

Weed management increases the detrimental effect of an invasive parasite on arboreal Darwin's finches

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ABSTRACT

The detrimental effects of invasive parasites on hosts often increase under poor environmental conditions. Both natural fluctuations in environmental conditions and habitat management measures can temporarily cause adverse environmental effects. In this study, we investigated the interaction between the invasive parasitic fly *Philornis downsi*, control of invasive plants and precipitation on the breeding success of Darwin's finches. Introduced plant species have invaded a unique forest on the Galapagos island of Santa Cruz, which is a key habitat for Darwin's finches. The Galapagos National Park Directorate applies manual control and herbicides to combat this invasion. We hypothesized that these measures led to a reduction in the arthropod food supply during chick rearing, which in turn caused mortality in chicks that were already weakened by parasitism. We compared food availability in three study sites of varying degrees of weed management. To assess the interaction of parasitism and weed management, we experimentally reduced *P. downsi* abundance in nests in all three study sites. The key result suggests that there is an increase in the adverse effect of parasitism under unfavourable habitat conditions. As predicted, we found a negative additive effect of parasitism and weed management on the breeding success of the insectivorous warbler finch (*Certhidea olivacea*), but not on the omnivorous small tree finch (*Camarhynchus parvulus*), which was strongly affected by parasitism independently of weed management. Management measures can temporarily decrease environmental quality and reduce resistance/tolerance to invasive species. This should be considered when applying management measures to habitats of vulnerable species.

1. Introduction

Avian parasite invasions are responsible for much of the decline in avian biodiversity (Atkinson and LaPointe, 2009) and are increasing, as a result of an expanding global network of transport pathways (Westphal et al., 2008). In addition, the detrimental effects of parasites on hosts often increase under poor environmental conditions (Delope et al., 1993; Goulson et al., 2015; Lafferty and Kuris, 1999). For example, endemic birds on oceanic islands are especially at risk when they are already weakened by other factors, such as habitat change (Atkinson and LaPointe, 2009; Pimm et al., 2014). In Darwin's finches, which are endemic to the Galapagos Archipelago, such additive effects may be responsible for poor breeding success (Cimadom et al., 2014). Breeding success is adversely affected by invasive weed management

and climatic conditions, but also by the invasive parasitic fly *Philornis downsi* (Cimadom et al., 2014; Dudaniec et al., 2007; Koop et al., 2013a). The larvae of *P. downsi* suck blood from bird nestlings and observational as well as experimental studies have shown that *P. downsi* has a negative impact on nestling growth, nestling haemoglobin levels and fledgling success (e.g. Dudaniec et al., 2006; Fessl et al., 2006; Huber, 2008; Kleindorfer and Dudaniec, 2009; Knutie et al., 2013; Knutie et al., 2016; Koop et al., 2011). *Philornis downsi* is now considered one of the biggest threats to Galapagos landbirds (Causton et al., 2006) and has led to the dramatic decline of several populations of endemic Darwin's finch species (e.g. Cimadom et al., 2014; Dvorak et al., 2012; Dvorak et al., 2017; Fessl et al., 2010; O'Connor et al., 2010). In addition to parasitism, large-scale habitat loss and degradation due to the spread of invasive plant species have a negative impact

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on bird populations, especially in the humid highlands of the Galapagos Islands (Dvorak et al., 2012; Dvorak et al., 2017). The remnant *Scalesia* forest in the highlands of Santa Cruz, dominated by the endemic tree *Scalesia pedunculata*, is the area with the highest density of arboreal Darwin's finches. This forest has been invaded by introduced plant species, especially by blackberry (*Rubus niveus*, Jäger et al., 2017; Rentería and Buddenhagen, 2006). The Galapagos National Park Directorate is using manual control and herbicides to manage blackberry and other invasive species. These management efforts may have a negative impact on the birds' breeding success, as the removal of the entire understory likely reduces the arthropod food supply of insectivorous species. Management measures, such as herbicides, have been shown to indirectly affect both arthropods and birds in different agricultural systems (e.g. Boatman et al., 2004; Chiverton and Sotherton, 1991; Giuliano et al., 2018; Moreby and Southway, 1999; Morris et al., 2005). Beside habitat degradation, climatic conditions during breeding can influence breeding outcome. Although rainfall triggers an increase in food abundance for Darwin's finches and thus has a positive effect on breeding activity in general (Grant, 1999; Hau et al., 2004), intensive rainfall during the nestling period might negatively affect parents' feeding rates, as shown e.g. in great tits (Radford et al., 2001). Additionally, rainy periods can lead to higher energetic demands of nestling as nests get wet and cold (Heenan, 2013). The correlational study of Cimadom et al. (2014) suggested that there is a detrimental effect of *P. downsi* which increases under harsh environmental conditions. The authors hypothesized that invasive plant management and high precipitation during the nestling period negatively affected food supply and/or increased energetic needs during chick rearing, which in turn caused mortality in chicks that had already been weakened by parasitism.

In the present study, we experimentally tested whether the interaction of two external stress factors (the parasite *P. downsi* and weed control measures) and a natural stressor (intensive rainfall during nesting) have a supplemental negative effect on the breeding success. We compared breeding success in experimentally parasite-reduced nests with untreated nests in areas of different weed management regimes (not controlled, recently controlled and long-term management), and related the results to daily precipitation data. This allowed us to test how these factors and possible interactions between them contribute to the nesting failure of two closely related Darwin's finch species, the warbler finch and small tree finch (*Camarhynchus parvulus*).

