PRIMARY RESEARCH ARTICLE

WILEY **Global Change Biology**

Species' traits as predictors of range shifts under contemporary climate change: A review and meta-analysis

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Abstract

A growing body of literature seeks to explain variation in range shifts using species' ecological and life-history traits, with expectations that shifts should be greater in species with greater dispersal ability, reproductive potential, and ecological generalization. Despite strong theoretical support for species' traits as predictors of range shifts, empirical evidence from contemporary range shift studies remains limited in extent and consensus. We conducted the first comprehensive review of species' traits as predictors of range shifts, collecting results from 51 studies across multiple taxa encompassing over 11,000 species' responses for 54 assemblages of taxonomically related species occurring together in space. We used studies of assemblages that directly compared geographic distributions sampled in the 20th century prior to climate change with resurveys of distributions after contemporary climate change and then tested whether species traits accounted for heterogeneity in range shifts. We performed a formal meta-analysis on study-level effects of body size, fecundity, diet breadth, habitat breadth, and historic range limit as predictors of range shifts for a subset of 21 studies of 26 assemblages with sufficient data. Range shifts were consistent with predictions based on habitat breadth and historic range limit. However, body size, fecundity, and diet breadth showed no significant effect on range shifts across studies, and multiple studies reported significant relationships that contradicted predictions. Current understanding of species' traits as predictors of range shifts is limited, and standardized study is needed for traits to be valid indicators of vulnerability in assessments of climate change impacts.

KEYWORDS
body size, diet breadth, fecundity, global change, habitat breadth, life history, range expansion

1 | INTRODUCTION

Although species' functional traits have long been recognized as being both products and drivers of ecological processes (Stearns, 1977; Tilman, Wedin, & Knops, 1996), a renewed focus on trait diversity has grown in recent years (Gibert, Dell, DeLong, & Pawar, 2015). Ecological and life-history traits shared by groups of organisms have been used to create frameworks for community assembly (Laughlin, Joshi, van Bodegom, Bastow, & Fulé, 2012) and nutrient cycling (Zuo et al., 2015), predict species and community responses to disturbance (Mouillot, Graham, Villéger, Mason, & Bellwood, 2013; Pellegrini, Franco, & Hoffmann, 2016; Pryde, Nimmo, Holland, & Watson, 2016), and evaluate ecosystem functions and services (Cardinale et al., 2012; Schmitz, Buchkowski, Burghardt, & Donihue, 2015). Species' traits are also well-known drivers of invasion ecology and range dynamics (Chuang & Peterson, 2016; Clark, 1998), making them promising candidates to explain species-specific variation in range shifts under contemporary climate change (Estrada, Morales-Castilla, Caplat, & Early, 2016). Range shifts observed under recent climate change appear highly idiosyncratic (Parmesan & Yohe, 2003;

Wiens, 2016) and are thought to be driven by exposure (as measured by the magnitude of climate change experienced by a species; Loarie et al., 2009; Dawson, Jackson, House, Prentice, & Mace, 2011) and mediated by species-specific capacities to move to more suitable locations (Dawson et al., 2011; Williams, Shoo, Isaac, Hoffmann, & Langham, 2008). Traits have important influences on how species respond to exposure and their range expansion capacity. Therefore, traits could provide valuable evidence-based tools for conservation and management that could increase the accuracy of extinction risk projections (La Sorte & Jetz, 2010; Thomas et al., 2004), vulnerability assessments (Foden & Young, 2016; Foden et al., 2013), and predictions of novel community assemblages (Stralberg et al., 2009; Williams & Jackson, 2007).

Hypotheses for how species' traits should relate to range shifts are based largely on assumptions that patterns will be similar to those observed in studies of abundance shifts, range size, range filling, and invasion potential (Estrada et al., 2016). For the margin of a species' range to expand, individuals must possess the physical capacity to disperse into previously unoccupied areas. Therefore, species with greater dispersal potential (e.g., larger body size or more migratory behavior) are expected to show larger range shifts (Angert et al., 2011; Buckley & Kingsolver, 2012). Once individuals of a species disperse into previously unoccupied areas, high reproductive potential (e.g., fast life history strategies such as high fecundity and low longevity) facilitates the establishment of viable populations (Angert et al., 2011; Perry, Low, Ellis, & Reynolds, 2005). Persistence in areas beyond the historic range limit will also depend on the ability to find appropriate food and habitat. Generalist species (e.g., those with greater diet or habitat breadth) should be more likely to find suitable resources in novel areas and should therefore show greater range shifts than specialists, which require concomitant range shifts of species on which they depend (Angert et al., 2011; Berg et al., 2010; Buckley & Kingsolver, 2012). Finally, although not strictly a species' trait, species with initial range limits located at higher latitudes or altitudes are expected to show smaller range shifts over time; for example, mountaintop species have less room to shift their altitudinal limit upward (Angert et al., 2011).

