ORIGINAL ARTICLE

Associations between a range-shifting damselfly (*Erythromma viridulum*) and the UK's resident Odonata suggest habitat sharing is more important than antagonism

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Abstract

1. Species shifting their ranges under climate change are a conservation dilemma. Range-shifters may be threatened by climate change in their historic range. However, range-shifters are likely to be generalist opportunists, which could mean they could harm aspects of biodiversity in their new ecosystems. Therefore, we need approaches to rapidly assess how range-shifters may integrate into the community of historically resident species.

2. The small red-eyed damselfly (*Erythromma viridulum*) has shifted into the United Kingdom since 1999 and may affect resident Odonata via intraguild predation. We asked whether the damselfly's arrival is associated with a decline in resident Odonata.

3. We harnessed the British Dragonfly Society's dataset, using records from 49,788 site visits between 2000 and 2015 to construct dynamic species occupancy models for 17 resident UK Odonata. We estimated the potential effect of *E. viridulum* presence on the probability that each species would persist at a given site, while controlling for potential effects of climate and recording effort.

4. On average, dragonflies (Anisoptera) persisted more frequently at sites where *E. viridulum* had established, while damselflies (Zygoptera) showed no change in persistence. Nevertheless, two resident damselflies, including *E. viridulum*'s congener, disappeared more frequently when the range-shifter established.

5. We suggest that *E. viridulum* poses minimal risk to most UK resident Odonata. Rather, *E. viridulum* may be differentially establishing in areas with good habitat quality, where many species of historically resident Odonata are also found. Therefore, high quality, biodiverse sites may become home to increasing numbers of range-shifters in future. Our approach permits rapid detection of how range-shifters are integrating into resident biota.

KEYWORDS
aquatic systems, biotic interactions, climate change, community ecology, novel species, range shifts

INTRODUCTION

Novel species interactions are occurring around the world as anthropogenic environmental change causes species distributions to shift with increasing frequency (Bonebrake et al., 2018; Gurney, 2015; Mason et al., 2015). These interactions may lead to a range of both positive and negative effects, often depending on the local environmental and social context (Pecl et al., 2017; Pettorelli et al., 2019). Despite their potential to alter recipient ecosystems, species that are losing historic range will be at increased risk of extinction if they cannot establish in new areas (Araújo et al., 2011; Thomas et al., 2004). Therefore, we may sometimes see a conservation dilemma between protecting the new arrivals and protecting historically resident species.

Range-shifters, that is, species immigrating to novel communities without human assistance, are often expected to have minimal effects on recipient ecosystems (Urban, 2020; Wallingford et al., 2020; Wilson et al., 2016). Nevertheless, some studies have found negative impacts such as: out-competing residents (Fitt & Lancaster, 2017; Yackulic et al., 2019), disease spill over (Dobson, 2009), direct predation, and hybridisation (Sánchez-Guillén et al., 2013; Steeves et al., 2010). On the other hand, species that are losing historic range will be at increased risk of extinction if they cannot establish in new areas (Araújo et al., 2011; Thomas et al., 2004). Understanding local factors associated with range-shifter establishment, including the resident species with which they are co-occurring, is therefore important for conservation planning for both resident and range-shifting species. It therefore seems prudent to develop tools to assess how range-shifters integrate into resident biota, and whether undesirable effects are occurring.

Horizon scanning (Roy et al., 2014), risk assessment (Hawkins et al., 2015) and proactive monitoring (Kennedy et al., 2018) are often used to identify threats from introduced invasive species. However, such efforts, as well as legal or management frameworks for alien species, focus on species that have been introduced by humans—not range-shifting species moving under their own powers of dispersal (Trouwborst et al., 2015). The large number of range-shifters (Lenoir et al., 2020) and concomitant stress from changes to the physical environment suggests we should not overlook this phenomenon. Being able to monitor and quantify the potential for novel interactions between range-shifters and residents is important for two reasons. First, in the short term, quantification allows limited conservation resources to be spent on the species of greatest impact or need (Carrasco et al., 2010; Kumschick et al., 2012). Second, in the longer term, the resultant knowledge base could be used to compare the impacts of range-shifting species at regional and global levels relative to other risks to biodiversity (Turbelin et al., 2017). However, detecting novel interactions is challenging. There is little systematic data on range-shifters' distributions in recently occupied parts of their ranges and even less on their abundance or interactions with residents. Most available data are opportunistically collected rather than using standard protocols (Amorim et al., 2014). Unfortunately, opportunistic data can suffer from several biases, which can lead to flawed inferences over species trends (Isaac & Pocock, 2015). Furthermore, it can be challenging to separate the effects of the arriving species from other environmental changes. If environmental change increases both the probability a new species will establish and the probability a resident species will go locally extinct, this could lead to a correlation between new species arrival and resident species decline (Parmesan et al., 2011). Climate change is a quintessential example. It allows new thermophilic species to establish but by exceeding current residents' thermal limits causes their probability of persistence to decrease (Pinkert et al., 2022). These indirect associations, as well as sampling biases, mean that we should be cautious when inferring biotic interactions from correlations between resident and range-shifting species using opportunistic data (Blanchet et al., 2020; Dormann et al., 2018). Nonetheless, one advantage of modelling over (most) experimental studies, in that it can integrate data from a much wider geographic area and time period. Moreover, models can be more easily replicated and adapted, for example, different environmental covariates or different model formulations can be statistically compared, than field or laboratory experiments can be rerun. Therefore, modelling the occupancy of multiple species using opportunistic data can act as useful starting points for generating hypotheses and general patterns so long as consideration is paid to the risk of assigning causality.