Both study species differ in body mass, parasite load and diet, but do not differ in clutch size (Cimadom et al., 2014). These factors can influence the impact of parasitism and habitat change on breeding success. In general, *P. downsi* abundance varies among host species, with larger-bodied hosts and larger nests experiencing higher parasite numbers (Dudaniec et al., 2007). Nests of the smaller warbler finch on average contain fewer parasites than nests of the larger small tree finch (Cimadom et al., 2014). While there is no clear correlation between parasite intensity and in-nest mortality between species (reviewed in Kleindorfer and Dudaniec, 2016), *P. downsi* abundance per chick decreases with increasing brood size, an indication of a parasite dilution effect (Dudaniec et al., 2007). Diet niche breadth, on the other hand, can influence how birds can cope with habitat change. Generalists should be better at coping with changing environments than specialists as they can switch more easily to alternative food sources (e.g. Begon et al., 2014). In our study we compared two arboreal finch species that differed in diet niche breadth. Warbler finches are mainly insectivorous (arthropods are consumed in 96% of observed foraging events), while small tree finches also forage on fruits and seeds (66% of observed foraging events, Filek et al., 2018). Both species forage mainly in the canopy, but warbler finches use the understory to a larger extent than the small tree finches (37% versus 28%, Filek et al., 2018).

We hypothesized that total arthropod biomass (food availability) would be lower in areas where blackberry had recently been controlled and that the insectivorous warbler finch would be more affected than

the small tree finch by this removal of the understory as it is highly dependent on arthropod food. Furthermore, we predicted that the breeding success of both species would increase when parasite abundance in nests was experimentally reduced. In addition, we expected a stronger interaction of weed management and *P. downsi* parasitism in the warbler finch than in the small tree finch. Hence, we hypothesized that the lowest levels of breeding success would be in the parasitized warbler finch nests in recently controlled areas. Finally, we predicted that precipitation during nesting would enhance the negative effects of weed management and *P. downsi* parasitism, as it poses an additional stressor.

2. Material and methods

2.1. Study site and weed management

The study was conducted at the “Los Gemelos” site in the humid highland of Santa Cruz Island, Galapagos (S 00°37'20"–45" W 90°23'00"–15", 500–600 m a.s.l.) during the breeding season from January–March 2012 (data also included in Cimadom et al., 2014), January–April 2014, January–May 2015, January–April 2016 and January–April 2017. The study site comprises one of the last remnants of native *Scalesia pedunculata* forest of ca. 100 ha on Santa Cruz (Mauchamp and Atkinson, 2011). The forest has been invaded by several introduced plant species, such as *Rubus niveus* (blackberry), *Cestrum auriculatum* (sauco) and *Tradescantia fluminensis* (Jäger et al., 2017). *Rubus niveus* is now dominant or co-dominant throughout the forest's understory (Jäger et al., 2017; Rentería et al., 2012). To preserve these last *Scalesia* remnants, the Galapagos National Park Directorate (GNPD) controls *R. niveus* by cutting down the adult plants with machetes and subsequently applying a herbicide mixture of Glyphosate and COMBO® (Picloram and Metsulfuron-Methyl) on the regrowth. These large-scale control measures lead to the removal of almost the entire understory. Within the forest, we defined three study areas that differed in the degree and timing of the management of invasive plants: (1) the invaded area (8 ha) that was heavily invaded by *R. niveus* but had never been exposed to any control measures; (2) the C12-area (9.7 ha), where *R. niveus* had been manually and chemically controlled since 2012 by the GNPD, and (3) the C15-area (6.8 ha), where *R. niveus* had been controlled since August 2014 by the GNPD (see Fig. S1). As the intensity of invasive plant management changed over time and natural succession took place as a result of the initial removal of the understory, we additionally defined three management stages: (1) not controlled (NC): never controlled and heavily invaded by *R. niveus*, (2) recently controlled (RC): less than two years after initial intense control measures, (3) long-term management (LTM): more than two years after the initial intense control measures. Table S1 gives an overview of the management stages in the three different study areas from 2012 to 2017. To access the study areas in the not controlled management stage, a 50 × 50 m grid trail system was cut into the dense invaded understory vegetation by rangers from the GNPD.

2.2. Sampling of arthropod biomass

Small tree finches and warbler finches mainly forage in the canopy, understory and in the moss growing on tree trunks (Filek et al., 2018) and we sampled arthropod biomass in each of these micro habitats. Canopy samples were taken by branch clipping (adapted from Johnson, 2000, see supplementary material for details). Arthropods within the moss were collected from the same trees as the corresponding canopy samples (see supplementary material for details). To sample the understory, 5 m long transects with a buffer of 1 m width in each direction amounting to an area of 10 m² were visually searched for 15 min by one person. Arthropods encountered on vegetation up to 1.7 m above the ground were collected either by hand or with an aspirator and stored in 70% alcohol. Flying insects could not be recorded by this method.

Standard methods to sample insects from understory vegetation (e.g. using a sweep net) could not be used, as the understory vegetation in our study area was invaded by spiny *R. niveus*. A canopy, understory and moss sample were collected in ten randomly selected sampling points in each of the three study areas (invaded, C12 and C15) in February and April of 2015, 2016 and 2017. In total 540 samples were taken.

All collected arthropods were identified to the order level and their body length was measured (accuracy: ± 0.5 mm). Additionally, the dry weight (dried for 72 h at ca. 60 °C in a drying chamber) was measured for a subset of specimens of each order. Only Lepidoptera, Coleoptera, Orthoptera, Hymenoptera, Hemiptera, Diptera and Arachnida were used in the analysis because they were recorded as food source for both focal bird species (Filek et al., 2018). Separate regression functions were then calculated to describe the length-weight relationships of individual taxonomic groups. Following recommendations by Ganihar (1997), a power function for Coleoptera, Orthoptera, Formicidae, Hymenoptera (except Formicidae), Diptera and Arachnida, and an exponential function for Lepidoptera (larvae) and Hemiptera were used (see Table S2). Subsequently, the fitted functions were used to calculate the dry weight for all sampled specimens of the relevant orders. To standardize the arthropod biomass per sampled canopy or moss plant material, total arthropod biomass per sample was divided by the dry mass of the corresponding sampled plant material (mg arthropods/plant material). As it was not feasible to collect the understory vegetation, understory samples were not standardised for quantity of sampled vegetation.