Despite strong theoretical support for these traits as predictors of climate-induced range shifts, empirical support is limited in extent and consensus (Angert et al., 2011; Buckley & Kingsolver, 2012). At the species and community scales, considerable controversy remains over the mechanistic justification for traits (Estrada et al., 2016), particularly under varying contexts of environmental matching (Sol et al., 2012), biotic interactions (Angert et al., 2011), and trait covariance (Laube et al., 2013; Sekar, 2012). At broader geographic and taxonomic scales, traits are increasingly being incorporated into multispecies range projections (Barbet-Massin, Thuiller, & Jiguet, 2012; Bateman, Murphy, Reside, Mokany, & VanDerWal, 2013; Iverson, Prasad, Matthews, & Peters, 2011; Midgley, Hughes, Thuiller, & Rebelo, 2006; Schloss, Nuñez, & Lawler, 2012) and climate change vulnerability assessments (Foden et al., 2013; Gardali, Seavy, DiGaudio, & Comrack, 2012; McClure et al., 2013). Such models may provide a useful approximation of heterogeneity in species-specific

range shifts when mechanistic data are not available or feasible to incorporate (Buckley & Kingsolver, 2012), but they assume trait-based relationships that at present remain largely unvalidated. Recently, Pacifici et al. (2017) examined whether life-history traits explained whether bird and mammal populations were positively or negative affected by climate change, but there has been no global analysis of how traits influence recent range shifts of species.

Two approaches can be used to quantitatively synthesize the strength of current evidence for traits as predictors of recent range shifts. The first approach is to conduct a meta-analysis of primary data (Mengersen, Gurevitch, & Schmid, 2013) compiled from existing studies of range shifts of individual species and their corresponding traits to produce a fine-scale investigation of the influence of traits in different phylogenetic, geographic, and biotic contexts. While meta-analysis of primary data is often championed, valid applications must address problems of comparability among studies due to ecological and methodological heterogeneity, and it is often difficult, costly, and time-consuming to assemble a comprehensive and comparable dataset with all of the relevant data (Mengersen, Gurevitch, & Schmid, 2013). As a result, meta-analyses of primary data are rare in ecology (Mengersen, Gurevitch, & Schmid, 2013) as well as in the data-rich field of medicine (Simmonds et al., 2005). To the best of our knowledge, a data set compiling range shifts of species related to contemporary climate change and their corresponding traits does not currently exist. The second approach is to conduct a formal meta-analysis of study-level effect sizes for aggregated data from published studies that compared geographic distributions of assemblages (taxonomically related species occurring together in space; Stroud et al., 2015) sampled in the 20th century prior to climate change with resurveys of distributions after contemporary climate change and then tested whether species traits accounted for heterogeneity in range shifts. Meta-analysis of aggregated data encompasses a set of rigorous statistical techniques (Glass, 1976; Koricheva & Gurevitch, 2013) that have been used to synthesize evidence for over three decades in the social sciences (Hines, Hungerford, & Tomera, 1987; White, 1982) and over two decades in ecology (Aguilar, Ashworth, Galetto, & Aizen, 2006; Jarvinen, 1991; McKnight, García-Berthou, Srean, & Rius, 2016; Myers & Mertz, 1998; Weber, Stevens, Diniz-Filho, & Grelle, 2016). These methods estimate the mean effect size across multiple studies after weighting individual studies by their standard error (i.e., stronger studies with smaller standard errors weight more heavily) and can be designed to account for ecological and methodological heterogeneity among studies using covariates (Stewart, Côté, & Rothstein, 2013).

