

RESEARCH ARTICLE

Behavioural responses by a bumble bee to competition with a niche-constructing congener

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Abstract

1. While feeding, foragers can alter their environment. Such alteration constitutes ecological niche construction (ENC) if it enables future benefits for the constructor and conspecific individuals. The environmental modification may also affect non-constructing, bystander species, especially if they share resources with constructor species. If so, ENC could confer the constructor species a competitive advantage by both enhancing its foraging returns and reducing those of bystander species.
2. Expectations – (E1) ENC frequency should vary positively with the recent and current density of the constructor species, and (E2) constructors should use modifications disproportionately. In contrast, bystanders should (E3) experience intensified competition for the affected resource, and (E4) exhibit diverse, possibly mitigating, responses to ENC, depending on opportunity and relative benefits.
3. We investigated these expectations in Argentina for competition for *Fuchsia magellanica* nectar between an invasive bumble bee *Bombus terrestris* (*terr*: putative constructor), which often bites holes at the bases of floral tubes to rob nectar, and native *B. dahlbomii* (*dahl*: bystander), which normally accesses *Fuchsia* nectar through the flower mouth (front visits). Robbing holes constitute ENC, as they persist until the 7-day flowers wilt. The dynamics of the incidence of robbed flowers, abundance of both bees and the number and types of their flower visits (front or robbing) were characterised by alternate-day surveys of plants during 2.5 months.
4. After initially accessing *Fuchsia* nectar via front visits, *terr* switched to robbing and its abundance on *Fuchsia* increased 20-fold within 10 days (E2). Correspondingly, the incidence of robbed flowers varied positively with recent and past *terr* abundance (E1). In contrast, *dahl* abundance remained low and varied negatively with the incidence of robbed flowers (E3). When *terr* ceased visiting *Fuchsia*, *dahl* abundance increased sixfold within 10 days (E3), possibly because many *dahl* previously had avoided competition with *terr* by feeding on other plant species

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(E4). While *terr* was present, *dahl* on *Fuchsia* used front visits (tolerance) or used existing robbing holes (adoption: E4). The diverse *dahl* responses suggest partial compensation for competition with *terr*.

5. ENC alters competitive asymmetry, favouring constructor species. However, bystander responses can partially offset this advantage, perhaps facilitating coexistence.

KEYWORDS

bumble bee, ecological niche construction, exploitation competition, invasive species, nectar robbing, southern South America

1 | INTRODUCTION

In the process of accessing a resource, consumers can cause lingering changes to their abiotic or biotic environment that enhance future resource consumption by themselves and conspecifics, resulting in ecological niche construction (ENC; Kylafis & Loreau, 2011). ENC can enable ongoing access to a resource that would otherwise be unattainable by the constructor species and/or improve its foraging efficiency. ENC also has indirect benefits if it increases the constructor's competitiveness for shared resources with non-constructing 'bystander' species (Kylafis & Loreau, 2011). Thus, ENC can have diverse ecological consequences for individual performance and population dynamics of constructor and bystander species, and hence for community structure (see Bråthen & Ravolainen, 2015; Isbell & Loreau, 2014; Kylafis & Loreau, 2008, 2011). Depending on the magnitude, consistency and duration of the ecological effects of ENC, it could also impose selection on traits of the affected species, perhaps precipitating a between-generation evolutionary response known simply as niche construction (Barker & Odling-Smee, 2014; Matthews et al., 2014; Odling-Smee et al., 2013). Regardless of whether adaptation occurs, ENC could be ecologically relevant for many organisms.

Explicit consideration of ENC has focused on its population and community consequences (Bråthen & Ravolainen, 2015; Kylafis & Loreau, 2011), rather than the responses by individuals of constructor and bystander species that generate those consequences. Bystander species could be either beneficiaries of the constructor species if ENC improves bystander access to resources, or competitors if ENC hampers bystander consumption of a shared resource. Competitor bystanders could respond behaviourally to ENC in three ways (Figure 1; see Irwin et al., 2010). Two responses are typical reactions to competitive depletion of a shared resource (Wisheu, 1998). In the absence of reasonable alternatives, bystanders experiencing exploitation competition must tolerate the reduced resource availability and its consequences. If instead alternatives exist and offer greater foraging returns than the resource shared with constructor individuals, avoiding competition by a dietary switch (i.e. resource partitioning; Bolnick et al., 2003; Kotler & Brown, 2007) may be more profitable than tolerance. The third option is specific

to interaction with a niche constructor, namely for a bystander to adopt the environmental modification opportunistically and switch its mode of foraging on the shared resource. Whether individual bystanders tolerate, avoid or adopt ENC will depend on the relative foraging efficiencies associated with these alternative (see Dedej & Delaplane, 2005; Higginson & Ruxton, 2015; Lichtenberg et al., 2018, 2020). These responses need not be fixed (e.g. Bronstein et al., 2017; Lichtenberg et al., 2020), but instead likely vary with the prevailing frequency of ENC, as determined by the persistence of individual environmental modifications, the past and current densities of the niche constructor and the replenishment of unmodified conditions (see Jones et al., 1997).

A widespread case of ENC, known as nectar robbing (Irwin et al., 2010), occurs when a short-tongued flower visitor (primary robber; Inouye, 1980) bites holes at the bases of tubular flowers to ingest nectar that it cannot access readily by probing 'legitimately' through flower mouths (e.g. Navarro, 1999; Pyke, 1982; Varma & Sinu, 2019). Primary robbing constitutes ENC (Newman & Thomson, 2005) for several reasons. First, primary robbing can increase the robber's foraging returns compared to probing legitimately (Lichtenberg et al., 2018; Pyke, 1982). Second, by extracting more nectar by robbing than by visiting legitimately, a flower-biting (constructor) species depletes resources for legitimate (bystander) visitors (González-Gómez & Valdivia, 2005; Maloof & Inouye, 2000). Third, damaged floral tubes do not heal, so holes persist until the flower wilts. These holes provide continued nectar access for later visiting secondary robbers, either the original primary robbers or

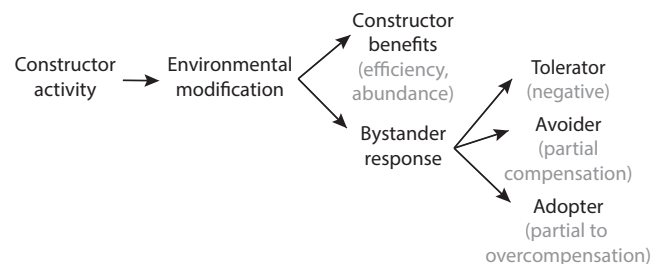


FIGURE 1 General effects of an ecological niche constructor on the environment and potential behavioural responses of bystander organisms

adopting bystanders of the same or difference species, that capitalise on the benefits of the holes without creating them (Bronstein et al., 2017; Irwin et al., 2010). Although interactions of nectar robbers and affected plants are well-studied, competition between robbing and legitimate flower visitors has received limited attention (Irwin et al., 2010).

