspallum distichum*.

Calopteryx exul is a large damselfly that lives in open rivers and streams with relatively fast-flowing water (Khelifa, 2013). In the Seybouse watershed, the species has patchy distribution (Khelifa, 2016) and lives in subpopulations that might be connected by dispersal. The species has a potential to disperse long distances (5 km) to seek favourable new habitats (Khelifa *et al.*, 2014). This damselfly is partially bivoltine with the main population emerging in late spring and a small cohort emerging in late summer-early autumn (Khelifa, 2016). In addition, it is territorial and shows a preference to lay eggs in floating leaves of *Potamogeton nodosus* (Khelifa R. unpublished data). Here, we considered a subpopulation of *C. exul* when the following conditions were met: (i) individuals successfully reproduce (copulation, oviposition and emergence) in a favourable habitat along the watercourse, (ii) the subpopulation has persisted for at least two generations, and (iii) the distance between one subpopulation and another is at least 300 m; otherwise is considered the same subpopulation.

We used data collected in the period 2007–2016 in the Seybouse watershed. A total of 33 sites lying in 24 quadrates (4 km²) (Table S1; Fig. S2) were surveyed three times every flight season (May–July). We recorded the number of individuals along a transect of 200 m in each site. Then, the counts were reduced to binary data referring to detection (coded 1) and non-detection (coded 0).

Due to the conspicuous coloration (both males and females) and the ease of identifying the species, detection was fairly straightforward.

Colonisation experiment

To assess species colonisation, we used capture-mark-recapture data of *Calopteryx exul* adults conducted daily (10:00–16:00) between 25 May and 21 June 2016 in one currently existing subpopulation (site 21 in Table S1; Fig. S3). By slowly walking along 400 m transect near the bank vegetation of the river, individuals were captured with a hand net and marked with alphanumeric codes on the hindwing with permanent markers. We recorded the sex and the reproductive state of individuals (reproductive: territorial male, tandem, in copula or female oviposition; non-reproductive: single). Estimations of abundance were accurate since most of individuals were marked during each sampling occasions. To increase the subpopulation size of the species, a field experiment was conducted consisting of translocating patches of *Potamogeton nodosus*, the favourite host-plant for the species (Fig. 1). Our hypothesis is that subpopulation size is limited by the availability of the host-plant where eggs are laid, and that by providing this plant the abundance of the species will increase. Before conducting the experiment, we divided the 400 m study site into accessible stretches and labelled each one with coded small flags that were attached to the vegetation (Fig. S3). From 25 May to 21 June 2016, abundance (number of reproductive and non-reproductive adults) of *C. exul* was surveyed daily in two subsequent 14-days periods in the morning along the study transect. We consider an individual in reproductive state when we recorded territorial behaviour (defending a patch), courtship, copulation or oviposition. In the first period (pre-management), the two parameters were surveyed under natural conditions where only three natural patches of *Potamogeton spp.* (two patches with *P. pectinatus* and one patch of *P. nodosus*) were available, whereas in the second period (post-management), the habitat was improved by adding eight 1 m²-patches of *Potamogeton nodosus* (Fig. S3; hereafter referred as *substrate augmentation*). Then, changes in abundance and site occupancy were surveyed. We have reasons to think that there was no bias related to emergence since the experiment was performed during the peak abundance of the species where most individuals have already emerged (Khelifa, 2016; Fig. S4). In fact, only 25 tenerals were marked during the study period of which 19 (76%) were recorded during the pre-management period. In addition, the number of marked individuals was higher during the pre-management period (58.1%, $n = 139$) than during the post-management period (32.6%, $n = 78$) (Fig. S5). After the experiment, we continued our capture-mark-recapture efforts until the end of the flight season where we marked 22 individuals (last one on 2 July) which correspond to 9.2% of all individuals marked (Fig. S5). This shows that our substrate augmentation experiment was conducted during the second half of the flight season of the species where the number of individuals is not expected to increase. Furthermore, the possibility that individuals might have matured in terrestrial habitats and returned to the water, as many odonates do, is unlikely since immature individuals of *C. exul* remain near the water course and hence our daily MCR sampling took into account all individuals from different ages. Finally, weather conditions were not different during the two 14-day periods since mean wind speed (Welch two sample *t*-test: $W = 98$, $P = 0.99$) and minimal and maximal air temperature (Welch two sample *t*-test: $W = 63$, $P = 0.12$; $W = 59$, $P = 0.07$; respectively) did not differ between the pre- and post-management period.