Here, we evaluate empirical support for the leading hypotheses that climate-induced range shifts are larger in species with greater dispersal ability, reproductive potential, and ecological generalization (Angert et al., 2011; Buckley & Kingsolver, 2012; Estrada et al., 2016). We present the first comprehensive review of species' traits as predictors of recent range shifts, using vote counting to summarize results from 51 studies encompassing over 11,000 species responses across 54 assemblages of multiple taxa. We then conduct a formal meta-analysis to quantitatively assess study-level mean

effect sizes on range shifts for five focal traits with sufficient sample sizes—body size, fecundity, diet breadth, habitat breadth, and historic range limit. This two-step procedure of vote counting followed by formal meta-analysis is recommended to avoid a loss of information (Koricheva & Gurevitch, 2013, page 11). Our meta-analysis objectives were to (i) calculate the mean effect size of each trait on observed range shifts, and (ii) test whether study-level ecological and methodological covariates explain variation in effect sizes of traits across studies. While our meta-analysis is unlikely to control for all sources of heterogeneity among studies, it provides an informative first assessment of traits as predictors of climate-induced range shifts at the broad taxonomic and geographic scales currently used to project future ranges and to conduct vulnerability assessments for scenarios of climate change.

2 | MATERIALS AND METHODS

We searched the literature for studies that related species' traits to range shifts (either range margin or range center) for assemblages of any taxa. We searched the online database Web of Science for papers published between 2000 and 2015 with keywords "climate" and "range shift/expansion," "latitudinal shift/expansion," or "elevational shift/expansion." The search produced approximately 11,200 results. From this set, we chose papers for closer scrutiny if they directly analyzed potential range shifts by explicitly comparing 20th century and contemporary assemblages. These studies included both single-year resurvey efforts and multiyear resurveys of atlas data; for the latter studies, we compared the first and last years of atlas data. Of the 145 papers that met the above criteria, 50 studies (54 analyses of assemblages, accounting for studies that performed separate analyses for different taxa) measured the effect of at least one species trait on variation in range shifts (see Table S1). While it would have been ideal to further refine studies to those that accounted for differences in detection probability or survey effort that could bias observed range shifts between 20th century and contemporary surveys, the limited number of studies (Moritz et al., 2008; Tingley, Monahan, Beissinger, & Moritz, 2009) made this unfeasible.

We began analysis by qualitatively summarizing results (significant positive, significant negative, or nonsignificant) for the eight most commonly tested traits across studies: body size, migratory strategy, movement ability (including seed dispersal mode, flight behavior, or dispersal distance), fecundity, longevity, diet breadth, habitat breadth, and historic range limit. We then carried out meta-analyses for five focal traits that were measured consistently by at least six studies: body size (13 studies; 13–1075 species/study), fecundity (nine studies; 13–143 species/study), diet breadth (14 studies; 13–282 species/study), habitat breadth (10 studies; 13–1075 species/study), and latitudinal or altitudinal limit of the historic range (eight studies; 13–143 species/study). Raw data on effect sizes are given in Tables S2–S6. Body size was quantified as average length or mass, and fecundity as the number of eggs or live young produced annually per female. Most studies quantified diet breadth

and habitat breadth using a discrete numerical scale that represented the number of diet or habitat types used by a species; for studies that presented only categorical diet or habitat categories, we reduced the data to a binary comparison between the omnivore or generalist category (as identified by the original study) and any other categories. Studies documented shifts in the margin ($n = 22$ with 7–13 studies per trait) or center ($n = 4$ with 0–1 studies per trait) of either elevational ($n = 13$ with 4–5 studies per trait) or latitudinal ($n = 13$ with 3–9 studies per trait) ranges, and encompassed a variety of taxa and geographic locations (Fig. S1). Migratory strategy, movement ability, and longevity traits were included in our literature review and a vote count tally of studies evaluating predictions, but could not be included in our formal meta-analysis due to insufficient sample size or noncomparable trait measurement schemes across studies.