We considered competition between *Bombus dahlbomii* Guérin-Méneville (hereafter *dahl*), the only native bumble bee in Patagonia, and *B. terrestris* Linnaeus (hereafter *terr*), a recent invader, for nectar of *Fuchsia magellanica* Lam. (Onagraceae; hereafter *Fuchsia*; Figure S1). *Terr* is short-tongued (mean \pm SE for workers = 6.3 ± 0.5 mm; Goulson et al., 2008) and a notorious primary and secondary nectar robber of long-tubed flowers throughout its native and invasive ranges (Goulson, 2010), including those of *Fuchsia* (Figure S1c,d; Valdivia et al., 2016; Stanley & Cosnett, 2021). Thus, *terr* is a putative niche constructor. In contrast, *dahl* is likely a bystander species in this case, as its relatively long proboscis (11.10 ± 0.17 mm; Madjidian et al., 2008) is similar in length to the basal nectar tube of *Fuchsia* flowers (range = 7–15 mm, Berry, 1989; Figure S1d). Using daily observations during 11 weeks, we characterised the dynamics of resources (*Fuchsia* flower abundance), environmental modification (robbed flowers) and the densities and behaviours of *terr* and *dahl*. These observations allowed assessment of the expectations that:

1. Environmental modification (robbed flowers) varies positively with past and present densities of the putative constructor species;
2. The constructor species benefits from its environmental modification by improving its foraging efficiency and disproportionately increases its use of the affected resource;
3. The bystander species experiences competition with the constructor species for the modified resource; and
4. The bystander species experiences increased interspecific competition owing to ENC and exhibits diverse, possibly mitigating, responses to the associated environmental modification.

As we observed bees only visiting *Fuchsia* flowers, tolerance and adoption of the constructor's environmental modification could be detected directly, whereas avoidance could only be inferred.

2 | MATERIALS AND METHODS

2.1 | Study species and site

Fuchsia is a shrub native to temperate regions of Chile and Argentina along the Andes Mountains (Berry, 1989). It flowers continuously for up to 6 months during austral summer (Dzendoletas et al., 2003). Individual *Fuchsia* flowers are pendent with a basal nectar tube, flaring red sepals and a distal purple corolla tube formed by separate overlapping petals (Figure S1a). They remain open for a mean \pm SD

of 7.1 ± 1.6 days (median = 7 days), producing copious nectar (volume \pm SD = 0.563 ± 0.301 μ l/hr, concentration = $21.8 \pm 5.1\%$; Rosenberger, N.M., unpubl. data). Native *Fuchsia* pollinators include *dahl* and the hummingbird *Sephanoides sephanioides* Lesson (Traveset et al., 1998; Valdivia et al., 2016). We do not consider *S. sephanioides* further, as it represented only 2.8% of flower visitors recorded during 129.5 hr of observation.

This study was conducted at Puerto Blest, Parque Nacional Nahuel Huapi, Río Negro, Argentina (-41.033333 , -71.816667), at the end of the western arm of Lago Nahuel Huapi near the Andean continental divide. Puerto Blest is located in Valdivian temperate rainforest dominated by *Nothofagus dombeyi* (Mirb.) Oerst., which also includes various herbaceous species and hummingbird-pollinated shrubs (Aizen & Rovere, 2010; Dzendoletas et al., 2003). Other nectar-producing, native species that flower during the study period at Puerto Blest include *Berberis darwinii*, *Campsidium valdivianum*, *Dasyphyllum diacanthoides*, *Desfontainia spinosa*, *Discaria chacaye*, *Escallonia rubra*, *Fragaria chilensis*, *Gaultheria mucronata* and *Luma apiculata* (Dzendoletas et al., 2003). The Administración de Parques Nacionales Argentinas permitted this study under project permit 1430, and no ethics approval was required as animal visitors were not handled or captured.

2.2 | Plant surveys

This study considered daily records of *dahl* and *terr* visiting flowers of 22 *Fuchsia* plants. We selected these plants haphazardly throughout the study area to represent habitat variation, including four along the beach of Lago Nahuel Huapi, four in *N. dombeyi* forest, 10 along forest streams and four in an open, disturbed area around the Puerto Blest Hotel. The study plants varied in size, with a maximum of 34–510 flowers open simultaneously. Maximum display size did not differ significantly among habitats ($F_{3,18} = 1.46$, $p > 0.25$; GLM with negative binomial distribution).

Two observers sampled plants daily from 1 December 2015 to 8 April 2016 between 07:00 hr and 20:00 hr. *Dahl* and *terr* were first observed visiting *Fuchsia* flowers on 9 and 28 December respectively; however, our analyses consider observations from only 20 January to 8 April 2016 when bumble bees visited *Fuchsia* flowers consistently. Individual plants were surveyed on alternate days, with half the plants observed each day (see Table S1). For analyses of bee abundance and visit behaviour, we excluded surveys for 21 January, 17 March and 7 April, when no bees were observed owing to inclement weather.

While surveying a plant, an observer counted all open flowers and observed visits to some or all of them for 10 min (i.e. total 110 observation min per day). When floral display size exceeded 30 flowers, a subset of observation flowers was selected on one or more branches. For each visitor to observation flowers, the observer recorded its species and the numbers of flowers visited by probing the distal end of the floral tube (front visit) or through a hole in the side of the floral tube (tube visit or robbing). For tube visits, observers

also recorded whether the visitor created the hole (primary robbing) or used an existing hole (secondary robbing). Observation of a visitor ceased when it left the observation flowers or the 10-min survey ended.

Additional flowers were monitored to quantify the proportion of robbed flowers (i.e. extent of ENC). Every 4 days, an observer haphazardly selected five mature flower buds per plant and attached a uniquely numbered jeweller's tag to each flower's pedicle. Every sampling day thereafter until wilting, the nectar tubes of tagged flowers were inspected for the presence of holes caused by primary robbing.

2.3 | Data analysis

We primarily report analyses that assessed statistical effects on daily variation of three dependent variables—the per-plant proportion of robbed tagged flowers, the numbers of bees of both species visiting flowers during 10-min observations of individual plants (local bee abundance) and the numbers of front or robbing flower visits by those bees (flower visitation). A fourth analysis, described and presented in Appendix S1, considered effects on the proportion of *dahl* that engaged solely in front or robbing visits. These analyses involved GLMMs (Stroup, 2013), as implemented in the glimmix procedure of SAS/STAT 14.2 (SAS/STAT® 14.2 User's Guide, 2016; robbed flowers and visit types) or the glmmTMB procedure (version 1.0.2.9000; Brooks et al., 2017) of R (version 4.0.2; R Core Team, 2020; bee abundance). Each analysis included bee species (except robbed flowers and *dahl* visit type) and habitat as fixed factors, as well as relevant continuous covariates (see below and Table S2). General among-plant variation was assessed by including plant as a random factor. We also accounted for correlated responses arising from repeated measurement of sampling units (robbed flowers—study plant; bee abundance—bee species per plant; flower visits—bee species per observation period). Specifically, the temporal covariance between pairs of observations within sampling units was modelled as a declining exponential function of the intervening interval (Stroup, 2013). Sample date was not additionally included as an independent variable, as the relevant influences involved the daily dynamics of flower abundance and bee abundance and behaviour, not the specific date.