Dynamic multispecies occupancy models (DMSOs) have been used successfully to link environmental change to biodiversity impacts using occurrence records (Woodcock et al., 2016). Including environmental covariates can help to rule out possible confounding factors such as climate or habitat. In addition, including ecological processes such as dispersal in sub-models can also help to build more biologically realistic models. Our understanding of range-shifters effects can also be updated as more data become available to estimate parameters, allowing near real-time inputs into conservation strategy (Mancini et al., 2019).

Here, we apply DMSOs to examine a range-shifting species—the small red-eyed or small redeye damselfly (*Erythromma viridulum*). The species was first detected in the United Kingdom in 1999 and has continued to establish over the last two decades. Originally a Mediterranean species, the damselfly has spread gradually northwards, arriving in the United Kingdom via multiple irruptive waves from 1999 and becoming established by 2002, at times appearing abundant at certain sites (Watts et al., 2010). The damselfly is at the current poleward edge of its distribution in the United Kingdom (GBIF Secretariat, 2019) and thus breeds less frequently there, either annually or biennially, than in the warmer core of its range. It favours static pools or slow-flowing rivers for egg-laying as they have requisite macrophytes, particularly Hornwort and Water Milfoil. It flies principally between May and September (Brooks & Cham, 2014).

E. viridulum is a representative and timely study species for investigating measures of impact since several new Odonata are expected to establish in upcoming years (Parr, 2010). There are reasons to think range-shifting Odonata both may and may not have effects on UK resident Odonata. Odonata are known for their strong inter-specific interactions in both their adult and larval stages, including predation, which constitutes a biologically plausible mechanism for impact (Cerini et al., 2019; Wissinger & McGrady, 1993). There are numerous examples of range-shifting Odonata with competitive advantages over

resident species (Pinkert et al., 2022 and references therein; Siepielski et al., 2022). Interactions in the larval stage are hard to observe directly and therefore inferring through modelling could be particularly useful. In addition, the UK Odonata is relatively species-poor compared to similar latitudes in mainland Europe (Kalkman et al., 2018). This is concerning as low biodiversity has been shown to decrease resistance to invasion (Kennedy et al., 2002). Impacts may also be amplified since several UK Odonata species are already locally threatened (Daguet et al., 2008). Odonata are range-shifting rapidly within the United Kingdom and Europe, so are of particular interest (Pinkert et al., 2022). Within the Odonata, *E. viridulum* is one of two species (both damselflies) to have arrived in the United Kingdom within recent decades and is the most numerous (Parr, 2010; Watts et al., 2010). It displays aggressive flight behaviour towards six resident Odonata and has high dietary overlap with at least one other damselfly (*Coenagrion puella*, Cox, 2013). *E. viridulum* is one of the most rapidly range-shifting species in Europe, it forms large populations where it establishes (Trippier et al., 2014), can become one of the most abundant species in the odonate community (Ketalaar, 2002). *E. Viridulum* seems to be showing some form of adaptation to local conditions (Hassall et al., 2014), which can alter the balance of inter-specific interactions (Lancaster et al., 2017; Therry et al., 2014). These traits, often found in other range-shifting odonata (Pinkert et al., 2022), mirror those found in many invasive species (Estrada et al., 2016; Wallingford et al., 2020). *E. viridulum* has a congener in the United Kingdom (*Erythromma najas*) with whom it overlaps in habitat preference and flight season (Powney et al., 2014). This could result in a negative impact, or the presence of *E. najas* could stall the establishment of *E. viridulum*.

On the other hand, Odonata have fairly generalist diets, meaning that competition for food and intraguild predation between *E. viridulum* and most resident species may be low unless external conditions led to severe food shortages. *E. viridulum's* short flight periods might also minimise the effects of territoriality. In addition, low Odonata species richness in the United Kingdom may mean that there are vacant niches to exploit (Gauzere et al., 2020), reducing other forms of resource competition. Therefore, some resident Odonata, particularly the larger dragonflies, may be unlikely to suffer negative effects from *E. viridulum*, than others, for example, the damselflies. Because the larger dragonflies are well recorded through the same methods as other Odonata and found in the same habitat, they potentially provide a good control. If negative associations between *E. viridulum* and many species of dragonflies were found, this could indicate a third factor is causing joint declines, and confounding detection of biotic interactions.

Data on *E. viridulum* are some of the best available to test our approach given that the United Kingdom has some of the best Odonata recording globally. Within our study area, a team of 51 volunteer County Dragonfly Recorders (CDRs) solicit, collect, collate and verify records contributed by recorders over a fairly small geographic area, manually determining whether a record is accepted (Taylor et al., 2021). CDRs know local sites very well, and given that the arrival of *E. viridulum* has generated substantial interest, CDRs are likely to verify new sightings in their vice county rigorously. The rigour with which records of many potentially interacting species are verified means that

DMSO techniques may be readily and accurately applied. We note that there is potential for misidentification between *E. viridulum* and *E. najas*. The added noise in the data is likely to make it harder for models to detect species associations, rather than detect spurious associations.