2.3. Nest monitoring and experimental manipulation of parasite abundance

We monitored the nests of both Darwin's finch species in all three study areas, except for 2012, when we only investigated the invaded and C12-area (sample size overview see Table S3). Nest monitoring followed exactly the procedure described in Cimadam et al. (2014). To quantify the effect of *P. downsi* on breeding success, we experimentally reduced *P. downsi* abundance in nests. Small tree finch nests were treated with 10 ml of a 1% permethrin solution (Permethrin™ II). Because pre-trials revealed that warbler finches tended to give up nests treated with Permethrin™ II, 5 ml of a 0.5% permethrin solution of Permacap CS was used instead for the smaller warbler finch nests. Permacap CS contains micro-encapsulated permethrin, which allows a slower but constant release of the insecticide and has a less intense smell than Permethrin™ II (from a human perspective). We decided not to change the product midway for the small tree finch as both products effectively reduced parasite numbers in nests (see results Section 3.2). Nests were treated only once within 3 days before or after the chicks hatched. Nests were often impossible to reach directly so the insecticide was injected from the outside into the bottom layer of the nests without removing eggs or chicks. To reach nests in up to 7–8 m height, a 5 ml syringe was placed at the end of a 3 m fishing pole into which a second slightly thinner pole was inserted to push the plunger of the syringe. Parents usually quickly returned to the nest after this treatment. Nests which were abandoned within one day of treatment and for which treatment could not be excluded as the cause of abandonment, were not considered in our analysis.

After breeding failure or successful fledging, all monitored nests were collected in separate sealed plastic bags and dismantled in the laboratory on the same day in order to count *P. downsi* larvae, pupae and empty puparia. Parasite abundance per nest was defined as the total number of *P. downsi* individuals per nest. As the number of *P. downsi* can only be counted by destroying the nest, parasite abundance was assigned to the age of the chicks at the time breeding activity terminated. Additionally, the date of the start of incubation, the hatching date of first chick, age of oldest chick at termination of breeding activity and nest height were recorded for each nest (for details see Cimadam et al., 2014). Because the onset of the breeding

seasons differed between years and bird species, we standardised the start of incubation for each nest by setting each nest in relation to breeding attempts from the first to the last recorded nest for each of the two bird species in each year separately: standardised start of incubation = $(DIS - \min DIS) / (\max DIS - \min DIS)$, where DIS is the date of incubation start for a given nest, minDis is the earliest recorded date of incubation start and maxDis is the latest recorded date of incubation start for each species in each year (values span between 0 and 1).

2.4. Precipitation data

Data on daily precipitation was provided by the nearest weather station (operated by Rolf Sievers, S 0°39'57.49" W 90°22'35.04") located about 4.5 km south and 150–200 m lower than the study site Los Gemelos. Precipitation data were available over the entire study period except for January 2017.

2.5. Statistical analysis

2.5.1. Arthropod biomass

To investigate the effect of weed management on arthropod biomass in the canopy, understory and moss layers, separate linear mixed models (LMM) were calculated. To obtain normally distributed data and because there were some samples without arthropods that yielded a biomass value of zero, a $\log(x + 1)$ transformation of the arthropod biomass was performed. Weed management (not controlled, recently controlled, long-term management) and year were taken as fixed effects and individual sampling point were nested in the three study areas (invaded, C12, C15) as random effects (random intercept). p-Values were obtained by likelihood ratio tests of the full model with the effect in question (weed management) against the model without the effect in question. Tests for spatial autocorrelation of arthropod biomass (e.g. caused by edge effects) within the three plots using Moran's I did not indicate any significant effects for understory, moss and canopy samples for any of the sampling rounds (p values calculated for 10 bins all > 0.10). Hence, the spatial setting of our sampling sites within the three study plots was not further considered in the calculated LMMs.

2.5.2. *Philornis downsi* abundance

Effects of host species, age of chicks at failure or fledging, year, standardised start of incubation and weed management (not controlled, recently controlled, long-term management) on parasite abundance (number of *P. downsi* individuals per nest) were evaluated using a generalized linear mixed model (GLMM) with a negative-binomial error structure (because of overdispersion) and area (invaded, C12, C15) as random effect (random intercept). For this analysis, only non-treated nests with chicks were used ($N = 513$). We are aware that brood size is a relevant factor, as *P. downsi* abundance per chick decreases with increasing brood size, an indication of a parasite dilution effect (Dudaniec et al., 2007). However, there was no indication that clutch size differed between the two species (warbler finch: 2.28 ± 0.62 , mean \pm SD, $N = 113$; small tree finch: 2.38 ± 0.76 , $N = 78$; Mann-Whitney test: $U = 4798.5$, $p = 0.25$). To test whether the permethrin treatment was successful in reducing *P. downsi* numbers, GLMs with quasi-Poisson error structure and treatment (yes/no) and year as fixed factors were calculated for the small tree finch ($N = 186$) and the warbler finch ($N = 155$) separately. Significance of individual model terms was tested with Type II tests using the Anova procedure in the car package (Fox and Weisberg, 2011). Model's predicted values for each set of observed values of the independent variables were used for graphical representation.

2.5.3. Breeding success

We performed χ^2 -tests to compare the breeding success (defined as nests which produced at least one fledgling) between the two bird species and between years. To test which factors influenced the

breeding success (yes/no) of each of the two target species, we constructed a set of GLMMs (binomial family and logit link function) with area (invaded, C12, C15) as random effect (random intercept) and compared them using a model selection approach based on Akaike's information criterion (AIC, Burnham and Anderson, 2002). In a first analysis, we considered only non-treated nests, which allowed us to also include nests which had failed during incubation. Over all five breeding seasons parasite prevalence in nests that failed during incubation ranged from 0% to 80% and in nests with chicks from 83% to 100%. For this first general analysis of breeding success, we used management stage, median daily precipitation during nesting (from the start of incubation to nesting failure or success), standardised start of incubation and year and the interaction of management and median precipitation as fixed effects. Data for all factors were available for 337 warbler finch nests and 277 small tree finch nests. For the second analysis, we were explicitly interested in the impact of *P. downsi* parasitism and its interaction with management stage and precipitation. Thus, we reduced the sample size to only nests with chicks. Only data from years in which nests were treated with permethrin were entered into the analysis (small tree finch 2015–2017, $n = 186$ nests; warbler finch 2016–2017, $n = 151$ nests). We used management stage, median daily precipitation during the nestling period (from hatching day to nest failure or success), treatment (yes/no), standardised start of incubation, year and the interaction terms treatment \times management and treatment \times median precipitation as fixed effects. For each of the GLMM analyses, a set of models containing no factors (null model), single factors or all possible combinations of factors were developed. All models within a set were ranked according to their AIC with adjustment for small sample size (AICc). AICc differences compared to the top ranked model (Δ AICc) and Akaike weights (ω) are reported for each model to evaluate the strength of evidence for each model compared to the set of respective candidate models (Table S4). To account for model selection uncertainty, we averaged across all models with a Δ AICc ≤ 4.0 from the top model (Richards et al., 2011; Symonds and Moussalli, 2011) in order to get model-averaged estimates with shrinkage (full average), standard errors and 95% confidence intervals for each factor (Burnham and Anderson, 2002). This method of multimodel inference enables one to use the entire set of candidate models to judge the importance of a parameter, rather than basing conclusions on a single best-fit model (Burnham and Anderson, 2004). Model-averaged predicted values for each set of observed values of the independent variables were used for graphical presentation.