The analysis of daily variation in the proportion of robbed flowers per plant addressed Expectation 1, that the putative constructor species, *terr*, modified the foraging environments of both bee species (see Table S2). If so, the proportion of robbed flowers should have varied positively with total *terr* abundance, as measured by the daily sum of *terr* counts for all study plants. Given the average 7-day life span of individual flowers, both current and recent total *terr* abundances are relevant. As a measure of past abundance, we used the average *terr* count for the preceding two samples of a plant (i.e. 2 and 4 days prior). We also included total current flower number on all study plants as a measure of overall flower abundance. This analysis involved a quasi-binomial

distribution (logit link function) to account for overdispersion in the dependent variable.

The analysis of daily variation in local bee abundance simultaneously assessed numerical responses of both bee species to the current total abundance of each species (i.e. among all study plants), resource availability (open flowers per plant) and environmental modification (proportion of robbed flowers per plant; Table S2). We interpret negative effects of conspecific and heterospecific total abundance as intra- and interspecific competition respectively (Expectations 2 and 3). Negative or positive effects of the proportion of robbed flowers similarly indicate competitive or facilitative effects of environmental modification respectively (Expectations 2 and 3). Note that considering the effect of total *terr* abundance on the proportion of robbed flowers (above) and the effect of the proportion of robbed flowers on local *terr* abundance does not involve circularity because of the contrasting scope of analysis (total versus local bee abundance) and the fact that almost all robbing bees used existing floral holes that may have been created up to 6 days earlier. The distribution of local abundance of each bee species included more zeroes than expected for a negative binomial distribution. Therefore, we used the glmmTMB procedure to assess simultaneously the (possibly different) influences on: the probability that bees were not available to be detected during an observation period (zero-inflation component; binary distribution, logit link function); and the number of bees recorded visiting the observation flowers (possibly 0) if they were available on the plant (conditional component; negative binomial distribution, ln link function).

The analysis of daily variation in the numbers of front and tube visits to observation flowers by individual bees during 10-min observations assessed the effects of environmental modification (proportion of robbed flowers per plant), the current local (per plant) and total (all plants) densities of both bee species, and resource availability (open flowers per plant; Table S2). The use of tube visits should vary positively with the proportion of robbed flowers to the extent that perforated flowers increase a bee's foraging efficiency. This visit type should be especially prevalent for the constructor species, *terr*, given its relatively short tongue (Expectation 2). For the bystander species, *dahl*, the use of front versus tube visits indicates whether individuals tolerated or adopted the constructor's environmental modification respectively (Expectation 4). The visitation analysis considered only the 97.5% of the 1,313 observed bees that exclusively used one behaviour or the other, with visit type included as a categorical factor. The remaining 33 bees (5 *terr* and 27 *dahl*) used front and tube visits interchangeably to extract nectar from individual plants. This analysis involved a log-normal distribution and identity link function.

The three analyses incorporated two common features concerning the handling of independent variables. First, all analyses initially included pairwise interactions between independent variables to account for heterogeneous effects. As sampling did not involve a balanced, fully crossed design, collinearity is likely between interactions and their constituent variables, hampering characterisation of statistical effects. Therefore, we used backward elimination to

exclude interactions that did not statistically influence (i.e. $\alpha > 0.05$) variation in the dependent variable (Kutner et al., 2005). Second, as independent variables, bee abundance (+1) and flower counts were ln-transformed for all analyses. Consequently, the analyses of bee abundance (conditional component only) and visit behaviour considered linear ln–ln relations (power functions) for the effects of these independent variables. In these cases, a partial regression coefficient of $\beta = 1$ indicates proportional variation of the dependent variable with an independent variable, $\beta < 1$ indicates a decelerating relation and $\beta > 1$ indicates an accelerating relation.

To illustrate the relations of dependent variables to independent variables, we present partial effects that account for variation in other independent variables in a final statistical model. For categorical independent variables, we present back-transformed marginal means (Milliken & Johnson, 1984) for categories represented by >4 observations, unless indicated otherwise. We illustrate the effect of a focal continuous independent variable, X_p , as the associated variation in adjusted values of the dependent variable. For observation i , this value is

$$\hat{Y}_i = g' \left(\beta_0 + \beta_f X_{f,i} + \sum_{j=1}^k \beta_j \bar{X}_j + e_i \right),$$

where g' is the inverse link function, β_0 is the intercept, β_f and β_j are the partial regression coefficients for the focal and j th non-focal independent variables, \bar{X}_j is the mean of the j th non-focal independent variable and e_i is the observation's residual.2322

3 | RESULTS

3.1 | Dynamics of flowering, bee visitation and robbed flowers

The daily surveys revealed differing phenologies for *Fuchsia* and its *dahl* and *terr* visitors (Figure 2). During the last third of January, relatively few *Fuchsia* flowers were open (Figure 2a) and both bee species visited them relatively infrequently, with *dahl* being about 60% more abundant than *terr* (Figure 2b,c). Throughout this period, all *Fuchsia* flowers were intact (Figure 2d) and bees of both species used only front visits to ingest nectar (Figure 2e,f).

On 2 February, *terr* began robbing *Fuchsia* flowers and within 3 days it robbed almost exclusively until it ceased visiting *Fuchsia* (Figure 2f, red line). During the first 10 days of February, mean *terr* abundance per *Fuchsia* plant increased almost 20-fold (Figure 2b), 72 times faster than the concurrent 27% increase in *Fuchsia* flowering (Figure 2a). In contrast, after a slight peak on 2 February, *dahl* abundance per plant declined during the first 10 days of February (Figure 2c). Both *terr* abundance and the proportion of robbed flowers peaked on February 10 (Figure 2b,d), one month before peak *Fuchsia* flowering (Figure 2a). *Terr* abundance then generally declined until late March, after which *terr* was not observed visiting *Fuchsia* (Figure 2b). The proportion of robbed flowers declined from 0.8 to

0.2 from 10 February to 29 February. It then rose again to an average of about 0.5 in mid-March before declining (Figure 2d), roughly paralleling the phenology of flowering (Figure 2a). On the final sampling day (8 April), no observation flowers had been robbed, despite moderate *dahl* abundance (Figure 2c). The lagged persistence of robbed flowers until 8 days after *terr* ceased visiting is consistent with the average longevity of *Fuchsia* flowers.