In this study, we investigated whether we could detect and quantify associations between the occurrences of the range-shifting *E. viridulum* and the UK's resident Odonata. Specifically, we asked whether there was a net change in the persistence probability of dragonflies (Anisoptera) and damselflies (Zygoptera) at sites where *E. viridulum* had arrived. We also examined changes in the persistence of individual species. Our study incorporated data from 2609 1 km^2 sites, 49,788 site visits from 2000 to 2015, 10 historically resident dragonfly species and 7 historically resident damselfly species, compensating for differential recorder effort through a detectability sub-model. We controlled for the potentially confounding effects of climate and recorder effort.

MATERIALS AND METHODS

Occurrence data

We obtained the locations of Odonata from the British Dragonfly Society (BDS) database. This dataset includes data from the National Biodiversity Network and the BDS' iRecord database. We used all available species records, which had a spatial resolution sufficient to place them at 1 km^2 resolution on the British National Grid (EPSG:27700) and a recorded date between 2000 and 2015. We obtained 509,723 records across the United Kingdom with records from 39,719 sites in total. For every grid cell, following (Roy et al., 2012; Woodcock et al., 2016), we assumed records on the same day could be treated as recorded on the same visit and we excluded grid cells that were only visited in a single year.

In order to reduce confounding effects, we compared cells where *E. viridulum* has established against cells without *E. viridulum* but which have similar potential compositions of resident species, habitat, and climate by further restricting the dataset in two ways. First, we included only 1 km^2 grid cells within 100 km cells of the British National Grid (e.g. TF) containing at least 50 records of *E. viridulum*. Second, we included only grid cells that had a confirmed record of either *E. viridulum* or its congener red-eyed damselfly (*E. najas*) at some point in the study period. We only modelled associations with resident dragonfly and damselfly species that had a habitat overlap with *E. viridulum*, following Powney et al. (2014) (Table S1). Thus, we removed species that are unlikely to interact with *E. viridulum* as they do not occur in the same habitats. Finally, we removed 10 resident species with <2000 records in the dataset as these species had very few co-occurrences with *E. viridulum* (on average co-occurring in 66 1 km^2 grid cells, across 16 years) and thus would not provide information relevant to our hypothesis.

After filtering, our dataset covered 17 resident species, 7 damselflies and 10 dragonflies, not including *E. viridulum*. Across 2609 sites, there were in total 49,788 visits by recorders. *E. viridulum* was

reported at 1190 of those sites at least once and was in total reported in 3350 distinct visits. We used these data to model resident species distributions in 1 km² grid cells as independent sites, assuming that if a species was detected in a grid cell at least once in a year it was present that whole year, regardless of any subsequent failure to redetect it by surveys in that year (MacKenzie et al., 2003). For each of these sites, we used 1 km² resolution annual climate data from the Met Office (Hollis et al., 2019) to find the mean spatial climate anomaly for the site between 2000 and 2015. For each site, we calculated the yearly difference in its mean annual temperature from the mean annual temperature across all sites in that year. This adds information on how unusual a grid cell's temperature is each year, which is important given that cells with different temperatures will have different species assemblages (i.e. species in a grid cell with a temperature of 10°C in 2000 will respond differently to an annual temperature of 15°C than will species in a grid cell that started at 14°C). However, the estimated magnitude of the effect of climate on persistence will not be substantially different from using raw climate data.

We could not be certain of the true extent of *E. viridulum* occurrence in each year because not all sites were visited annually. Some records, especially in early years, represent ephemeral appearances rather than established populations. In other cases, a population may have persisted after being initially recorded but not recorded in later years. Therefore, we constructed occupancy models using two final datasets, based on two different assumptions about the true presence of *E. viridulum*. In the first dataset, *E. viridulum* presence was taken at face value, that is, considered present in a site only in years when it was recorded (EV$_{AsReported}$); (Roy et al., 2012). In the second dataset, we instead assumed that once *E. viridulum* was established at a site it was not subsequently extirpated and therefore was present in all subsequent years (EV$_{NoExtinction}$). It is probable that the true state of *E. viridulum* occupancy lay between these two bounds, as the risk of identifying *E. viridulum* at unsuitable sites is low and as a new species to the United Kingdom, there is a higher risk of the species not being reported relative to a resident species, for example, due to omission in less recent field guides. Nonetheless, differences in the results of the two analyses would indicate if under-recording might affect results. All analyses below were repeated for each dataset.

Model description

In order to estimate the effect of *E. viridulum* on the persistence of UK resident Odonata, we used DMSO models derived from the study by Ruiz-Gutierrez et al. (2016). The parameter of interest—occupancy—cannot be directly observed (i.e. it is a latent state). We can only infer it from separate detections of species' presences on a particular visit (*k*) at a site (*j*). Therefore, the model describes two sub processes: occupancy and detection. We fitted our models using a Bayesian approach, which permits full propagation of uncertainty. This approach synthesises information from assumptions about the probability of different parameter values (priors) with information from the

observed data (Y) to find the most likely parameter values given the data (posteriors).