All statistical analyses were performed in the program RStudio (2018), version 3.4.2 (R Core Team, 2017) using the packages lme4 (Bates et al., 2015) and MuMin.

3. Results

3.1. Biomass

Arthropod biomass was lower in the recently controlled management stage compared to the not controlled and long-term management stages in the understory ($\chi^2 = 7.00$, $df = 2$, $p = 0.03$, Fig. 1A) as well as in the moss layer ($\chi^2 = 7.34$, $df = 2$, $p = 0.03$, Fig. 1B). A similar pattern was detected for canopy arthropod biomass, but the differences were not significant ($\chi^2 = 4.39$, $df = 2$, $p = 0.11$, Fig. 1C).

3.2. *Philornis downsi* abundance

Small tree finch nests contained a higher parasite load than warbler finch nests in all years ($\chi^2 = 72.1$, $df = 1$, $p < 0.001$, Fig. 2). Furthermore, *P. downsi* numbers in nests increased with chick age ($\chi^2 = 97.2$, $df = 1$, $p < 0.001$, Fig. 2) and nests later in the breeding season showed higher parasite loads than earlier nests ($\chi^2 = 4.5$, $df = 1$, $p = 0.034$). There was no significant difference in *P. downsi* abundance between the three different management stages ($\chi^2 = 0.4$, $df = 2$, $p = 0.805$).

Lastly, *P. downsi* abundance differed between years ($\chi^2 = 13.6$, $df = 4$, $p = 0.009$), with the lowest numbers in 2017.

The experimental treatment of nests with permethrin was effective at reducing *P. downsi* abundance. In both Darwin's finch species, the respective GLMs indicate that treated nests had fewer parasites than untreated nests (small tree finch: *P. downsi*/nest (mean \pm SE), treated 9.2 ± 2.0 , untreated 35.2 ± 2.3 , estimate (\pm SE) = -1.32 ± 0.20 , $p < 0.001$; warbler finch: *P. downsi*/nest (mean \pm SE), treated 6.5 ± 1.7 , untreated 19.8 ± 1.7 , estimate (\pm SE) = -1.11 ± 0.25 , $p < 0.001$), with year heaving no discernible effect (small tree finch: $\chi^2 = 2.6$, $df = 2$, $p = 0.268$; warbler finch: $\chi^2 = 2.7$, $df = 1$, $p = 0.103$).

3.3. Breeding success

Breeding success of the warbler finch and small tree finch varied substantially across years (warbler finch: 16–67% success, χ^2 -test: $\chi^2 = 50.3$, $p < 0.001$; small tree finch: 7–32% success, χ^2 -test: $\chi^2 = 18.2$, $p = 0.001$) and overall was higher in the warbler finch than in the small tree finch (χ^2 -test: $\chi^2 = 36.70$, $p < 0.001$). The results of the model selection exploring the relative importance of fixed factors on the breeding success of the warbler finch and the small tree finch are shown in Fig. 3 and in Tables S4 and S5. For the general analysis of the breeding success in both species all top models included the effect of year and start of incubation (selection probability = 1.0). Breeding success differed between years (for details see Table S5) and decreased over the breeding season (GLMM, warbler finch: $b \pm SE = -1.19 \pm 0.27$, -1.72 to -0.65 95%CI; small tree finch: $b \pm SE = -1.31 \pm 0.39$, -2.08 to -0.54 ; see Fig. 4). In the warbler finch model, median precipitation during nesting showed strong support (selection probability = 1.0) and negatively correlated with breeding success (GLMM, $b \pm SE = -2.52 \pm 1.03$, -4.55 to -0.50), whereas in the small tree finch model median precipitation received relatively weak support (selection probability = 0.38). Similarly, management was an important factor affecting the breeding success in the warbler finch (selection probability = 0.92) but not in the small tree finch (selection probability = 0.15). Warbler finch nests in recently controlled areas had a lower probability of succeeding than nests in not controlled (GLMM, NC vs. RC: $b \pm SE = -1.00 \pm 0.51$, -1.93 to -0.25 95%CI) or long-term managed areas (GLMM, RC vs. LTM: $b \pm SE = 1.01 \pm 0.59$, 0.08 – 2.14 95%CI). Nest height and the interaction management \times precipitation were weakly supported in the general breeding success models of both the warbler finch (nest height: selection probability = 0.29; management \times precipitation: selection probability = 0.32) and small tree finch (nest height: selection probability = 0.53, management \times precipitation: not included in the top models).

The analysis, including the effect of parasitism (nest treatment with insecticide), showed similar results for the factors included in the previous models (Fig. 3B, Table S4 and S5). The additional factor, insecticide treatment, was more strongly supported in both species' models (small tree finch: selection probability = 1.0, warbler finch: selection probability = 0.85). Treated small tree finch nests had a much higher probability of succeeding than non-treated nests irrespective of management (GLMM, non-treated vs. treated: $b \pm SE = 2.09 \pm 0.38$, 1.34 – 2.84 95%CI; Fig. 5A). In the small tree finch model, the interaction term management \times treatment received no support in the top set of models. In the warbler finch, this positive effect of treatment seemed to be present only in the recently controlled management stage (Fig. 5B, Table S5), indicated by the interaction management \times treatment (although with low selection probability = 0.21) and the 95% CI of the respective interaction barely crossing zero (Fig. 3B, Table S5). In both species, the interaction term precipitation \times treatment was only weakly supported (warbler finch: selection probability = 0.15; small tree finch: selection probability = 0.07).