Statistical analyses

Occupancy models. Dynamic occupancy models, also known as multiseason occupancy models, are a class of occupancy models that account for changes of occupancy over seasons. Instead of imposing a static state of occurrence y_{ij}, which represents detection/non-detection observation at site i during survey j, dynamic occupancy models have two temporal scales (robust design). This allows occurrence to change across seasons (primary sampling occasion), but not within season occasions (secondary sampling occasion), yielding detection/non-detection data y_{ijk} for site i, within-season survey j, and season (year) k (Kéry & Schaub, 2012).

The classic DOM involves four parameters, namely occupancy in the first season (Ψ_1), colonisation (γ), local extinction (ε) and detectability (p). First, we used DOM to assess changes in occupancy of the study species from 2007 to 2016. Here, we have 10 primary sampling periods (years), and three secondary sampling periods (replicates). An example of capture history of year 2007 and 2008

Fig. 1. Oviposition of two marked females of *Calopteryx exul* in a translocated patch of *Potamogeton nodosus*. [Colour figure can be viewed at wileyonlinelibrary.com]

looks like '110 000,' which means that the species was recorded during the two-first occasions of 2007, but has not been observed at any occasion of 2008. The probability of this capture history equals: $\Psi_1 p^2 (1 - p) \times \{\varepsilon + (1 - \varepsilon) (1 - p)^3\}$, such that the probability that the site was initially occupied and the damselfly was detected on two occasions and not detected in the last occasion of the year, and either the site was deserted in the following year or the damselfly was not detected on all occasions.

Using the package *unmarked* (Fiske & Chandler, 2011), we tested for the effects of some covariates on occupancy, colonisation, extinction and detection processes. We introduced a missing value when sites were not visited in a particular year or occasion. Site covariates included elevation, water flow and width of watercourse (with and without quadratic effect), whereas yearly varying covariates were *Potamogeton nodosus* occurrence (presence/absence) and disturbance. Disturbance here is estimated based on anthropogenic factors that affect directly or indirectly the subpopulation, and varies from 0 (no disturbance) to 4 (complete fragmentation of the habitat). Four sources of disturbance were considered: grazing (scored as 1), water pumping (scored as 2), bank vegetation fragmentation (scored as 3) and waterbed enlargement (scored as 4). When there are different sources of disturbance, we summed up the scores but the highest score is fixed to 4 (even if the sum exceeds 4). For instance, when both grazing and water pumping are recorded, we score it as 3 (1 + 2). We used Akaike's information criterion (AIC) to select the best model from candidate models with increasing complexity in terms of covariates, following Kéry *et al.* (2013). Models with ΔAIC <2 were considered as the best to explain our data, and we (mostly) selected the least parametrised one (parsimony). We first fitted a model with constant parameters and compared it with time-dependent colonisation, extinction and detection. Covariates were then added successively to detection probability (*p*), and selected the best model. The same procedure was performed with the initial occupancy parameter (Ψ_1), using site covariates and their interactions. Then, we repeated the modelling approach first starting by the probability of local extinction (ε) and then probability of colonisation (Υ) (variant one) and second starting by the probability of colonisation, then the probability of local extinction (variant two). Since both variants showed similar results, we show only one variant in (Table 1). The goodness of fit of the chosen models was assessed with the *mb.gof.test* function of the *AICcmodavg* package (Mazerolle, 2016) with 5000 simulations, which yielded a *P*-value >0.05, indicating that there was no evidence of lack of fit. The *predict* function of *unmarked* package was used to estimate the four parameters and their relationship with covariates.

Colonisation experiment.   A quasi-Poisson generalised linear model was used to test for differences in the number of imagoes and reproductive individuals before and after substrate augmentation. Since capture-mark-recapture was conducted during the study period, detection probability was estimated with a Cormack-Jolly-Seber (CJS) model using *RMark* package (Laake, 2013). Detection probability can be used as a surrogate of philopatry, so high detection probability indicates high philopatry. Our hypothesis is that substrate augmentation increases philopatry of the species, which may increase population size through repeated oviposition. We fixed survival as constant and allowed detection to vary. We started by fitting a temporal-dependent model, then a model with a single covariate (sex), time and sex, and including the interaction between the latter. We selected the best model based on the AICc (corrected Akaike's Information Criterion). The goodness of fit of the model was checked with the *release.gof* function from RMark (Amstrup *et al.*, 2010). We estimated a variance inflation factor (c-hat) of 0.678 by dividing the overall χ^2 (sum of the TEST 2 and TEST 3 component tests) by the overall degrees of freedom (Cooch & White, 2006). Since c-hat <1, no adjustment were made to our models.