Throughout February and the first 3 weeks of March, *dahl* abundance per plant remained relatively constant, compared *terr* abundance (Figure 2b,c). *Dahl* was first observed using robbing holes 5 days after *terr*, but this behaviour by *dahl* was not observed daily for another 6 days (Figure 2e,f), after the availability of robbed flowers peaked (Figure 2d). *Dahl* mostly used front visits to access *Fuchsia* nectar, except during the first 2 weeks of March (Figure 2f). During the last 10 days of March, when *Fuchsia* flowering declined and *terr* was rarely observed visiting *Fuchsia*, *dahl* abundance increased six-fold and more *dahl* than *terr* were observed using robbed flowers (Figure 2e, compare blue and red lines). During April, *dahl* abundance declined with flower availability (Figure 2a,c).

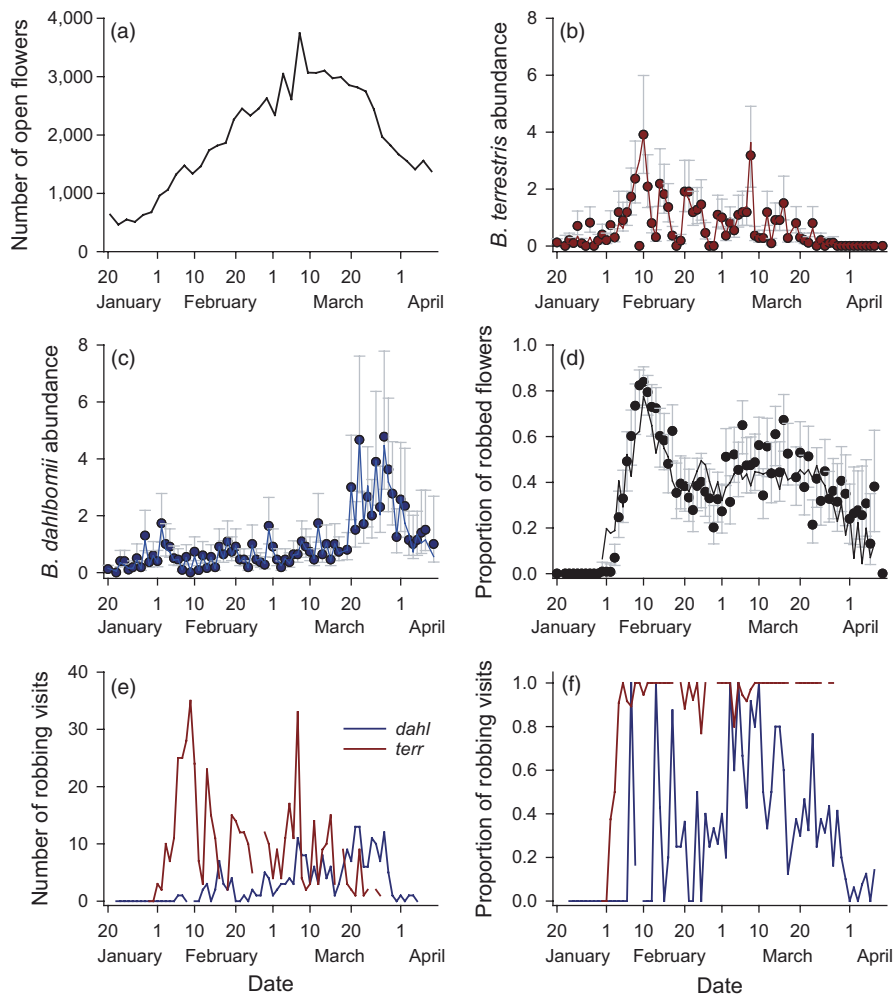
3.2 | Incidence of robbed flowers

Consistent with *terr*'s reputation as a primary nectar robber and Expectation 1, its abundance had diverse, interacting effects on the daily proportion of robbed flowers (Table 1; Table S3; Figure 3). Of particular relevance, the incidence of robbed flowers varied positively and synergistically with recent and current total *terr* abundance (Figure 3a). In addition, the effects of recent and current *terr* abundance each varied with total flower availability, being strongest when relatively few flowers were open (Figure 3b,c) as robbing began during early February (see Figure 2a). In contrast, during peak flowering, the proportion of robbed flowers varied largely independently of recent and current *terr* abundance (Figure 3b,c). The incidence of robbed flowers did not differ statistically among habitats, but it varied somewhat among plants within habitats (Table 1). Unsurprisingly, given the longevity of individual flowers, the proportion of robbed flowers correlated strongly between sampling days (Table 1; e.g. $r \approx 0.75$ between successive samples).

3.3 | Local bee abundance

Two processes determined the local (per plant) abundance of bees on individual plants during observation periods, as indicated by the improved fit of an analysis that accounted for zero inflation ($\Delta AIC = 32.1$). The first process governed the presence of bees of a given species on a plant during an observation period, which varied with four detected influences (Table 1; Table S4). Bee presence differed consistently among plants, but not among habitats (Table 1). Unsurprisingly, bees were least likely to be present when plants displayed few flowers (Figure S2a; Table S4), which primarily occurred early during the study. Bee presence also varied with overall *dahl*

FIGURE 2 Daily variation of (a) overall flowering by 22 *Fuchsia magellanica* plants, (b, c) *Bombus terrestris* and *B. dahlbomii* abundance (bees per plant per 10-min observation), (d) the proportion of robbed flowers per plant and (e) the numbers and (f) proportions of nectar-robbing flower visits by *B. terrestris* and *B. dahlbomii* per observation period. Panels b–d depict marginal (\pm SE) and predicted means (solid line) based on the respective statistical analyses (which did not explicitly include date). Gaps in lines in panels e and f indicate days when no bees of the associated species were observed visiting *Fuchsia* flowers



abundance and the proportion of robbed flowers per plant, with contrasting relations for the two bee species (Table S4). Specifically, the presence of *dahl* per plant varied positively with total *dahl* abundance, but independently of the proportion of robbed flowers, whereas *terr* presence varied independently of *dahl* abundance, but positively with the availability of robbed flowers (Figure 4a; Figure S2b). The latter association is consistent with Expectation 2. Given these effects, the per-plant presence of both species did not vary statistically with overall *terr* abundance; however, indirect effects are likely, given the influence of total *terr* abundance on the proportion of robbed flowers (Figure 3).

The second process affecting local bee abundance determined the number of bees seen visiting observation flowers if they were present on a plant (Table 1). The observed bee number correlated strongly between sampling days for each species (Table 1; e.g. $r \approx 0.92$ between successive samples). In addition, more bees visited observation flowers on plants with larger displays (Figure 4b; Table S4). Similarly, local bee abundance increased in proportion to total conspecific abundance for both species (*terr* – Figure 4c, red line; test of $\beta = 1$, $t_{1525} = 1.35$, $p > 0.15$; *dahl* – Figure 4d, blue line; $t_{1525} = 1.52$, $p > 0.1$). In contrast, the local abundance of both species varied independently of the total abundance of the other species (Figure 4c,d; Table S4). The proportion of robbed flowers on a plant

did not affect local *terr* abundance statistically, whereas fewer *dahl* were observed on plants with high proportions of robbed flowers (Figure 4e; Table S4), signalling a competitive effect (Expectation 3). In addition to the preceding overall effects, local abundance of the two bee species varied heterogeneously among habitats (Table 1), with more *dahl* than *terr* observed visiting *Fuchsia* in disturbed and stream sites, but not in beach or forest sites (Figure 4f). Together these influences on bee presence and conditional abundance accounted for most daily variation in local bee abundance (compare means and solid lines in Figure 2b,c).