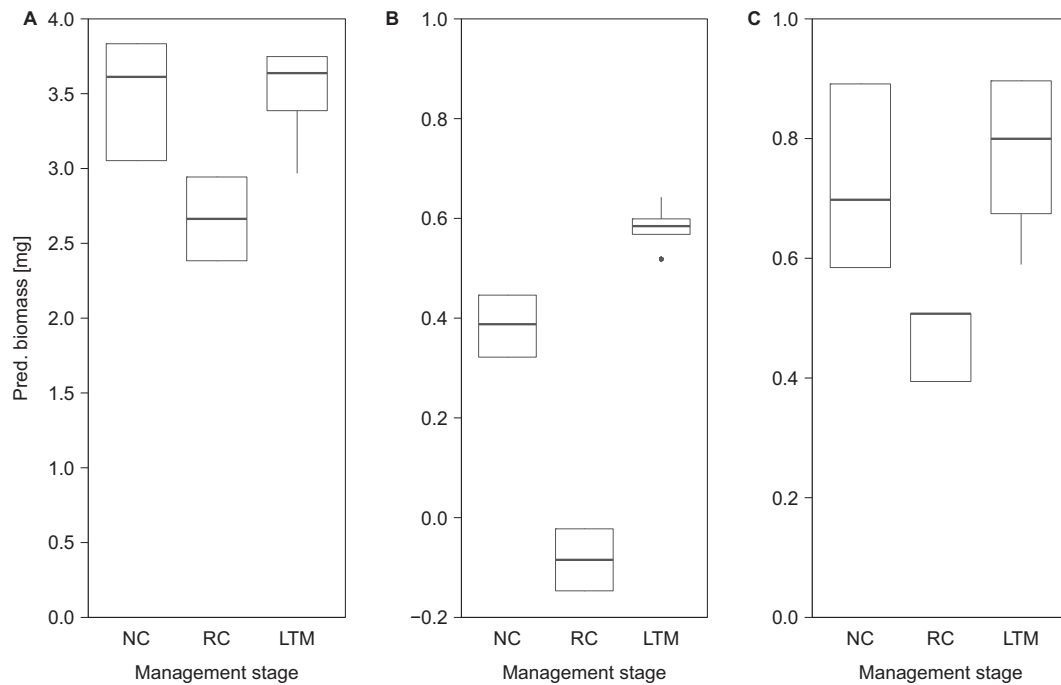


Fig. 1. Predicted arthropod biomass in the three different management stages (NC: not controlled, RC: recently controlled, LTM: long-term management) quantified separately for (A) understory, (B) moss and (C) canopy samples. Arthropod biomass values were $\log(x + 1)$ transformed. Values represent model averaged predicted values for each set of observed values of the independent variables. Boundaries of the boxes represent 1st and 3rd quartile, black line within the boxes marks the median and whiskers extend from the median to the largest and lowest value within 1.5*IQR (inter quartile range).

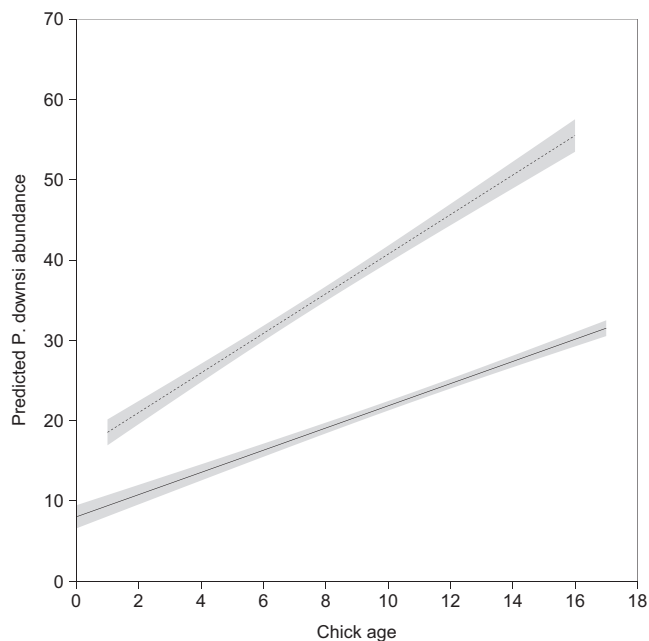


Fig. 2. Predicted *Philornis downsi* abundance (\pm 95% CI) in warbler finch nests (solid line) and small tree finch nests (dashed line). Fitted lines indicate model's predicted values for each set of observed values of the independent variables.

4. Discussion

The results of our study suggest that there is an increase in the adverse effect of *P. downsi* under unfavourable habitat conditions. This is in line with several studies of different taxa, which have shown that the detrimental effect of parasites increases under poor environmental conditions (e.g. Gehring and Whitham, 1992; Goulson et al., 2015; Hoi-Leitner et al., 2001; Lafferty and Kuris, 1999). In our study the poor

environmental conditions are caused by habitat change due to weed management, leading to a reduction in arthropod biomass. Such changes are expected to affect the specialist insectivorous species more than the generalist feeder (e.g. Begon et al., 2014). As predicted, we found a negative additive effect of parasitism and weed management on the breeding success of the insectivorous warbler finch, but not on the omnivorous small tree finch, which was strongly affected by *P. downsi* regardless of management treatment. These results suggest that food availability is limiting the breeding success of the insectivorous species and that parasitism is the main cause for breeding failure in the omnivorous species. Management measures might temporarily decrease environmental quality (e.g. food availability) and so reduce resistance/tolerance to invasive species.