Results

Geographic distribution

Of the 33 sites surveyed during the period 2007–2016, *C. exul* was recorded in 15 sites (Fig. 2a), of which 13 harboured a subpopulation (Fig. 2b). A total of 11 subpopulations went extinct, representing an extinction of 77% of all subpopulations during a decade. To estimate the rate of extinction, we used two time windows corresponding to 6 years (2010–2016, $n = 13$) and 10 years (2007–2016, $n = 7$) because not all sites were monitored for 10 years and the least surveyed sites were monitored for 6 years (Table S1). The extinction rate was 0.77 subpopulations per year and 0.57 subpopulations per year for 6 and 10 year windows respectively.

The occupancy of *C. exul* in the Seybouse watershed was assessed based on the geographic distribution of the 13 subpopulations recorded during the past decade (Fig. 2b). To estimate the temporal pattern of the occupancy of the species in the Seybouse watershed, we divided the main watercourse of the watershed (the preferred habitat of *C. exul*) into 283 quadrates of 4 km² (Fig. 2a). During 2007–2016, the species was recorded in seven quadrates (28 km²), which represents 2.5% of the total watershed area. In each quadrate, the number of subpopulations varied between 1 and 4 (Fig. 2b). Of the 13 subpopulations occurring in seven quadrates (28 km²), 10 subpopulations were recorded as extinct in six quadrates (24 km²) (Fig. 2c). This accounts for a geographic loss of five quadrates (20 km²), corresponding to 71.4% loss of the total area where the species existed in the watershed. Thus, total area covered by *C. exul* in the Seybouse watershed is currently restricted to 8 km² occupied by three subpopulations (Fig. 2d).

Table 1. Results of model selection for *Calopteryx exul* range dynamics from 2007 to 2016 in the Seybouse watershed, Algeria.