3.4 | Flower visits

Of the 4730 flower visits observed during flower sampling, 53.7% involved robbing. Among the 2,542 robbing visits, only 1.3% involved primary robbing, including 28 visits by 20 *terr* and four by two *dahl*. Primary robbing by *dahl* was observed late during the sampling period (28 and 29 March), after *terr* ceased visiting *Fuchsia* flowers. Whereas 96.7% of the 519 *terr* observed visited only robbed flowers (Figure 2f), 31.8% of the 695 *dahl* used only front visits, 64.2% only robbed and 4.0% used both visit types, indicating both tolerance and opportunistic adoption of robbed flowers (Expectation 4).

TABLE 1 Overall results of GLMMs evaluating effects on the proportion of robbed flowers, the local abundance of each bumble bee species and flower visits by individual bees. The analysis of local bee abundance involved a zero-inflated negative binomial distribution, allowing joint assessment of effects on bee presence on sample plants and the number that visited observation flowers. Local bee abundance, open flowers and observed flowers refer to counts on individual plants during individual surveys, whereas total abundance and open flowers refer to the sum over all observation plants per sampling day

Effect	Dependent variable			
	Robbed flowers ^a	Local bee abundance		
		Presence ^b	Number observed ^c	Flower visits ^d
Species		$\chi^2_1 = 1.32$	$\chi^2_1 = 54.90^{***}$	$F_{1,1238} = 4.52^*$
Habitat	$F_{3,17.2} = 1.48$	$\chi^2_3 = 3.74$	$\chi^2_3 = 19.27^{***}$	$F_{3,34.08} = 1.16$
Species × Habitat			$\chi^2_3 = 16.30^{***}$	$F_{1,1205} = 1.90$
ln(Total <i>dahl</i> abundance + 1)		$\chi^2_1 = 0.90$	$\chi^2_1 = 25.37^{***}$	$F_{1,579.9} = 25.06^{***}$
Species × ln(Total <i>dahl</i> abundance + 1)		$\chi^2_1 = 4.22^*$	$\chi^2_1 = 47.74^{***}$	
ln(Local <i>dahl</i> abundance + 1)				
ln(Total <i>terr</i> abundance + 1)	$F_{1,600.5} = 16.30^{***}$		$\chi^2_1 = 114.1^{***}$	$F_{1,556.8} = 6.10^*$
Species × ln(Total <i>terr</i> abundance + 1)			$\chi^2_1 = 152.6^{***}$	
ln(Past total <i>terr</i> abundance + 1)	$F_{1,559.0} = 13.71^{***}$			
ln(Total <i>terr</i> abundance + 1) × ln(Past total <i>terr</i> abundance + 1)	$F_{1,636.9} = 6.89^{***}$			
Proportion robbed flowers		$\chi^2_1 = 8.92^{**}$	$\chi^2_1 = 1.61$	$F_{1,573.6} = 10.35^{**}$
Species × Prop. robbed flowers		$\chi^2_1 = 8.35^{**}$	$\chi^2_1 = 4.15^*$	
Visit type				$F_{1,1142} = 1.02$
Species × Visit type				$F_{1,1209} = 3.95^*$
Habitat × Visit type				$F_{3,1170} = 2.29$
Species × Habitat × Visit type				$F_{3,1218} = 3.35^*$
Visit type × Prop. robbed flowers				$F_{1,958.5} = 11.96^{***}$
ln(Total open flowers)	$F_{1,524.3} = 28.86^{***}$			
ln(Open flowers per plant)		$\chi^2_1 = 5.39^*$	$\chi^2_1 = 19.68^{***}$	
ln(Observed flowers)				$F_{1,579.9} = 25.06^{***}$
ln(Total <i>terr</i> abundance + 1) × ln(Total open flowers)	$F_{1,590.9} = 18.17^{***}$			
ln(Past total <i>terr</i> abundance + 1) × ln(Total open flowers)	$F_{1,568.5} = 13.41^{***}$			
Among-plant variance	$\chi^2_1 = 4.65^*$	$\chi^2_1 = 34.5^{***}$		$\chi^2_1 = 21.69^{***}$
Temporal autocorrelation	$\chi^2_1 = 338.2^{***}$		$\chi^2_2 = 11.3^{**}$	$\chi^2_1 = 17.89^{***}$

^aOverdispersed binomial distribution, logit link function.

^bBinary distribution, logit link function.

^cNegative binomial distribution, ln link function.

^dLog-normal distribution, identity link function.

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

The average proportion of robbing *dahl* largely equalled the proportion of robbed flowers (Figure S3c), especially on plants with few *terr* (Figure S3d; see Appendix S1 and Table S5).

The number of flowers visited per bee during individual survey periods was subject to diverse influences (Table 1; Table S6, Figure 5). Unsurprisingly, the recorded flower visits per bee varied positively with the number of flowers observed (Figure 5a). Overall, bees generally visited more flowers when *terr* was abundant (Figure 5b) and on plants with few *dahl* during a survey

(Figure 5c). Front-visiting bees probed fewer observation flowers on plants with a high proportion of robbed flowers, whereas this proportion did not influence the number of flowers visited by robbing bees (Figure 5d). On average, *dahl* individuals generally visited equivalent numbers of observation flowers whether using front or tube visits, except on beach plants where they probed more flowers while front visiting (Figure 5e). In contrast, *terr* generally probed fewer flowers while front visiting than while robbing, especially on plants at the beach and disturbed sites (Figure 5f). The