Although weed management led to a reduction of total arthropod biomass it did not influence the abundance of *P. downsi* larvae in nests. This result can be interpreted in two ways: either adult flies live mainly in the canopy (Kleindorfer and Dudaniec, 2016) and are therefore less affected by weed management, or adult fly numbers do not strongly affect larval abundance. Currently we lack knowledge about the microhabitat use of adult flies and more studies about the biology of *P. downsi* are needed. A study by Causton et al. (unpublished) found no relationship between catch rates of adult *P. downsi* females and parasite abundance in nests of the warbler finch and the small tree finch.

4.1. Interaction between parasitism and weed management

In the case of the warbler finch, we found the expected interaction between parasitism and weed management. In the recently controlled area where arthropod biomass was low, breeding success only increased when the parasite load was reduced. To our knowledge, this is the first study on Darwin's finches that shows an interaction between parasitism and habitat quality, suggesting that there is an additive negative effect. However, our study also shows that the warbler finch can tolerate parasitism under favourable habitat conditions: in areas with high arthropod abundance (not controlled and long-term managed area),

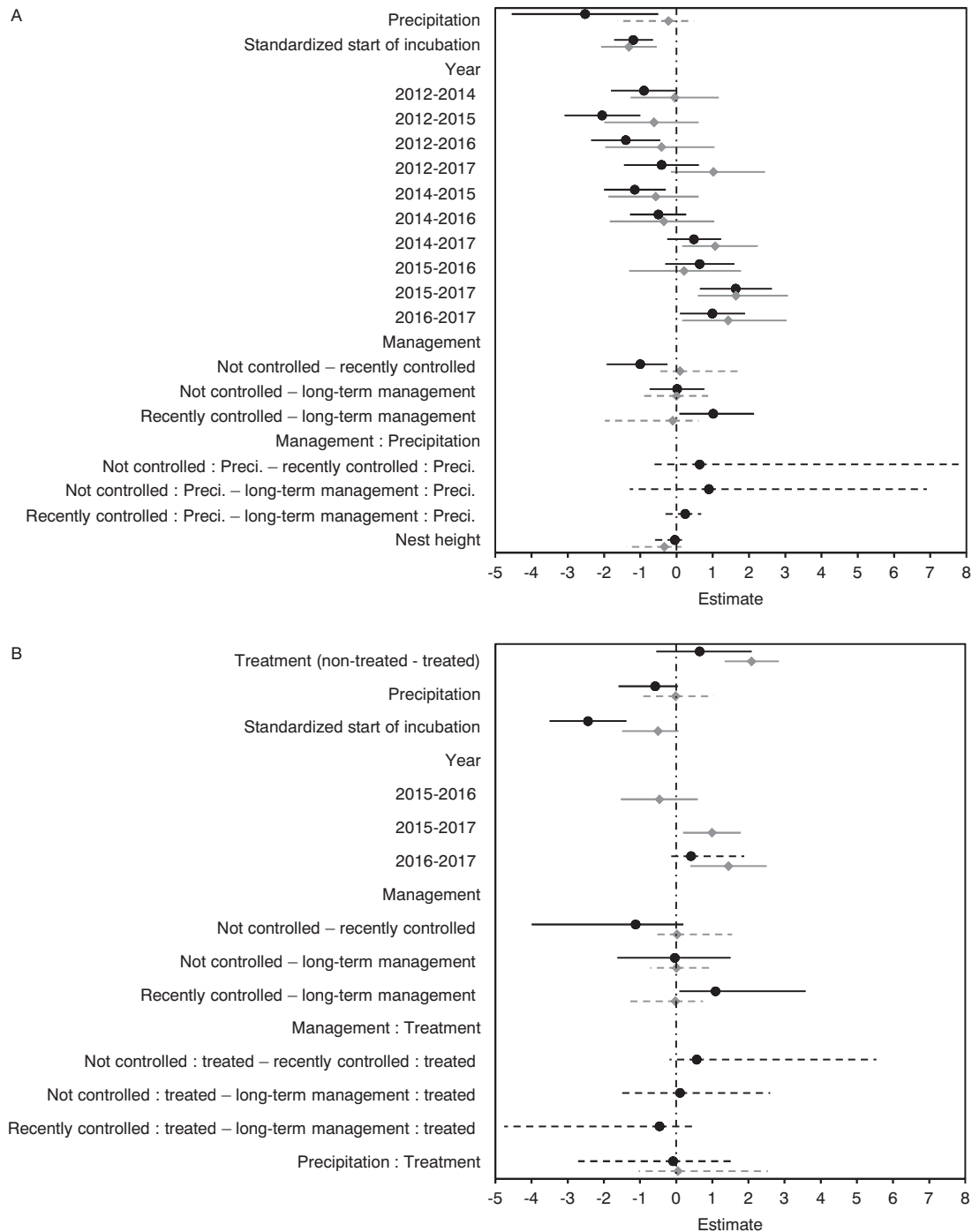


Fig. 3. Outcomes from model averaging procedure (A) of the first general analysis including only non-treated nests and (B) of the second analysis including treated and non-treated nests with chicks investigating the breeding success of the warbler finch (in black) and the small tree finch (in grey) using a subset of models with $\Delta AICc < 4.0$ (see Table S4 and Table S5). Estimates (95% CI) of each factor included in the models' subset are shown. Solid lines indicate relative variable importance of ≥ 0.5 , dashed lines indicate relative variable importance of < 0.5 .

breeding success was high, irrespective of parasite load and the reduction of parasite abundance had no enhancing effects. This contrasts with previous studies on Darwin's ground finches in the lowlands of Santa Cruz and Floreana showing an increase in breeding success when *P. downsi* burdens were experimentally reduced (Fessl et al., 2006; Knutie et al., 2014; Knutie et al., 2016; Koop et al., 2013b; Koop et al., 2011; O'Connor et al., 2014, but see Koop et al., 2013a). A study that can disentangle effects of habitat quality and parasitism in Darwin's ground finches would be needed to interpret this difference. To date, the only resilient species that has a high breeding success despite high

P. downsi loads is the Galapagos mockingbird (*Mimus parvulus*). In parasitized nests mockingbirds increase parental food provisioning rates, a behaviour that is induced by higher hatchling begging rates (Knutie et al., 2016). Whether a similar mechanism operates in the warbler finch needs to be investigated. Closely related medium ground finches and small tree finches did not show increased begging or parental food provisioning in response to higher parasite loads (Knutie et al., 2016; O'Connor et al., 2014; Heyer et al. unpublished).