Model	nPars	AIC	ΔAIC
(a) Modelling time dependence in parameters			
Ψ1(.) Υ(.) ε(.) p(.)	**4**	**333.12**	**0.00**
Ψ1(.) Υ(Y) ε(Y) p(Y)	29	348.25	15.14
(b) Modelling patterns in detection probability (p)			
Ψ1(.) Υ(.) ε(.) p(Wf + Wf²)	6	332.44	0.00
Ψ1(.) Υ(.) ε(.) p(P)	5	333.03	0.59
Ψ1(.) Υ(.) ε(.) p(.)	**4**	**333.12**	**0.68**
Ψ1(.) Υ(.) ε(.) p(Rw)	5	334.08	1.64
Ψ1(.) Υ(.) ε(.) p(Wf)	5	334.64	2.20
Ψ1(.) Υ(.) ε(.) p(Rw + Rw² + Wf + Wf²)	8	334.77	2.34
Ψ1(.) Υ(.) ε(.) p(Y × Wf + Wf²)	24	335.96	3.52
Ψ1(.) Υ(.) ε(.) p(Rw + Rw²)	6	335.96	3.53
Ψ1(.) Υ(.) ε(.) p(Y + Wf + Wf²)	15	340.88	8.45
Ψ1(.) Υ(.) ε(.) p(Y + P)	14	341.07	8.63
Ψ1(.) Υ(.) ε(.) p(Y)	13	341.47	9.04
Ψ1(.) Υ(.) ε(.) p(Y + Wf + P)	15	343.06	10.63
Ψ1(.) Υ(.) ε(.) p(Y + P + Wf)	15	343.06	10.63
Ψ1(.) Υ(.) ε(.) p(Y + P + Wf + Rw)	16	344.96	12.53
(c) Modelling patterns in first-year occupancy probability (Ψ1)			
Ψ1(P) Υ(.) ε(.) p(.)	**7**	**321.41**	**0.00**
Ψ1(.) Υ(.) ε(.) p(.)	4	333.12	11.70
Ψ1(Wf) Υ(.) ε(.) p(.)	5	334.70	13.29
Ψ1(Rw) Υ(.) ε(.) p(.)	5	334.86	13.45
Ψ1(Wf + Wf²) Υ(.) ε(.) p(.)	6	336.69	15.28
Ψ1(Rw + Rw² + Wf + Wf² + Rw*Wf + Rw²*Wf) Υ(.) ε(.) p(.)	10	338.67	17.26
Ψ1(P + Wf + Wf²) Υ(.) ε(.) p(.)	7	360.76	39.35
Ψ1(Ev) Υ(.) ε(.) p(.)	5	499.34	177.93
Ψ1(Rw + Rw²) Υ(.) ε(.) p(.)	6	501.35	179.94
Ψ1(Rw + Rw² + Wf + Wf²) Υ(.) ε(.) p(.)	8	504.69	183.28
Ψ1(Rw + Rw² + Wf + Wf² + Rw*Wf) Υ(.) ε(.) p(.)	9	510.25	188.84
Ψ1(Ev + Ev²) Υ(.) ε(.) p(.)	6	895.50	574.09
(d) Modelling patterns in colonisation probability (Υ)			
Ψ1(P) Υ(P) ε(.) p(.)	**5**	**320.56**	**0.00**
Ψ1(P) Υ(P + Y) ε(.) p(.)	13	321.16	0.60
Ψ1(P) Υ(P*Y) ε(.) p(.)	21	328.41	7.85
Ψ1(P) Υ(.) ε(.) p(.)	4	333.12	12.56
Ψ1(P) Υ(Y) ε(.) p(.)	12	334.68	14.12
Ψ1(P) Υ(Y + Wf + Wf²) ε(.) p(.)	14	336.64	16.08
Ψ1(P) Υ(P + Wf + Y) ε(.) p(.)	14	442.35	121.79
Ψ1(P) Υ(Ev) ε(.) p(.)	5	500.70	180.14
Ψ1(P) Υ(P + Wf) ε(.) p(.)	6	502.73	182.18
Ψ1(P) Υ(P*Wf) ε(.) p(.)	7	504.73	184.18
(e) Modelling patterns in extinction probability (ε)			
Ψ1(P) Υ(P) ε(Dst + P) p(.)	8	314.64	0.00
Ψ1(P) Υ(P) ε(P) p(.)	7	314.83	0.19
Ψ1(P) Υ(P) ε(.) p(.)	**6**	**315.15**	**0.51**
Ψ1(P) Υ(P) ε(Dst) p(.)	7	315.69	1.04
Ψ1(P) Υ(P) ε(Wf) p(.)	7	317.15	2.51
Ψ1(P) Υ(P) ε(Wf + Wf² + P) p(.)	9	318.02	3.38
Ψ1(P) Υ(P) ε(Wf + Wf²) p(.)	8	318.83	4.19
Ψ1(P) Υ(P) ε(.) p(.)	15	319.27	4.63
Ψ1(P) Υ(P) ε(.) p(.)	14	319.99	5.35
Ψ1(P) Υ(P) ε(.) p(.)	16	323.75	9.11
Ψ1(P) Υ(P) ε(.) p(.)	15	351.84	37.20