To control for the potential effects of climate on species persistence, we parameterised two similar models differing only in whether a parameter for a climate effect was included. For both models, the probability of occupancy $E[(z_{i,j,t})]$ for each resident species (*i*), at site (*j*) in year (*t*) is modelled as either a persistence probability ($\phi_{i,j,t}$) or a species immigration probability (γ_i)—depending on if the modelled occupancy state of the site in the previous year ($z_{i,j,t-1}$) was present or not (Equation 1), respectively. We did not include distance to other occupied sites.

$$E\left[z_{i,j,t}\right] = z_{i,j,t-1} * \phi_{i,j,t} + (1 - z_{i,j,t-1}) * \gamma_i \tag{1}$$

In the model without climate (Clim$_{Exc}$, Equation 2), we modelled persistence probability ($\phi_{i,j,t}$) as a linear function, converted to the probability scale with a logit link. Our model had two parameters: a species-specific intercept β_{0i} (the probability that a population of a resident species will persist from 1 year to the next in the absence of *E. viridulum*) and β_{1i} (the difference in persistence associated with *E. viridulum* being present at the site (*j*) in the previous year (EV[*j*, *t* − 1])). In the climate model (Clim$_{Inc}$, Equation 3), we also included an effect (β_{2i}) of the previous year's climate anomaly (SpatAnol[*j*, *t* − 1]).

$$\text{Clim}_{Exc} \ \text{logit}\left(\phi_{i,j,t}\right) = \beta_{0i} + \beta_{1i} * \text{EV}[j, t-1] \tag{2}$$

$$\text{Clim}_{Inc} \ \text{logit}\left(\phi_{i,j,t}\right) = \beta_{0i} + \beta_{1i} * \text{EV}[j, t-1] + \beta_{2i} * \text{SpatAnol}[j, t-1] \tag{3}$$

To test the hypothesis that dragonflies (Anisoptera) and damselflies (Zygoptera) differ in their response to *E. viridulum*, we estimated their β terms as being drawn from two different distributions, allowing the suborders to diverge:

$$\beta_{1i} = \text{Aniso}_i(\beta_{Aniso} + \varepsilon_{Aniso}) + \text{Zygo}_i(\beta_{Zygo} + \varepsilon_{Zygo})$$

$$\varepsilon_{Zygo} \sim N(0, \sigma_{Zygo})$$

$$\varepsilon_{Aniso} \sim N(0, \sigma_{Aniso}) \tag{4}$$

These occupancy states were linked to the observed data—a logical matrix of which species were detected on each visit ($Y_{i,k}$)—through a detection sub-model. The probability of detecting a species on a visit ($P_{i,k}$) is modelled as a logit linked linear function of the number of species recorded on that visit, which provides a measure of sampling effort (Szabo et al., 2010). This function included three binary variables, indicating whether two ($LL2_k$), three ($LL3_k$), or four or more ($LL4_k$), species were recorded on the visit (Equation 5).

$$\text{logit}(P_{i,k}) = \beta_{3i} + \beta_{4i} * LL2_k + \beta_{5i} * LL3_k + \beta_{6i} * LL4_k \tag{5}$$

Thus, the logit probability that a visit list recording only one species is a record of focal species *i* is β_{3i}. The other three parameters

$(\beta_{4i}, \beta_{5i}, \beta_{6i})$ then capture how the logit probability of detection varies with increasing recorder effort, that is, if two species were recorded on that visit ($LL2_k = 1$) then the probability of detecting the focal
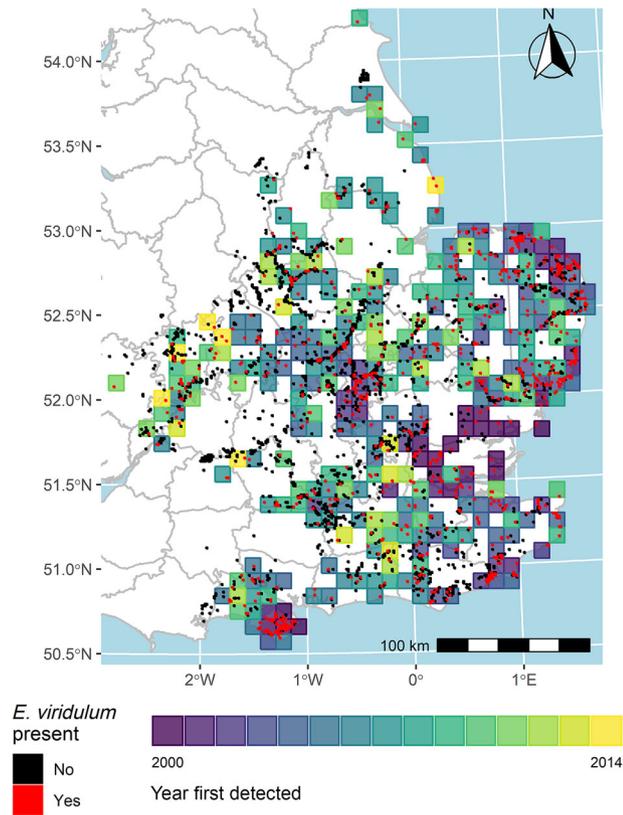
FIGURE 1 Distribution of *E. viridulum* in the United Kingdom in cells from the filtered dataset. Colour scale (blue to yellow) shows the first year *E. viridulum* was reported in that 10 km cell. The 1 km cells included in the study are shown in red, if *E. viridulum* was recorded at the site or black if absent.