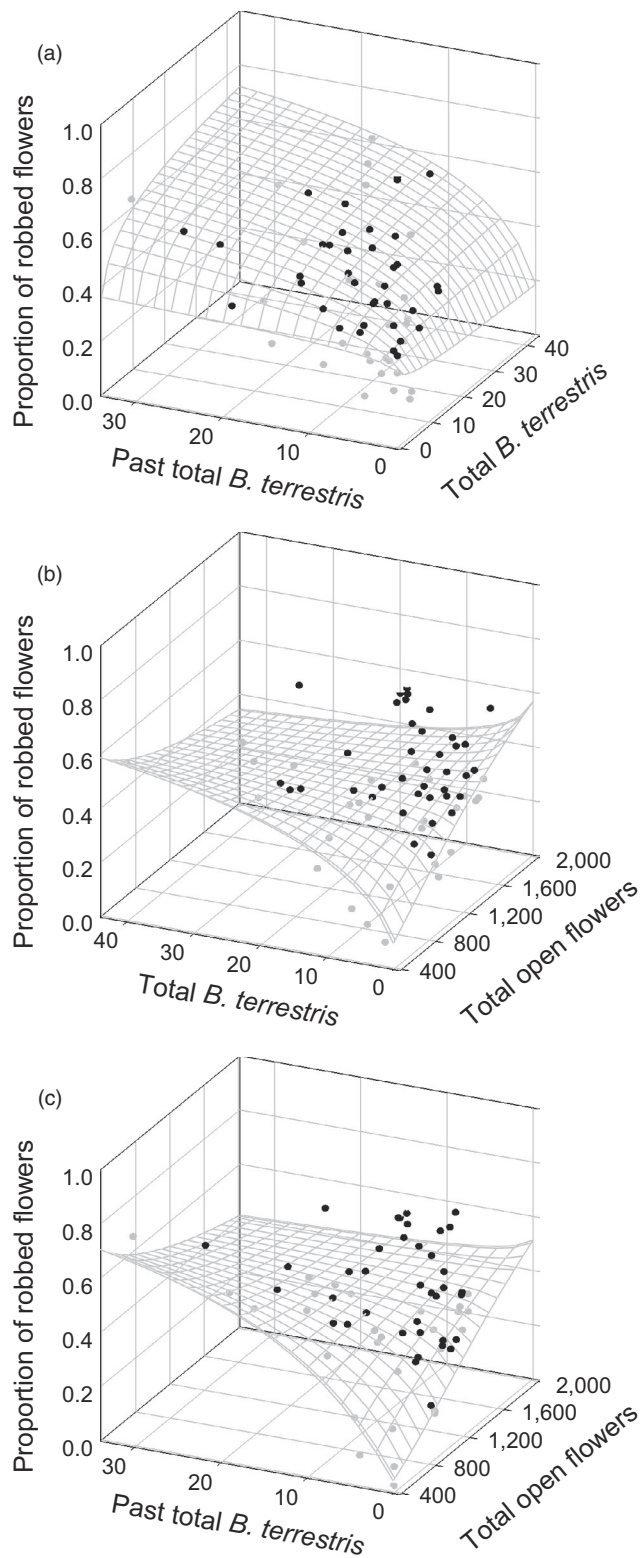


FIGURE 3 Partial effects on the daily incidence of nectar-robbed *Fuchsia magellanica* flowers, including pairwise interactions between the daily past and current total abundances of *Bombus terrestris* and the total number of open flowers on all study plants. See Tables 1 and S3 for statistical details

number of flowers visited also varied statistically among plants within habitats and correlated positively among bees within observation periods (Table 1).

4 | DISCUSSION

4.1 | Species roles and ecological niche construction

Terr and *dahl* played contrasting roles as *Fuchsia* visitors, which affected their competition for nectar. Several lines of evidence identify *terr* as the ecological niche constructor and *dahl* as a bystander. First, although primary robbing was observed rarely, most primary robbers were *terr* and the observations of two *dahl* biting flowers occurred late during the study. Second, *terr* switched to robbing first and was responsible for almost all robbing visits observed as the proportion of robbed flowers peaked during the following two weeks (Figure 2d,e). Finally, the occurrence of robbed flowers varied with the past and current abundance of *terr* (Figure 3; Expectation 1) and the creation of robbed flowers essentially ended when *terr* ceased visiting *Fuchsia*. After that, *dahl* rarely used robbed flowers (Figure 2e, blue line), despite visiting *Fuchsia* much more frequently than when *terr* was present (Figure 2c).

The observed dynamics of *terr* and *dahl* abundance and behaviour demonstrate that nectar robbing constitutes ENC (see Kylafis & Loreau, 2011; Newman & Thomson, 2005). As summarised in Figure 1, the environmental modification (nectar-access holes in *Fuchsia* flowers) created by the biting constructor species, *terr*, persisted and increased its resource availability and competitiveness, motivating behavioural responses by the bystander species, *dahl*. Although the constructor species did not initially rob *Fuchsia* flowers, once robbing began, it used this foraging mode almost exclusively (Figure 2f, red line). By doing so, individuals of the constructor species benefitted from increased visitation of observation flowers (Figure 2f), likely enhancing their nectar intake per flower (Expectation 2). Furthermore, the inferred presence of constructors on *Fuchsia* varied positively with the frequency of its existing environmental modifications (Figure 4a, red symbols and line). ENC also enhanced the constructor's competitive advantage (Expectation 3), as demonstrated by the negative relation of the number of bystanders (*dahl*) visiting *Fuchsia* to existing environmental modifications (Figure 4e, blue symbols and line). This competition prompted diverse responses by the bystander species (Expectation 4). *Dahl* initially tolerated niche construction, continuing to probe the mouths of *Fuchsia* flowers to ingest nectar (Figure 2f, blue line). Only after ENC peaked during mid-February (Figure 2d) did an increasing proportion of *dahl* individuals adopt the environmental alteration (Figure 2f). By doing so, they may have partially compensated for competition with the constructor species, as robbing bees visited more flowers per observation than front-visiting individuals when most flowers had been robbed (Figure 5d). In addition, many unobserved individuals of the bystander species may have avoided competition for *Fuchsia* nectar during peak *terr* abundance by visiting other plant species (see below). We now consider insights revealed by the *terr*-*dahl*-*Fuchsia* interaction concerning the role of ENC in competition between constructor and bystander species.