Only one variant (colonisation first before extinction) is shown here because the same results were found for the two variants (see Materials and methods). The sequential approach of model selection here is structured such that it first compares a fully time-dependent and a fully constant model, then it compares candidate models for detection (p), initial occupancy (Ψ1), colonisation (Υ) and extinction (ε). The best model is selected based on the Akaike's information criterion (AIC) and parsimony. The model retained is shown in bold. nPars refers to the number of estimated parameters. Covariates are abbreviated as Wf (water flow), Rw (river width), P (*Potamogeton* occurrence), Dst (disturbance), Ev (elevation) and Y (year). Quadratic terms are denoted by a superscript 2 and interactions by an asterisk.
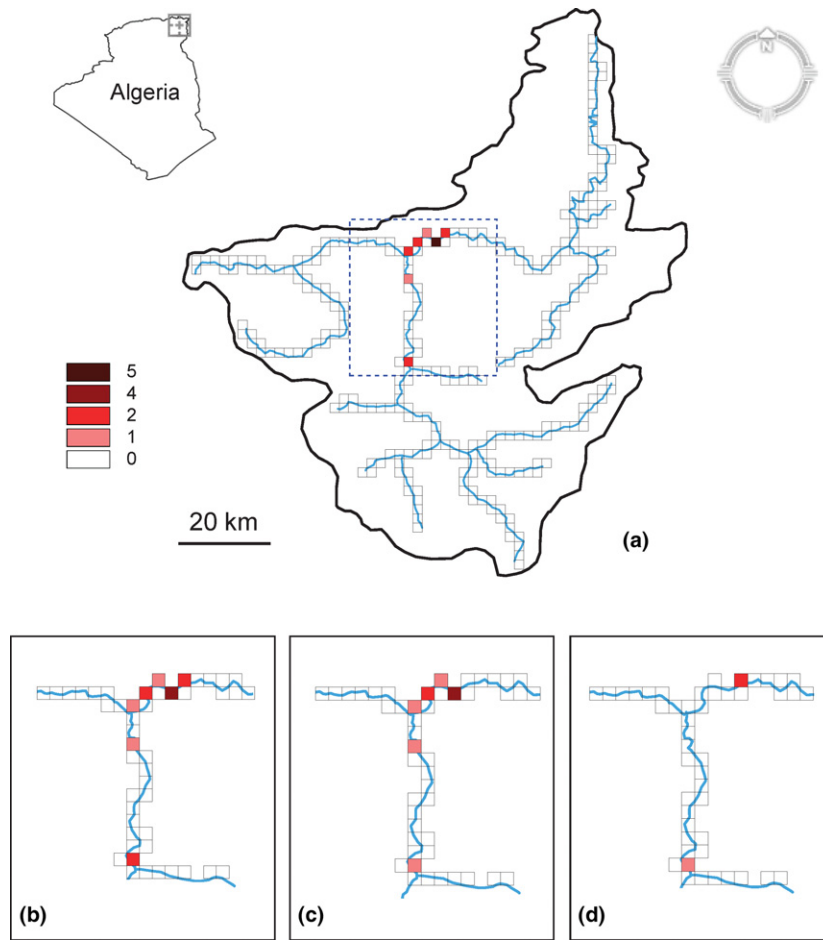
Fig. 2. Temporal dynamics of the distribution of *Calopteryx exul* in the Seybouse watershed during 2007–2016. The colour of the grid indicates the number of localities in (a) and the number of subpopulations in (b) (c) and (d). Dashed rectangle indicates the area zoomed in b, c and d. (a) All localities where the species was recorded. (b) All reproductive subpopulations. (c) Currently extinct subpopulations. (d) Currently existing subpopulations. Every grid is 2 × 2 km² size. [Colour figure can be viewed at wileyonlinelibrary.com]

Dynamic occupancy models

There was no evidence for time-dependence in colonisation, extinction and detection probability (Table 1a). Detection probability was not highly influenced by any environmental factor, showing a mean (±SE) of 0.676 ± 0.028 (Table 1b). Initial occupancy probability, however, was clearly dependent on the occurrence of *P. nodosus* (Table 1c, Fig. 3a). Occupancy probability was 0.537 ± 0.207 and 0.027 ± 0.027 for sites with and without *P. nodosus*, respectively. The colonisation probability depended on the occurrence of *P. nodosus* (Table 1d), revealing that sites where *P. nodosus* was present were more likely to be colonised by *C. exul* (Fig. 3b). Although the most parsimonious model for extinction probability was constant, three other models had a ΔAIC <2 including disturbance (ε ~ Disturbance), the occurrence of *P. nodosus* (ε ~ Potamogeton), and the additive effects of the two (ε ~ Disturbance + Potamogeton) (Table 1e).

Thus, it is fairly reasonable to consider that disturbance and *P. nodosus* play an important role in the extinction probability of the species, as described by the top model (ε ~ Disturbance + Potamogeton, Table 1e), which predicts that the greater the disturbance the higher the extinction probability; however, the occurrence of *P. nodosus* tended to buffer disturbance effects (Fig. 3c).

Increasing colonisation

A total of 222 marked individuals (91 males and 131 females) were recorded during the 28-day study period. The overall number of individuals and the number of reproductive individuals increased significantly after substrate augmentation (GLM quasi-Poisson: $\alpha = 0.3764$, SE = 0.1469, $t = 2.563$, $P = 0.0162$; $\alpha = 1.4960$, SE = 0.3571, $t = 4.189$, $P = 0.0002$ respectively), but the increase was more important for reproductive individuals.