species is $\beta_{3i} + \beta_{4i}$. Informing the model about the visit list length allowed it to estimate a possible impact of list length on detectability: our conception in this parameterisation is that longer list lengths imply higher search effort and thus detection probability on that visit (Outhwaite et al., 2019). However, the model formulation does not constrain this to be the case, that is ($\beta_{4i}, \beta_{5i}, \beta_{6i}$) can be negative. This might be the case if a species was particularly distinctive, leading inexperienced recorders to include just that species on their list as it was the only one they could identify. We did not estimate parameters for higher list lengths due to the small numbers of visits with lists of >5 species, which would make it hard to estimate the parameters. The observations on each visit inform the state sub-model via Equation (6), for example, if $Y_{i,k} = 1$ then $z_{i,j,t}$ must $= 1$.

$$Y_{i,k} = d\text{bern} \left(z_{i,j,t} * P_{i,k} \right) \qquad (6)$$

The priors used to fit this model were selected to be as weakly informative as possible and were the same for damselflies and dragonflies. The values are shown in the JAGS model code (Supporting Information Method S1).

Model fitting

In total, we ran four models. For both $EV_{AsReported}$ and $EV_{NoExtinction}$ datasets, we fitted the two models $Clim_{Exc}$ and $Clim_{Inc}$. These models were run to convergence using JAGS V4.3.0 (Plummer, 2003) and each model was run with three chains. We allowed our chains to run for 20,000 iterations, after adaptation (the sampling phase, determining how far the model moves in parameter space at each iteration). We discarded the first 10,000 iterations as burn-in and then thinned our chains by a factor of 20 to retain 500 samples of the posterior
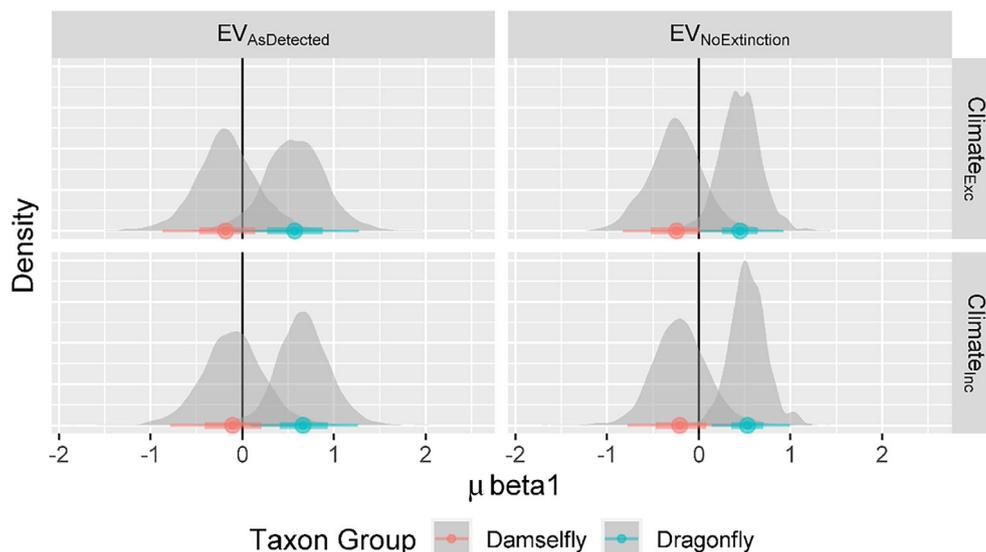
FIGURE 2 The posterior distributions for dragonflies (blue) and damselflies (red) from which *E. viridulum* (β1) species effects were drawn, credible intervals are shown for each model-data combination (point = mean, thick band = 66% CI, thin band = 95% CI). The central point represents the model's estimate for the effect of *E. viridulum* on an "average" damselfly's or dragonfly's probability of persistence at a site.

distribution per chain. Convergence was assessed by visual inspection and ensuring that Monte-Carlo Markov chains for all parameters had run to a point where they were sampling from the same area of parameter space (Brooks & Gelman, 1998). We checked for correlations between the sampled posteriors of the model parameters to assess model identifiability. Finally, we ensured that all parameters had an effective sample size of at least 1000. We describe the posterior distributions of our models' parameters using the mean and width of the 95% credible intervals. We report the Probability of Direction (PD), for our estimates of the effect of *E. viridulum*, which is the proportion of samples which have the same sign as the mean. PD is a metric of confidence in the direction of an effect if it exists.

RESULTS

E. viridulum was first recorded in the East and South of the United Kingdom, with high densities on the East Anglian Coast and the Isle of Wight (Figure 1). Sites were otherwise quite well distributed across the study area but with fewer in the North and West. The number of visits made to a site did not strongly relate to the year that *E. viridulum* was first detected which suggests that recording effort did not greatly affect the pattern of spread recorded (Figure S1).