For each study, we collected an effect size that measured the trait's influences on range shifts for assemblages of taxonomically related species. Studies varied in how they measured traits (e.g., mass or length for body size) and range shifts (e.g., distance of shift, rate of shift, or a binary shift v. no shift), so we standardized all effect sizes. For categorical trait variables, we calculated the standardized mean difference in range shifts between two groups (e.g., omnivores vs. specialists) using Cohen's D (Lipsey & Wilson, 2001; Rosenberg, Rothstein, & Gurevitch, 2013). For continuous variables, we used the beta coefficient reported from regression analysis. When standardized beta coefficients were not provided in the original study, we standardized the coefficients following Bring's (1994) equation:

$$\beta_s = \beta_{us} \frac{\sigma_x}{\sigma_y}$$

where β_s = the standardized beta coefficient, β_{us} = the unstandardized beta coefficient, σ_x = the standard deviation of the raw trait data, and σ_y = the standard deviation of the raw response data. In other words, the standardized beta coefficient quantifies how a change in x standard deviations of a trait variable is expected to produce a change of y standard deviations in extent of a range shift.

To explore sources of heterogeneity that may influence effect size, we compiled a set of study-level covariates related to both ecological and methodological factors. Ecological factors included taxa mobility (mobile birds and marine fish vs. other, less mobile taxa, with grouping based on patterns observed in the literature review; a full taxa-based analysis was impractical due to limited sample size) and range shift type (latitudinal or altitudinal). A covariate to control for whether a study analyzed the range center vs. margin was not feasible because only four studies quantified shifts in range centers. Visual inspection of the standardized effect sizes and variances for those four studies (Forero-Medina, Terborgh, Socolar, & Pimm, 2011; Nye, Link, Hare, & Overholtz, 2009; Perry et al., 2005; Reif & Flousek, 2012) indicated that they were within the values spanned by studies of range margins. Methodological factors included the number of species studied, study duration (number of years between

historic and modern data), exposure to climate change (change in mean annual temperature over the study period; when not reported, we calculated change in mean annual temperature between the first and last ten years of the study using WorldClim data; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), size of study area (km^2), and phylogenetic control (a binary indicator of whether or not a study controlled for phylogeny in the analysis). The latter is a reasonable approach given that meta-analytical methods cannot fully control for phylogeny, especially in our study where effect size is unable to be decomposed and taxa are so diverse that combining phylogenies would be difficult (Jennions, Lortie, Rosenberg, & Rothstein, 2013; Lajeunesse, Rosenberg, & Jennions, 2013).

We analyzed effect sizes using the METAFOR package in R (Schmid, Stewart, Rothstein, Lajeunesse, & Gurevitch, 2013; Viechtbauer, 2010). We used meta-analysis models to calculate mean effect size across studies by weighting each study-specific effect size by its corresponding standard error. We used random effects (RE) models that allowed effect sizes to vary around the mean due to unaccounted for heterogeneity in methodology or study system (Mengersen, Schmid, & Jennions, 2013). We used RE models as opposed to fixed effects models, because the latter assume a single common effect size across studies and assume that any heterogeneity across studies is due to chance alone (Trikalinos, Salanti, Zintzaras, & Ioannidis, 2008; Viechtbauer, 2010).

To calculate mean effect sizes, we modeled each trait individually without covariates to test whether the mean effect size across studies was significantly different from zero. Although a multivariate framework may be ideal to calculate the relative effects of and potential interactions among traits, the univariate approach was a limitation of our meta-analysis model and the small number of studies that analyzed similar sets of traits (see also McKnight et al., 2016). We also modeled effect size as a function of study-level covariates to explore drivers of heterogeneity across studies and to determine whether mean effect sizes were significantly different from zero when accounting for this variation. We present model sets consisting only of individual covariates; complex models consisting of additive combinations of two covariates and interactive effects between methodological and ecological covariates were not included in the model set due to limited sample size and to avoid overfitting. Exploratory analyses indicated that models with combinations of two or more covariates never performed better than models with one covariate. Model code is provided in Appendix S1.

We assessed publication bias through visual inspection of funnel plots, a scatterplot of effect size against standard error (Jennions et al., 2013). Although funnel plots are difficult to interpret when fewer than 30 studies are included (Jennions et al., 2013), funnel plots from the top model for each trait were relatively evenly and symmetrically distributed (Fig. S2). Additionally, the mean range shifts from studies included in our meta-analysis had a similar median and range when compared to the mean range shifts reported in the other studies of assemblages we identified in our literature review (Fig. S3).