The number of ovipositions per day increased by 1340% from 0.35 to 5.14.

There were no significant departures from assumptions that allow the use of CJS (Table 2). We found that the detection probability was best explained by time and sex (Table 3). Males were detected more frequently than females, but detection of both sexes increased substantially after substrate augmentation (Fig. 4). Mean detection probability was 0.39 ± 0.14 ($\pm$SD) and 0.68 ± 0.10 ($\pm$SD) in males and 0.18 ± 0.08 ($\pm$SD) and 0.42 ± 0.11 ($\pm$SD) in females during the pre- and post-management period respectively.

Discussion

Our study assesses, for the first time, the status of the threatened endemic damselfly, *Calopteryx exul*, and proposes conservation planning that likely improves the status of the species in the only (meta-)population known in Algeria. We first showed that the range of the species decreased substantially during the last decade, most probably due to habitat degradation. Second, we found that *Potamogeton nodosus* plays an important role in occupancy, colonisation and extinction processes. Third, we conducted a field experiment where we successfully increased the population size, reproductive events and philopatry of the species by augmenting the availability of *P. nodosus*. Based on these results, we will discuss a restoration plan which includes species and plant translocation to improve the conservation status of this species.

The range distribution of *Calopteryx exul* showed a severe retraction during the last decade with >70% loss of the entire range. The species area decreased from 28 km² to only 8 km² in 2016. Some of the extinct subpopulations were probably the largest of the global range of the species. Indeed, estimation of some subpopulations prior to their extinction yielded about 2200 individuals (Khelifa *et al.*, 2016a). Given that the Seybouse (meta-) population is the only one known in Algeria, it is reasonable to raise the species status from endangered to critically endangered at least at the national level, following IUCN

Table 2. Results of goodness-of-fit tests of the general Cormack-Jolly-Seber Model.

| Test	Chi square	d.f.	P
TEST2	49.1513	51	0.5474
TEST3	37.7356	77	1.0000
Total	86.8869	128	0.9979

TEST2 tests for trap-dependence effects (whether all individuals have equal recapture probabilities). TEST3 tests for transience (newly marked individuals at occasion t have less chance to be recaptured at $t + 1$ than animals already marked at t).

Table 3. Model selection results for detection probability of the Cormack-Jolly-Seber for capture-mark-recapture data of *Calopteryx exul*. The best model is in bold.