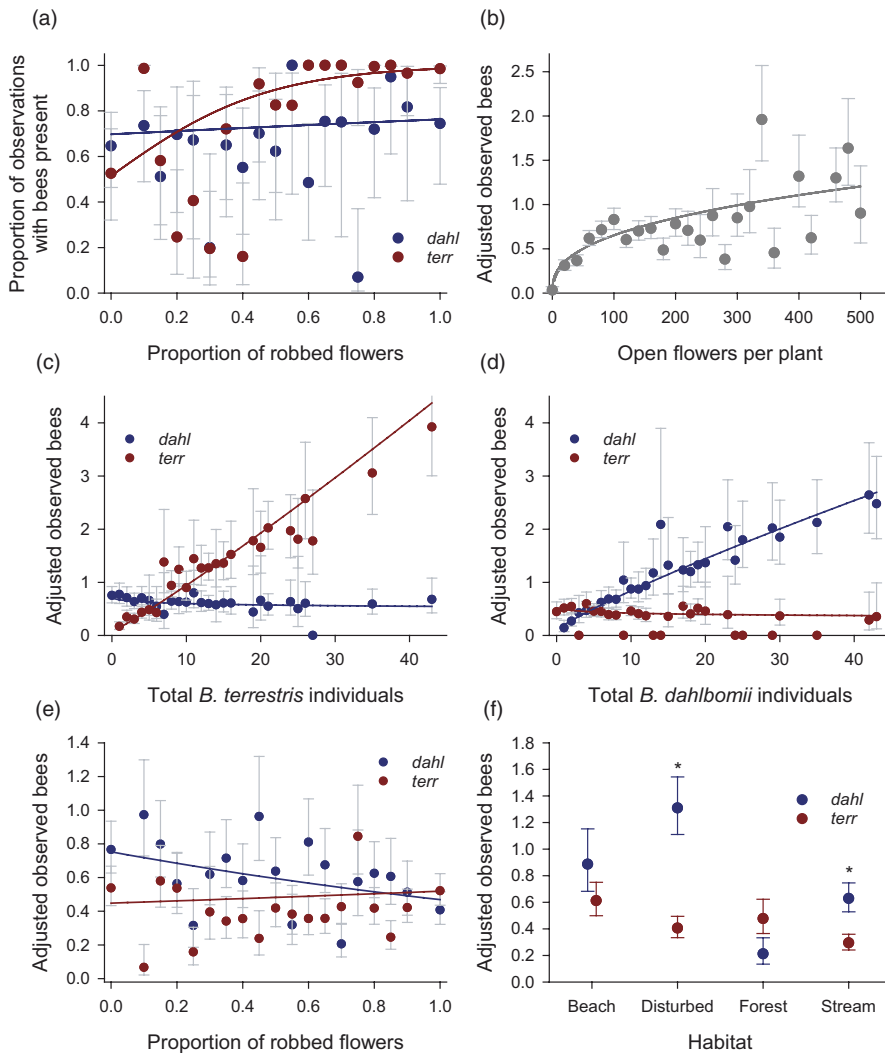


FIGURE 4 Partial effects on the marginal mean (\pm SE) numbers of *Bombus dahlbomii* and *B. terrestris* visiting *Fuchsia magellanica* plants during 10-min surveys, including: (a) the relation of bee presence on study plants to the proportion of robbed flowers; and the relations of observed bee numbers when bees were present to (b) the number of open flowers per plant, (c, d) the total numbers of *B. terrestris* and *B. dahlbomii* observed daily on all study plants, (e) the daily proportion of robbed flowers per plant and (f) habitat. See Tables 1 and S4 for statistical details and Figure S2 for additional effects on bee presence

4.2 | Ecological niche construction and competition asymmetry

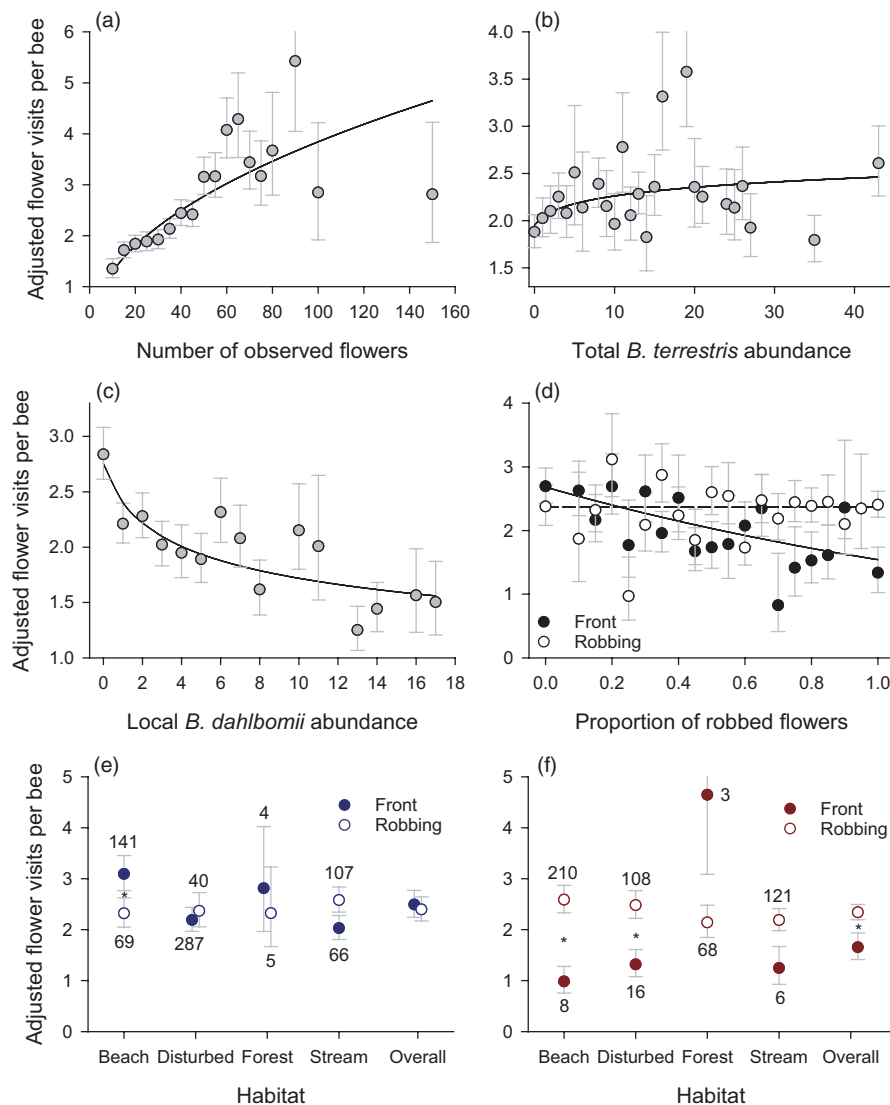
The extent to which a constructor's environmental modification improves its own resource access and foraging efficiency should also intensify its exploitation competition with other species vying for the same resource (Expectations 2 and 3). Thus, ENC should make interspecific competition more asymmetrical, favouring the constructor species. This expectation is evident in the apparent competitive release of *terr* and *dahl* as ENC began and ended respectively. Competitive release is evident when relaxation of interspecific competition increases a species' morphological or behavioural variation and/or its density or habitat use (Terborgh & Faaborg, 1973; Yoder et al., 2010; for *Bombus* examples, see Inouye, 1978; Laverty & Plowright, 1985).

The first relevant event occurred when *terr* began ENC and abruptly switched from front to robbing visits in early February (Figure 2f). Initially (late January), *terr* used only front visits to access *Fuchsia* nectar. In doing so, it was probably at a competitive disadvantage to *dahl*, which has a longer proboscis and so could access more of the nectar column in *Fuchsia* flowers (see Newman &

Thomson, 2005). The resulting limitation of accessible nectar likely prompted some *terr* individuals to begin robbing, allowing them to ingest more nectar per flower, alleviating their competitive disadvantage (see Dedej & Delaplane, 2005; Lichtenberg et al., 2018; Pyke, 1982). Correspondingly, *terr* abundance as a *Fuchsia* visitor increased 20-fold in just 10 days (Figure 2b), indicating extreme competitive release, perhaps aided by social transmission of nectar-robbing behaviour (see Leadbeater & Chittka, 2008). This increase was roughly 13 times faster than the maximal growth of *terr* colonies (see Duchateau & Velthuis, 1988), so it must have predominantly involved recruitment of individuals that previously fed on other plant species. Simultaneously, use of *Fuchsia* by *dahl* declined, so *terr* became the overwhelmingly dominant consumer of *Fuchsia* nectar (compare Figure 2b,c). Thus, through their environmental modification, primary-robbing *terr* individuals increased their own foraging efficiency, created foraging opportunities for secondary-robbing conspecifics (Figure 4a, red symbols and line) that had previously rejected *Fuchsia* as a profitable resource, and reduced the suitability of *Fuchsia* for *dahl* (Figure 4e, blue symbols and line).