3 | RESULTS

Figure 1 summarizes qualitative results for the eight most commonly tested traits (from 5439 species responses across 39 studies of 42 assemblages). The relationship between traits and range shifts varied greatly among studies. Significant effects were uniformly positive for habitat breadth and for traits related directly to movement ability (including seed dispersal mode or natal dispersal distance). Significant effects were uniformly negative for historic range limit. Migratory strategy, fecundity, longevity, diet breadth, and body size exhibited a mixture of significant positive and negative relationships with range shifts. When considering both significant and nonsignificant results, historic range limit was the strongest predictor of range shifts, with 60% of studies upholding the prediction that range shifts should be negatively related to historic range limit. Predicted relationships between traits and range shifts were weakly to moderately upheld for dispersal ability (22% for studies of body size, 10% for migratory strategy, and 50% for movement ability), reproductive capacity (36% for fecundity and 60% for longevity), and ecological generalization (27% for diet breadth and 43% for habitat breadth).

In the formal meta-analysis (based on 3123 species responses across 21 studies of 26 assemblages), effect sizes varied greatly among studies and included both positive and negative effects for all traits except historic range limit (Figure 2). Mean effect size did not differ significantly from zero for body size, fecundity, diet breadth, or habitat breadth (Table 1, Figure 1), indicating that these traits did not have a significant effect on range shifts across studies. However, historic limit had a significant mean effect size of -0.30 ($\tau^2 = 0.037$; 95% CI $= -0.48$, -0.12), indicating that for every standard deviation increase in latitude or altitude of the historic range limit of a species, its corresponding range shift decreased by 0.3 standard deviations.

Ecological and methodological differences among studies accounted for heterogeneity in effect sizes of some traits. Variation in effects of body size was best explained by taxa mobility (Table 2). Body size had a significantly negative mean effect on range shifts of birds and marine fish ($\mu = -0.275$, 95% CI $= -0.45$, -0.01), indicating that range shifts increased as body size decreased. In less mobile taxa, body size explained little variation in range shifts (Figure 2a; $\mu = 0.148$, 95% CI $= -0.07$, 0.36). Mean effect size of diet breadth (Figure 2c) was best explained by whether the range limit studied was altitudinal ($\mu = -0.23$, 95% CI $= -0.48$, 0.02) or latitudinal ($\mu = 0.08$, 95% CI $= -0.06$, 0.22), but mean effect sizes for these two groups did not differ significantly from zero (Figure 2c). Heterogeneity in mean effect size of habitat breadth was best explained by study area (Table 2); effect size increased as study area increased, with a positive relationship between habitat breadth and range shifts for study areas above 200,000 km^2 (Figure 2f). Results were unchanged when the largest study area (South Africa, 1.2 million km^2) was excluded from the analysis (AIC$_c$ w of top model declined from 0.99 to 0.78). Covariates explained little variation in mean effect sizes of fecundity or historic range limit (Table 2).
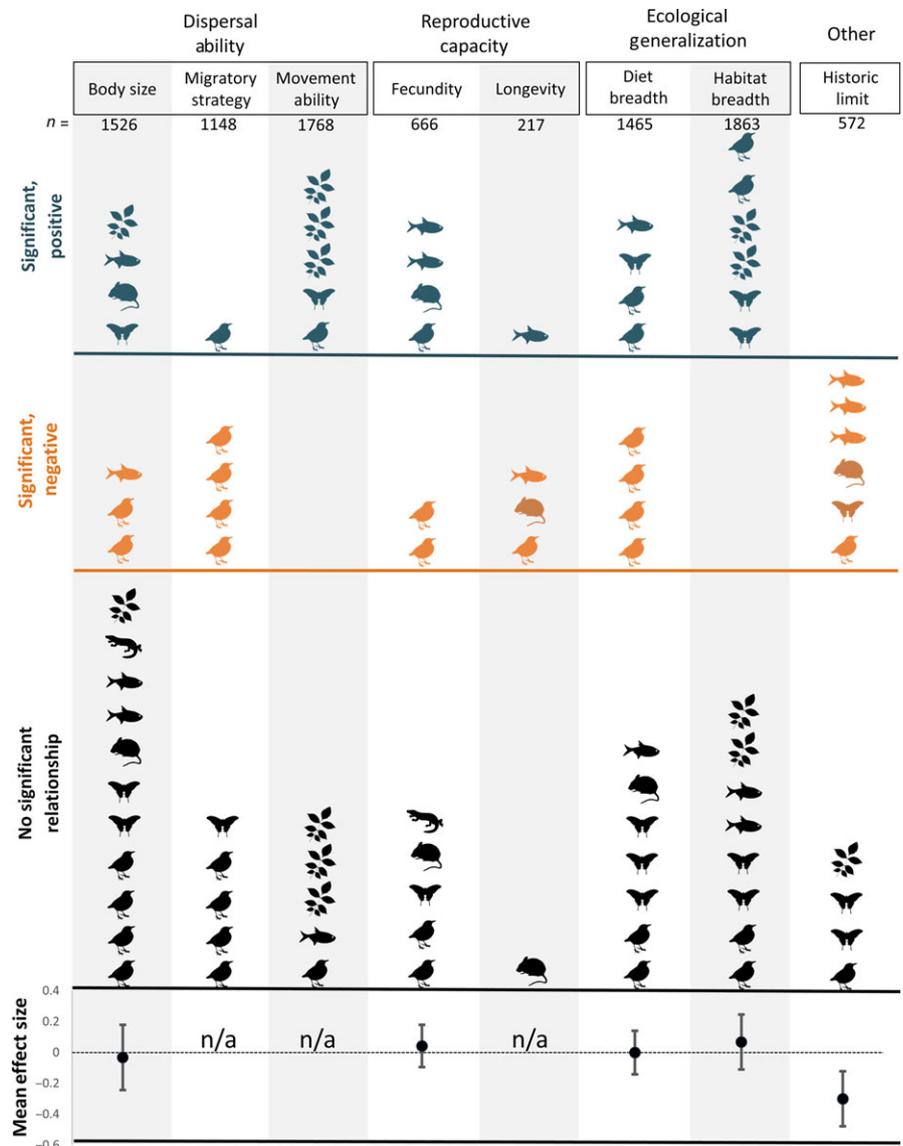
FIGURE 1 Summary of effects of species' traits on range shifts for the eight most commonly tested traits. Each icon represents the result from a single study of birds, small mammals, fish, invertebrates, reptiles, or plants, respectively, and n = the total number of species responses represented by all studies for each trait. Mean effect sizes ($\pm$ 2 standard errors) are based on meta-analytical models without covariates (see Table 1 for meta-analysis sample sizes).