Model	npar	AICc	ΔAICc	Weight	Deviance
Phi(.) p(sex + time)	**30**	**1582.678**	**0.000**	**1.000e+00**	**1052.644**
Phi(.) p(sex)	3	1622.061	39.383	2.805e−09	1149.380
Phi(.) p(time)	29	1624.316	41.637	9.087e−10	1096.507
Phi(.) p(sex × time)	57	1632.700	50.022	1.373e−11	1039.369
Phi(.) p(.)	2	1652.348	69.669	0.000e+00	1181.687
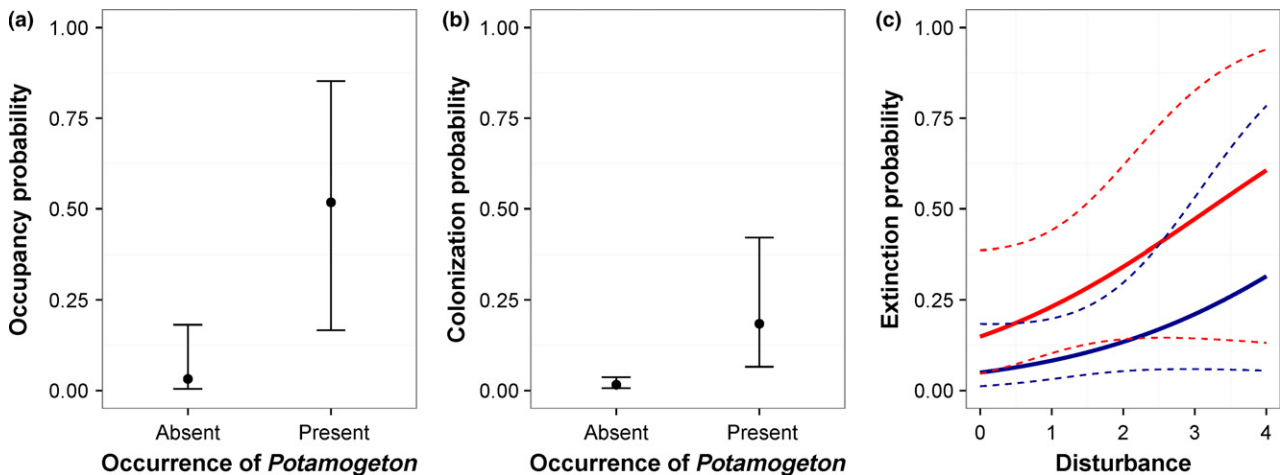
Fig. 3. Estimations of the dynamic occupancy model parameters. (a) Occupancy probability in sites with and without *Potamogeton nodosus*. (b) Colonisation probability in sites with and without *P. nodosus*. (c) Extinction probability as a function of disturbance and *P. nodosus* occurrence. In (c), continuous lines are the fitted mean, whereas the dashed lines are 95% confidence intervals. The blue and red colours indicate presence and absence of *P. nodosus* respectively. [Colour figure can be viewed at wileyonlinelibrary.com]
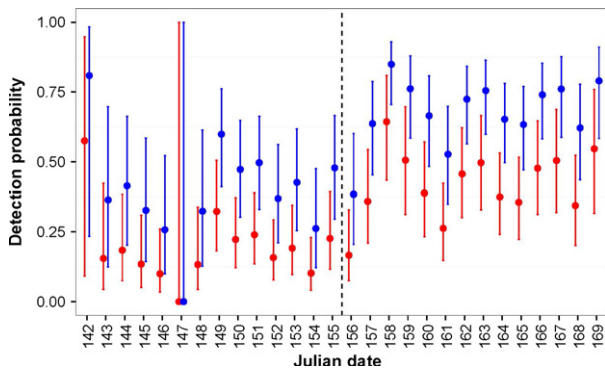
Fig. 4. Detection probability of *Calopteryx exul* estimated with a Cormack-Jolly-Seber model. Blue and red refer to male and female respectively. Dashed vertical line indicates the start of substrate augmentation experiment. Note that the detection probability of both sexes increases after substrate augmentation. [Colour figure can be viewed at wileyonlinelibrary.com]

criterial: B2 (occurring over less than 10 km², severe habitat fragmentation and decline in extent of occurrence) and E (at least 50% likely to go extinct in the wild over a decade).

There was an apparent intimate relationship between the occurrence of *P. nodosus* and *Calopteryx exul*. This odonate-plant relationship has been highlighted in different species of odonates (Corbet, 1999; Matushkina & Lambret, 2011; Andersen *et al.*, 2016), and its ecological understanding has important conservation value. The choice of *P. nodosus* as oviposition substrate likely improves larval survival and hatching success (Lambret *et al.*, 2015). Our analysis with the dynamic occupancy model showed that the occurrence of *P. nodosus* increases colonisation probability of the species, suggesting that this plant attracts males and females and promotes reproduction when the species seeks a new habitat. Furthermore, the top model for extinction probability was positively affected by disturbance, but negatively influenced by *P. nodosus* which gives evidence that the plant species reduces the probability of extinction and thus buffers the effects of habitat degradation and other disturbance factors. This suggests that the subpopulation size of the species may be larger when *P. nodosus* is present because it attracts more reproductive individuals, which reduces the extinction probability (Shaffer, 1981). In addition, *P. nodosus* may also decrease the pollution level of water (Peng *et al.*, 2008), as well as act like an umbrella that maintains the survival of local entomofauna.

Our experimental approach assessing colonisation in the field consisted of translocating the favourite plant substrate (*P. nodosus*) to reproductive sites of the species during the second half of the flight season, a period where the number of individuals is not expected to increase considerably. Our field experiment which was based on an extensive understanding of the temporal pattern of species emergence and habitat selection of adults demonstrated

the importance of *P. nodosus* in the colonisation process of *C. exul*. By augmenting the number of plant patches, both the number of individuals and the number of reproductive events (including oviposition) increased. Hence, *P. nodosus* is a valuable resource that determines habitat suitability for *C. exul*. As such, the availability of *P. nodosus* patches has crucial consequences on the population dynamics of the species because eggs represent the initial population size. In addition to the increased colonisation rate, this host-plant increases the philopatry of the individuals. Our analysis of capture-mark-recapture data highlighted that the frequency of observation of individuals in the site increases after substrate augmentation, which also plays a considerable role in egg laying in particular and population size in general. An extended version of the field experiment should be performed in the future at a larger scale (different sites) to strengthen our hypothesis that effective restoration of species and populations might be achieved with plant translocation.