In contrast to the warbler finch, we found no interaction between parasitism and weed management in the small tree finch. In parasitized

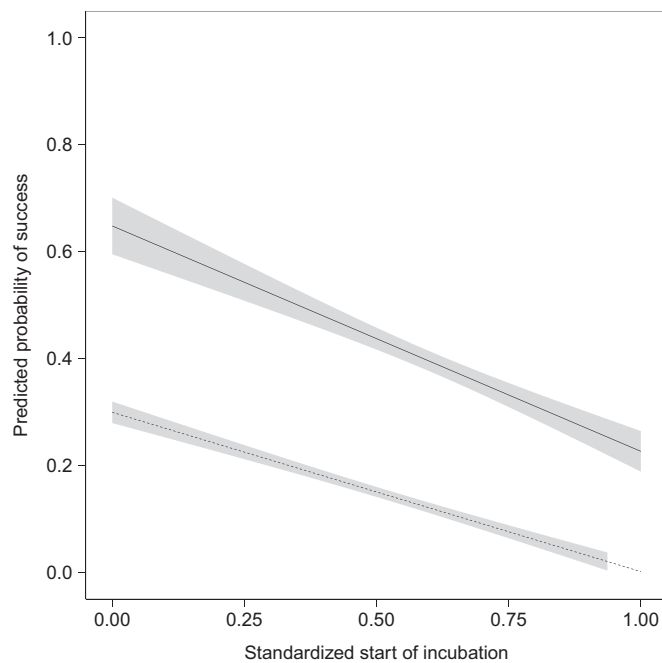


Fig. 4. Predicted probability (\pm 95% CI) of breeding success depending on standardised day of incubation start for the warbler finch (solid line) and the small tree finch (dashed line). Fitted lines indicate model averaged predicted values for each set of observed values of the independent variables.

nest, breeding success was extremely low in all three management stages. However, parasite reduction led to a considerable increase in breeding success, independent of weed management, comparable to that of the warbler finch (treated and non-treated nests) in good food conditions (NC and LTM). For the small tree finch, parasitism seems to be the main factor limiting breeding success. This raises the question as to why the small tree finch is more affected by *P. downsi* parasitism than the warbler finch.

4.2. Difference in host vulnerability

While we have already shown in a previous study that small tree finch nests contained higher *P. downsi* numbers than warbler finch nests, probably due to the former's larger body and nest sizes (Cimadam et al., 2014), the experimental approach of this study also indicates that this species is more vulnerable to the parasites. Host vulnerability may depend on parasite load in relation to host body mass and clutch size, expressed as the measure of parasite density, defined as the number of parasites per chick gram (Bush et al., 1997; Knutie et al., 2016). As both species have similar clutch sizes, the larger body size of small tree finch chicks should still make them more tolerant to higher parasite loads. However, while small tree finch chicks are approximately one third heavier than warbler finch chicks (Dudaniec et al., 2007), our analysis showed that an average small tree finch nest experienced approximately double the *P. downsi* load (GLMM, coefficient small tree finch vs. warbler finch = 1.96). This suggests parasite load per gram chick to be approximately 50% higher in small tree finch nests compared to warbler finch nests.

In addition to higher parasite abundance, the timing of infestation could also provide an explanation for the observed higher vulnerability of the small tree finch to parasitism. Long-term data showed that in recent years, *P. downsi* flies are attacking Darwin's finch nests earlier in the breeding cycle (Cimadam et al., 2016; Kleindorfer et al., 2014). Small tree finches might be more strongly affected by the early infestation of *P. downsi* and small tree finch nests do show higher parasite loads immediately after hatching compared to warbler finch nests (Cimadam et al., 2014). The presence of more and larger *P. downsi*