The second case of apparent competitive release involved *dahl*. During February and March, *dahl* abundance should generally

FIGURE 5 Partial effects of independent variables on marginal mean (\pm SE) visitation of *Fuchsia magellanica* flowers by *Bombus dahlbomii* and *B. terrestris* during 10-min surveys, including: (a) the number of observed flowers per plant; (b) the daily total number of *B. terrestris* observed on all survey plants; (c) the number of *B. dahlbomii* observed per-plant survey; (d) interacting effects of visit type and the proportion of robbed flowers per plant; and (e, f) the interacting effects of visit type and habitat for *B. dahlbomii* and *B. terrestris* respectively. For statistical details, see Tables 1 and S6



increase in the absence of *terr*, owing to colony growth. For example, during February 1994 and 1995, before *terr* invaded western Argentina, Aizen (2001) observed 5- and 3.5-fold increases in *dahl* abundance on *Alstroemeria aurea* in a drier forest 52 km east of Puerto Blest. In contrast, during our study, *dahl* abundance on *Fuchsia* remained consistently low throughout February and the first 3 weeks of March. However, this changed during the 10 days after 20 March, when *terr* largely ceased visiting *Fuchsia* (Figure 2c), probably owing to the end of its colony cycle, which typically lasts about 10 weeks (Gosterit, 2011). In response, *dahl* abundance increased sixfold, and it became more abundant than previously during the study. Like the earlier spike in *terr* abundance, the increase in observed *dahl* abundance occurred too rapidly to have resulted solely from colony growth. Rather, it likely involved recruitment of individuals that had previously avoided reduced resource availability associated with competition with a constructor and were instead visiting other plant species.

These results illustrate contrasting effects of ENC in these competitive-release episodes: the constructor species' environmental modification triggered its own release, whereas the absence of

the constructor and its modifications promoted the release of the bystander species. Despite the observational nature of this study, the synchrony of these numerical events with the dynamics of the constructor's environmental modification strongly imply that ENC asymmetrically altered competition between constructor and bystander species to the advantage of the constructor.

4.3 | Bystander responses

This study illustrates that ENC motivates a suite of behavioural responses by bystander species as they adjust to the associated environmental modification (Figure 1; Expectation 4). Specifically, direct evidence demonstrates that some *dahl* tolerated robbed flowers, continuing front visits of *Fuchsia* flowers, whereas others adopted the environmental modification and switched to secondary robbing (Figure 2e,f; also see, Lichtenberg et al., 2020; Newman & Thomson, 2005). That 96% of observed *dahl* used either front or robbing visits, rather than both, after robbed flowers became available, but the proportion of *dahl* using robbing visits

varied extensively during February and March (Figure 2d) suggests that both foraging modes were similarly rewarding (Bronstein et al., 2017). In addition, the spike in *dahl* observed visiting *Fuchsia* after *terr* ceased visiting (Figure 2c) suggests that many *dahl* had previously avoided the environmental modification by visiting other plant species.

Apparent co-occurrence of the three foraging responses to environmental modification suggests that *dahl* individuals assorted themselves among tolerance (front visits of *Fuchsia*), adoption (tube visits of *Fuchsia*) and avoidance (visits to species other than *Fuchsia*) in proportions that rendered all options equally rewarding, as in an ideal-free distribution (Dreisig, 1995; Fretwell & Lucas, 1970; Hamilton, 2010; Pleasants, 1981). Two observations support this conclusion. First, in contrast to the universal persistent switch from front visits to robbing by *terr*, the proportion of *dahl* that robbed *Fuchsia* generally increased and then declined during the study in concert with variation in factors that could affect resource dynamics (Appendix S1, Figure S3). Importantly, the average proportion of robbing *dahl* generally equalled the opportunity for secondary robbing, as governed by the proportion of robbed flowers (Figure S3c), in accordance with the input-matching rule of the ideal-free distribution (Houston, 2008). Second, the inferred rapid shift of *dahl* to *Fuchsia* when competition relaxed indicates awareness of the change in resource status, probably gained by sampling (Dall & Cuthill, 1997).

According to this interpretation, the various behavioural responses adopted by the bystander species partially compensated for the negative impact of competition with a niche constructor compared to its effect if adoption and avoidance had not been possible. Such compensation is possible because, like most bumble bees (Goulson, 2010), *dahl* is a behaviourally flexible ecological generalist (Abrahamovich et al., 2001; Aizen et al., 2002). In contrast, for bystanders with a limited behavioural repertoire, adoption may not be a feasible response to competition with a niche constructor. Similarly, bystanders with limited ecological range or those in environments with few suitable alternative resources may be unable to avoid constructor competition.

4.4 | Population and evolutionary implications

Foraging-based ENC can invoke diverse consequences for populations of constructor and bystander consumers and the affected food species that are the object of construction. Whereas ENC should generally enhance constructor abundance and distribution (Krakauer et al., 2009; Kylafis & Loreau, 2008), its effects on bystander populations and affected food species, including demographic consequences, can range from negative to positive (Kylafis & Loreau, 2011; Maloof & Inouye, 2000). For bystander species, positive effects (facilitation) arise if environmental modification creates new foraging opportunities, whereas negative effects result from increased exploitation competition. If such effects occur persistently

within and among generations and differentially affect individuals with particular heritable phenotypes, they could also precipitate evolutionary responses (Barker & Odling-Smee, 2014; Odling-Smee et al., 2013).

In the specific case of ENC by primary nectar robbing, the population consequences for constructor and bystander species are probably straightforward. For social species, including bumble bees, colony growth and production of sexual individuals vary positively with nectar intake (Requier et al., 2020; Rotheray et al., 2017). Consequently, populations of constructor species and facilitated bystanders should benefit from the actions of primary nectar robbers, whereas those of bystander species that experience increased competition should suffer. Thus, *dahl* populations likely suffer from competition with nectar-robbing *terr*. Unfortunately, this expectation can no longer be tested just 5 years after our study, as *dahl* populations have been largely extirpated from southern South America, apparently owing to a more severe environmental impact of invading *terr*, specifically its role as a parasite vector (Arbetman et al., 2013; Schmid-Hempel et al., 2014). In more persistent bee assemblages, competitive effects of ENC associated with nectar robbing should depend on the fraction of local plant species visited by both constructor and bystander species.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

N.M.R. and M.A.A. conceived and developed the study design; N.M.R. and R.G.D. collected the data; N.M.R. and L.D.H. developed and implemented the statistical analyses; N.M.R. wrote the first draft of the manuscript and all authors contributed substantially to the final manuscript. All authors gave final approval of the accepted manuscript.

DATA AVAILABILITY STATEMENT

Data used for this publication are available on Dryad Digital Repository <https://doi.org/10.5061/dryad.rbnz7hcj> (Rosenberger et al., 2021).

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