Habitat degradation is the main factor of extinction of *Calopteryx exul* subpopulations. Agricultural activity and pollution in the watershed are the main reasons behind the rapid range retraction of the species. The river is the main source of irrigation for agricultural lands of the region (Djabri *et al.*, 2003), and its banks are subject to fragmentation, including enlarging the waterbed, building small dams, and pumping the water near vegetation where *C. exul* larvae and other macroinvertebrates live. Water pollution which is known to be high in the region (Guettaf *et al.*, 2014), is also a factor that may have contributed to the extinction process of *C. exul* in the Seybouse watershed. Finally, the frequent grazing of bank vegetation is a non-negligible source of disturbance that alters the habitat structure and may force individuals to leave the site (Lee Foote & Rice Hornung, 2005). Therefore, there is an urgent need to protect riverbanks by building physical barriers that prevent human and livestock from approaching and fragmenting sites where *C. exul* exists or could exist.

The future of the Seybouse (meta-)population of *Calopteryx exul* is very uncertain. Without a restoration plan, the species will likely disappear after a few years. The first step is to maintain the two last subpopulations and increase the subpopulation size by augmenting the patches of *Potamogeton nodosus*. The second step is to re-introduce the species in areas where it used to exist, taking into account oviposition site availability. The final step is to identify potential habitats for the species (sink subpopulations) where the physico-chemical characteristics of the water are similar to those found in the existing subpopulations and to perform translocations of both final instar larvae and *P. nodosus* patches containing eggs from the source subpopulations (Khelifa *et al.*, 2016b). Final instar larvae should be introduced in order to ensure survival until emergence and potential reproduction because most odonates are philopatric to emergence sites (Utzeri *et al.*, 1984; Corbet, 1999; Dolný *et al.*, 2013). One biological feature of *P. nodosus* that might facilitate its translocation

is that it has a clonal reproductive mode (Spencer & Anderson, 1987), which will not harm the regrowth of the source patch and help the relative expansion of this locally rare plant in the Seybouse watershed.

This study highlights the importance of plants as a valuable resource for odonates, and represents a good example of how to proceed to restore a threatened species by increasing resource availability and promoting colonisation. Our restoration approach can also be applied to many other insect groups that show intimate ecological association with plants. Further studies should investigate the long-term effects of plant translocation at the community level and its effectiveness in maintaining biodiversity and ecosystem functioning.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/icad.12212:

Fig. S1. Study sites in the Seybouse watershed.

Fig. S2. Study sites clustered in 4 km² grids. Grid colours refer to the number of sites. In the legend, values between brackets are sample size of each category.

Fig. S3. Study site where translocation experiment of *Potamogeton nodosus* was conducted. Light blue is the river. The arrow indicates the water flow direction. Rectangles are the study sections (A-H). Natural patches of *Potamogeton* spp are in green, and translocated patches of *Potamogeton nodosus* are in dark blue.

Fig. S4. Timing of the translocation experiment of *Potamogeton nodosus* with respect to the theoretical phenology of *Calopteryx exul*. The phenology is based on Khelifa (2013, 2016). Blue curve refers to emergence, whereas the black curve refers to the adult flight season. The red rectangle indicates the period of translocation experiment. The vertical dashed red line divides this period into pre-management period and post-management period.

Fig. S5. Dual representation of the sum (left *y*-axis) and cumulative sum (right *y*-axis) of the number of marked individuals of *Calopteryx exul* during the study period. The three bars corresponds to the total number of marked individuals during pre-management, post-management, and post-experiment periods respectively. The red line is the cumulative sum, and the dots are daily cumulative numbers of marked individuals. Pink: pre-management period, dark pink: post-experiment period, and brown: post-experiment period.

Table S1. Geographic coordinates, elevation and the number of years sampled of the study sites. Sites in bold are those where *C. exul* was recorded at least once.

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