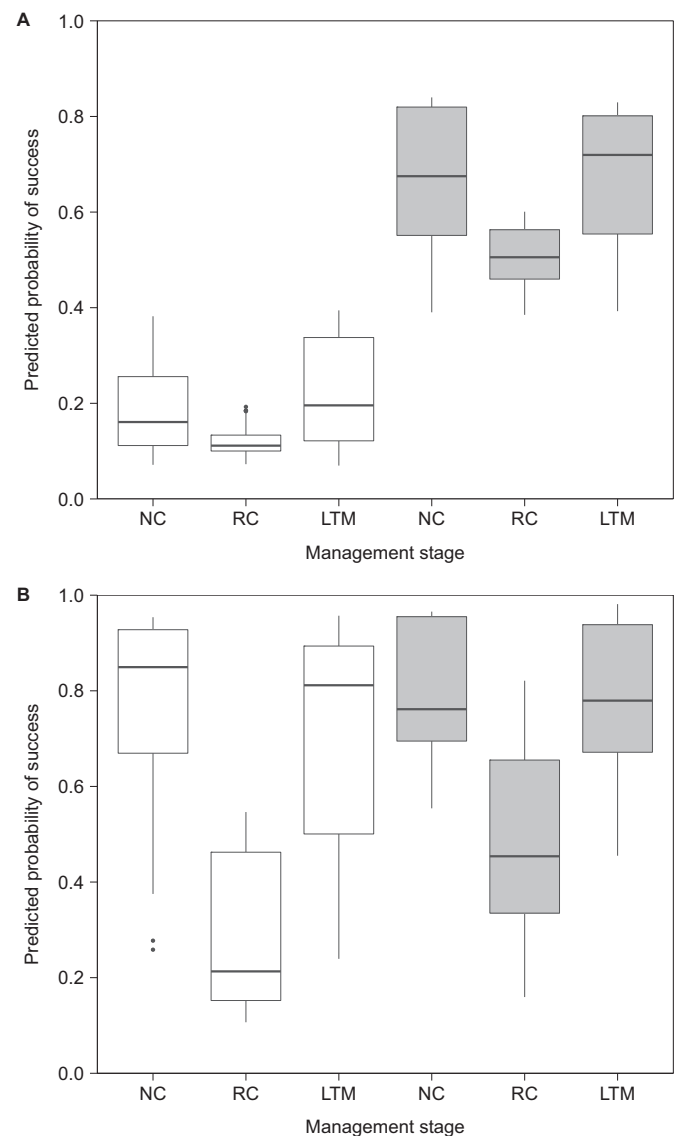


Fig. 5. Predicted probability of breeding success in un-treated (white) and treated (grey) small tree finch nests (A) and warbler finch nests (B) in the three different management stages (NC: not controlled, RC: recently controlled, LTM: long-term management). Values represent model averaged predicted values for each set of observed values of the independent variables. Boundaries of the boxes represent 1st and 3rd quartile, black line within the boxes marks the median and whiskers extend from the median to the largest and lowest value within 1.5*IQR (inter quartile range). Raw-data (percentage of successful nests) are shown in Fig. S2 (Supplementary material).

larvae in the very early nesting stages can lead to higher parasite virulence and further reduction in the breeding success, as young chicks are more vulnerable to parasites (Kleindorfer and Dudaniec, 2016).

4.3. Influence of precipitation

Contrary to our hypothesis, we found no evidence that precipitation during nesting increased the negative impact of weed management or *P. downsi* parasitism in either species. We did find a strong negative effect of precipitation during nesting – independent of weed management and parasite load – on warbler finch nests but not on small tree finch nests. The variation in the impact of precipitation on reproductive success may be explained by the large annual variation of total precipitation during the breeding season, ranging from 1174 mm in 2012 to only 457 mm in 2016. Also the frequency of heavy rain days (> 10 mm of

precipitation) varied between 4% in 2014 and 24% in 2012. The difference in breeding success between years may be partly explained by the variation in annual precipitation, as food abundance is lower in dry years (Grant, 1999). However, during intensive rainfalls parental food provisioning in small tree finches is reduced, which provides an explanation for the varying influence of rain on the breeding success (Heyer et al. unpublished). A similar study on the impact of rain on parental food provisioning in the warbler finch is still needed.

Precipitation may also influence *P. downsi* abundance but empirical results are contradictory. While Dudaniec et al. (2007) found the highest *P. downsi* abundance in nests in the years with the highest annual rainfall, Koop et al. (2013a) found no indication that *P. downsi* abundance was lower in a dry year compared to a wet year. These conflicting results may be explained by the fact that the relationship between precipitation and the abundance of *P. downsi* is affected by several factors, such as host availability and the timespan between breeding seasons which is triggered by precipitation patterns (Grant, 1999). For example, we recorded an extended dry period from March 2016 to January 2017 with non-existent or negligible bird breeding activity that resulted in a low *P. downsi* population at the onset of the 2017 breeding season, possibly as a consequence of there being no or few suitable hosts available for a prolonged period.

4.4. Variation of breeding success within breeding season

Apart from the year-to-year variation in breeding success, we also found variation within the breeding season. In both species, breeding success decreased later in the breeding season. Apart from the potential quality differences between early and late breeders, seasonal decline in reproductive success has been shown to be caused by seasonal environmental variation (reviewed in Verhulst et al., 1995). In closely related Darwin's ground finches, breeding activity is synchronized with rain events (Hau et al., 2004), as food abundance typically increases after the onset of rainfall (Grant and Grant, 1989). There may be a decrease in food abundance at the end of the breeding season as a result of dryer conditions. Furthermore, we found that *P. downsi* abundance increased over the breeding season, which could further exacerbate sub-optimal breeding conditions later in the season. Delope et al. (1993) found that breeding success in the house martin (*Delichon urbica*) was more affected by the presence of ectoparasites later in the breeding season, when environmental conditions for reproduction were suboptimal.

4.5. Conclusion

This and other studies have found an interaction between parasitism and poor environmental conditions (e.g. Gehring and Whitham, 1992; Goulson et al., 2015; Hoi-Leitner et al., 2001; Lafferty and Kuris, 1999). Ebert and Bull (2008) proposed that the negative effects of parasitism do not only depend on the traits of the parasite but also on the vulnerability of the host. Vulnerability depends on fixed host traits (e.g. body mass, nest size) but also on behavioural and physiological mechanisms that allow increased resistance or the ability to compensate for the detrimental effect of the parasite (e.g. tolerance, reviewed in Tschirren et al., 2009). The ability to compensate, for instance through increased feeding rates, can depend on ecological conditions, which can vary over time. Management measures, such as manual and chemical control, can temporarily decrease the quality of the environment and/or induce stress and reduce resistance/tolerance to invasive species. Management agencies need to take this into account, especially when applying management measures to the habitats of vulnerable species.

4.6. Implications for management strategies for the *Scalesia* forest

Our study has shown that intense invasive plant management, including the removal of nearly the entire understory and subsequent

large-scale application of herbicides, leads to a reduction in arthropod biomass and consequently to a reduction in the breeding success of some bird species, especially insectivorous species such as the warbler finch. However, only two years after the initial control measures, which were followed up by continuous applications of localized herbicide combined with the manual removal of invasive species' regrowth, arthropod biomass and the breeding success of the warbler finch returned to levels comparable to areas which were not controlled. Importantly, invasive plant management carried out in the *Scalesia* forest can be considered successful, as there were extremely high numbers of *Scalesia pedunculata* seedlings observed in controlled but not in not-controlled areas (Jäger et al., 2017). Consequently, although short-term negative effects were observed on some bird species and on arthropod biomass after initial control was carried out, we think that it is necessary to continue this management of invasive plant species, as it seems to be the only feasible course of action at this point to help the preservation of the last remnants of the *Scalesia* forest on Santa Cruz Island. We would suggest however that invasive species management should be conducted sequentially on a smaller scale in order to preserve sufficient suitable breeding habitat and so minimise the detrimental effect on breeding birds.

Declaration of interest statement

The authors declare that no competing interests exist.

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Appendix A. Supplementary material

Supplementary material to this article can be found online at <https://doi.org/10.1016/j.biocon.2019.02.025>.

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