We found that for all four model-data combinations, there was no net negative association between *E. viridulum* and UK damselfly (β_{Zygo}) and dragonfly (β_{Aniso}) site persistence (Figure 2). Climate itself seemed to have little effect on the persistence of residents, that is, posterior distributions for model parameters were qualitatively similar regardless of the input data or whether we included an effect of climate. We found that β_{Aniso} was more positive than β_{Zygo}, suggesting that *E. viridulum* had a different effect on damselflies as a suborder than dragonflies as a suborder. All four model-data combinations had over 90% of samples from the posteriors (probability of direction [pD]) with the same sign as the mean for this difference in *E. viridulum*'s effects between sub-orders (Table 1).

The species-level parameters for the effect of *E. viridulum* (β_{1i}) for the model where we included the effect of climate anomaly and used the unmanipulated *E. viridulum* occurrence dataset are shown in Figure 3. The species-level results for the other three models are shown in Figure S2 and are qualitatively similar. For damselflies, estimates of *E. viridulum*'s association with resident species (β_{1i}) fall either

side of 0, with a slight tendency towards a negative effect on persistence of resident species. The posterior means (μ) of the *E. viridulum* presence parameters (β_{1is}) suggested that *E. viridulum* establishment was associated with declines in the persistence of white-legged damselfly (*Platycnemis pennipes*) (pD = 1, $\mu = -1.1$) and *E. najas* (pD = 1, $\mu = -0.82$). The persistence of most dragonfly species was positively associated with *E. viridulum* establishment, with the exception of the brown hawker *A. grandis*. For only three dragonfly species was there less than 80% confidence in the direction of the effect (pD <= 0.8).

Damselfly

Dragonfly

beta1
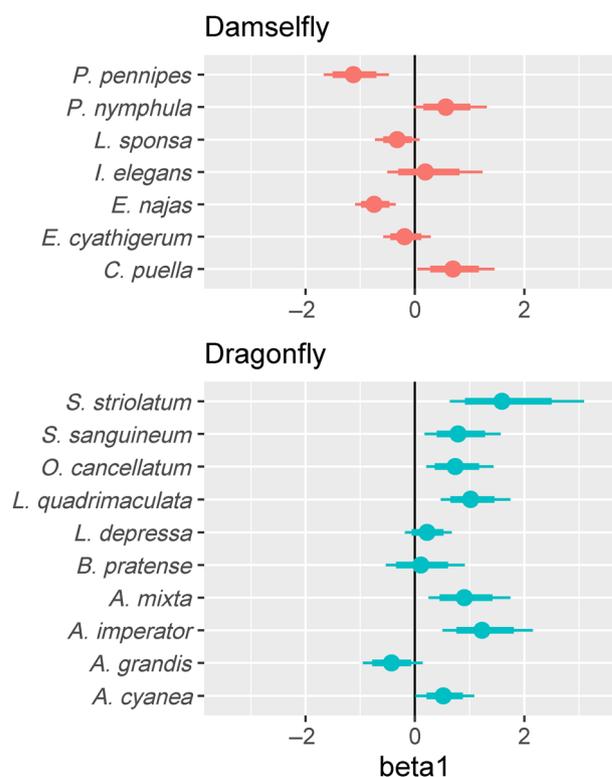
FIGURE 3 *E. viridulum*'s effect (β1) on persistence probability by species with credible intervals (point = median, thick band = 80% CI, thin band = 95% CI). Estimates shown are from the model where *E. viridulum* data was as detected and a climate effect was included (EV$_{AsReported}$ Clim$_{Inc}$). A positive coefficient indicates the species had a higher probability of persisting into the subsequent year, than if it was not present, and a negative coefficient a lower probability. See Figure S2 for results from other scenarios.

TABLE 1 Differences between *E. viridulum* effects on damselflies and dragonflies site persistence probability, shown by posterior mean (μ) and the proportion of samples matching the same sign as the mean (probability of direction [pD]) of the two distributions from which effects of *E. viridulum* were drawn.

Model	*E. viridulum* mean effect (damselflies)	*E. viridulum* mean effect (dragonflies)	Difference
EV$_{AsReported}$ Clim$_{Inc}$	$\mu = -0.10$, PD = 0.62	$\mu = 0.67$, PD = 0.99	$\mu = 0.77$, PD = 0.96
EV$_{AsReported}$ Clim$_{Exc}$	$\mu = -0.17$, PD = 0.71	$\mu = 0.58$, PD = 0.96	$\mu = 0.75$, PD = 0.93
EV$_{NoExtinction}$ Clim$_{Inc}$	$\mu = -0.20$, PD = 0.76	$\mu = 0.54$, PD = 0.99	$\mu = 0.73$, PD = 0.97
EV$_{NoExtinction}$ Clim$_{Exc}$	$\mu = -0.25$, PD = 0.81	$\mu = 0.45$, PD = 0.98	$\mu = 0.70$, PD = 0.96

Note: The pD for the difference in mean effect was calculated by comparing the two parameters in individual samples to derive a posterior distribution for the difference.

DISCUSSION

E. viridulum integration into UK resident biota

All four data-model combinations showed no clear negative association, on average, between *E. viridulum* presence and the persistence of either resident dragonflies or resident damselflies (which showed only a slight negative tendency). Rather, the mean association with resident dragonfly species was predicted as a positive effect. This suggests *E. viridulum* is not particularly harmful to resident Odonata as a whole. However, species-specific results may suggest a negative effect of *E. viridulum* presence on two resident damselfly species, including on its congener, *E. najas*. Alternatively, the two resident damselflies could be hindering the establishment of *E. viridulum*.

A possible explanation for this average positive association could be facilitative interactions (Rodriguez, 2006). However, it is hard to identify what these could be in practice. Positive indirect effects such as *E. viridulum* suppressing predators of resident species seem unlikely to affect such a broad range of species (Golubski & Abrams, 2011; Wissinger & McGrady, 1993). *E. viridulum* is a generalist rather than specialist predator so is unlikely to substantially change the food web by altering the abundance of one or a few species. *E. viridulum* could be a food source, particularly for the much larger dragonflies. However, Odonata larvae form only a small part of the diet of other Odonata (Kaunisto et al., 2017, 2020). *E. viridulum* is also not known to have any ecological engineering behaviour (Thomsen et al., 2010).

Rather than facilitation, it seems more likely that the positive association is because *E. viridulum* is differentially establishing in sites of high quality for resident Odonata and thus where historically resident species are persisting well (Balzan, 2012; Gibbons et al., 2002). *E. viridulum* may also be unlikely to establish in sites where resident species were declining. Hiley et al. (2014) found that wetland bird species range-shifting into the United Kingdom tended to establish first in protected areas and then spread out into surrounding areas. Our results suggest that high-quality aquatic habitat could be having a similar effect facilitating the settlement of range-shifting Odonata. This highlights that even rapid range-shifters can be dependent on high-quality habitat, and we might expect high quality, biodiverse sites to become home to increasing numbers of range-shifters in future.

If the interpretation that habitat quality is behind positive associations between *E. viridulum* and historically resident species is correct, then the effects shown in Figure 2 would represent the mean effect of habitat quality for dragonflies and damselflies, combined with any impacts of *E. viridulum*. The variation in the strength of the association between presence of *E. viridulum* and each resident species could be caused by variation in habitat preferences. More positive relationships could suggest that the resident species' habitat preferences more closely match those of *E. viridulum*. However, we cannot rule out that interactions between *E. viridulum* and resident species contribute to the associations seen, for example, lessening associations that would otherwise have been more positive.

Our ability to detect biotic interactions may have been reduced by the need to consider co-occurrence in 1 km² cells to indicate that species encounter one another. Damselfly home range size is much smaller than 1 km², meaning that such 'co-occurring' species may not actually share habitat or otherwise genuinely interact (Dormann et al., 2018; Montesinos-Navarro et al., 2018). Nonetheless, the positive mean association suggests range-shifter and the resident Odonata community are responding similarly to some environmental factor and given that we ruled out the effect of mean annual temperature, habitat seems the most likely.

We interpret the negative association between *E. viridulum* and persistence probability of *P. pennipes* and *E. najas* cautiously, given the potential effects of habitat and coarse spatial resolution discussed above, and because there was not a strong trend towards negative effects in damselflies (PD values, Table 1). However, the fact that one of the negative associations occurred with *E. viridulum's* congener species may suggest competitive displacement as functional traits such as flight period and habitat are likely to overlap. The stronger tendency for *E. viridulum* to form a negative association with other damselflies (including *P. pennipes*) than with dragonflies also matches the competitiveness-relatedness hypothesis (Cahill et al., 2008) and suggests that intra-suborder interactions may be a greater risk to resident species than inter-suborder interactions. However, this literature is still contested (Naughton et al., 2015). Another biotic interaction potentially underlying the negative association between related species may not be easily quantified but could be highly impactful: the spread of novel diseases or parasites such as *Arrenurus* mites (Forbes et al., 2002). Our findings suggest *P. pennipes* and *E. najas* as priorities for future autecological studies into negative effects. This prioritisation is particularly useful given the limited available resources for most non-pest entomological research.

Our results feed into a mixed literature on the effects of range-shifting *E. viridulum* on resident biota. Diet sampling of *E. viridulum* revealed no direct predation of other damselflies (Cox, 2013). However, Cox's study was conducted late in the larval growth period and may not have fully captured the potential complexity of intraguild predation (Frances & McCauley, 2018). Furthermore, Odonata larvae are known to predate voraciously on a range of non-Odonata taxa including, diptera and cladocerans, so *E. viridulum* could impact species from these taxa as well as other Odonata. New approaches such as meta-barcoding and stable isotope analysis may be able to clarify the trophic impacts of range-shifters (Do & Choi, 2019). Future DMSOs could complement these laboratory-based techniques by broadening to consider taxa outside the order Odonata (Kaunisto et al., 2020).

Annual climate did not appear to affect the population persistence of resident Odonata. This could be for several reasons: it is possible that at the spatial extent considered the effect of variation in climate is much smaller than the effects of other environmental variation; the spatial resolution of the data may be insufficient to reflect the microclimates actually experienced by the Odonata (Bütikofer et al., 2020); or more species-specific climate metrics may be necessary. Mean annual temperature has been shown to be important for the distributions of many Odonata (Termaat et al., 2019). However, temperature during species-specific flying seasons or key periods of

larval growth could be more informative in this case (Collins & McIntyre, 2015).

One detail we did not explicitly consider in our models is that several UK Odonata species are expanding their ranges (Mason et al., 2015) at the same time as *E. viridulum* is establishing. Therefore, range-expansion could create specious patterns in our data. For example, as *E. viridulum* is distributed in the south of the United Kingdom, it is more likely to overlap with the core ranges of resident species, rather than with their range-fronts. This discrepancy could affect our parameter estimates as core range populations may have more stable demographic rates than those at the range edge (where populations were more stochastic and had a greater potential to be population sinks) (Guo et al., 2005). This would result in a positive association between the presence of *E. viridulum* and the persistence of resident species, which could obscure the effects of any species interactions.

Improving models of range-shifter integration into resident biota

While we tried to reduce the effects of habitat variation by restricting analysis to sites with *E. viridulum* or *E. najas* reported, it was not possible to explicitly include habitat in our models. This is because the UK lacks data on the occurrence, characteristics, and water quality of small ponds and lakes. The challenge of obtaining sufficiently fine-resolution habitat data to study spatio-temporal trends in populations is true for most invertebrates, which make up the majority of species range-shifting into the United Kingdom and communities potentially affected (Gurney, 2015). Our results suggest that in the absence of high-resolution habitat data, trends in resident populations might themselves prove a useful proxy to inform where range-shifting species might establish next.

A limitation of our model is that the effect of *E. viridulum* presence on resident species was limited to two levels (i.e. present or absent). It could be that more complex functions, for example, a monotonic or logistic function parameterised with time since arrival could help capture effects dependent on *E. viridulum* population density (Sofaer et al., 2018). A monotonic or logistic function may be appropriate, given the delay in impact we might expect from when *E. viridulum* first arrives until it becomes locally abundant (Parker et al., 1999).

The detection sub-model of the DMSO also has scope for refinement (Boakes et al., 2016). Recorders are a diverse group and different sub-cultures within it can produce data of different information content, for example, those who keep complete lists versus single observations. It is currently challenging to incorporate these behavioural aspects into our models. We use the total list length on the visit as a proxy for recording effort. However, metrics such as recorder experience or even site knowledge could be more relevant. Another unknown aspect is to what extent new species like range-shifters attract different recording effort compared with resident species. Range-shifters could be both under-detected due to rarity or not being included in reference materials or be more likely to be reported

through the excitement of novelty (Cranston et al., 2021). In our study, we did not see a meaningful change in our results dependent on our two assumptions about recording effort (i.e. whether we assumed *E. viridulum* was present as reported or whether a single report indicated unobserved persistence thereafter). However, for other species, this distinction could be more impactful and efforts to understand how we can better model occurrences are the backbone for improving the outputs of DMSOs.

The likelihood that our results are caused by shared responses to habitat quality suggests that understanding the range-shift process of Odonata requires higher resolution location data and accompanying habitat data. High-resolution habitat information is increasingly available from remote sensing (Boyle et al., 2014), but metadata on spatial accuracy is often insufficient to link species records to such habitat data (Maldonado et al., 2015). Ideally, records of residents and range-shifters would be made available at an accuracy of tens of metres. Recorders could be encouraged to provide information that confirms population status, such as life-stage, sex, and whether breeding behaviour is observed (Patten et al., 2019; Raebel et al., 2010). Recorders could also be encouraged to report interactions that might reveal finer habitat requirements, for example, egg-laying on particular macrophytes. To be of most use for monitoring range-shifts, recording schemes could standardise habitat and breeding-status recording. It is also important to note that the timeliness and accessibility of occurrence data are crucial in the face of fast-moving environmental change. Therefore, it is also important to improve both local recording capacity (e.g. resourcing local environmental records centres to provide training and equipment) and national data infrastructure (e.g. continued development of the National Biodiversity Network Atlas).

Experimental data on *E. viridulum*'s rates of dispersal could also assist our ability to model drivers and impacts of range-shift (Jaeschke et al., 2013). Such empirical data could inform choices of priors in Bayesian models such as DMSOs and potentially reduce the required number of assumptions, increasing their realism.

CONCLUSION

The strength of DMSOs for assessing range-shifters' potential impacts lies in their ability to search for associations between spatio-temporal population trends in a broad range of species, while incorporating environmental effects. However, our findings show the current difficulty in interpreting potential biotic interactions inferred by these models due to the possibility of confounding factors such as habitat quality and spatial resolution. We argue *E. viridulum* is unlikely to be genuinely facilitating other species but rather responding to the same fluctuations in habitat quality as residents. This highlights that future approaches to identify the effects of range-shifting species should make use of the increasing availability of high-resolution habitat and microclimate data. Field or laboratory competition experiments will remain the gold standard for proving causal impacts but are prohibitively costly to perform for all species. Therefore, we can productively

use DMSOs to prioritise species at potential risk, such as the red-eyed damselfly (*E. najas*, *E. viridulum*'s congener), for further investigation by more sensitive methods.

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in British Dragonfly Society Recording Scheme at https://registry.nbnatlas.org/public/show/dp97.

ETHICS STATEMENT

No animals or museum specimens were used, or field work undertaken, in the research

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Supporting information