4 | DISCUSSION

4.1 | Degree of support for investigated traits as predictors of recent range shifts

Results from our literature review and meta-analysis indicated that ecological and life-history traits had limited success in accounting for variation among species in range shifts over the past century. Predicted relationships between traits and range shifts received only low-to-moderate levels of support (Figure 1). Of the five traits that received sufficient study to be included in our formal meta-analysis, only habitat breadth and historic range limit supported range shift predictions (Figures 1 and 2). All published significant relationships between habitat breadth and range shifts were positive (Alofs, Jackson, & Lester, 2014; Davey, Devictor, Jonzén, Lindström, & Smith, 2013; Hockey, Sirami, Ridley, Midgley, & Babiker, 2011; Jiménez-Alfaro, Gavilán, Escudero, Iriondo, & Fernández-González, 2014; Powney, Rapacciuolo, Preston, Purvis, & Roy, 2013; Pöyry, Luoto,

Heikkinen, Kuussaari, & Saarinen, 2009). Although the mean effect size of habitat breadth across all studies did not differ significantly from zero (Figure 1), range shifts increased with habitat breadth when we accounted for heterogeneity in size of study areas (Figure 2f). Our meta-analysis also found a significant negative mean effect size between historic range limit and range shifts (Figure 1), and all published significant relationships were negative (Alofs et al., 2014; Angert et al., 2011; Auer & King, 2014; Grenouillet & Comte, 2014; Menéndez, González-Megías, Jay-Robert, & Marquéz-Ferrando, 2013; Nye et al., 2009). Thus, species that occupied higher altitudes or latitudes tended to have smaller range shifts than species occupying lower altitudes or latitudes.

Some traits showed relationships that were contrary to range shift expectations under the leading hypotheses (Figure 1). Although species with longer migration distances typically have longer dispersal distances (Dawideit, Phillimore, Laube, Leisler, & Böhning-Gaese, 2009; Paradis, Baillie, Sutherland, & Gregory, 1998) and should show greater range shifts, multiple studies have documented smaller range
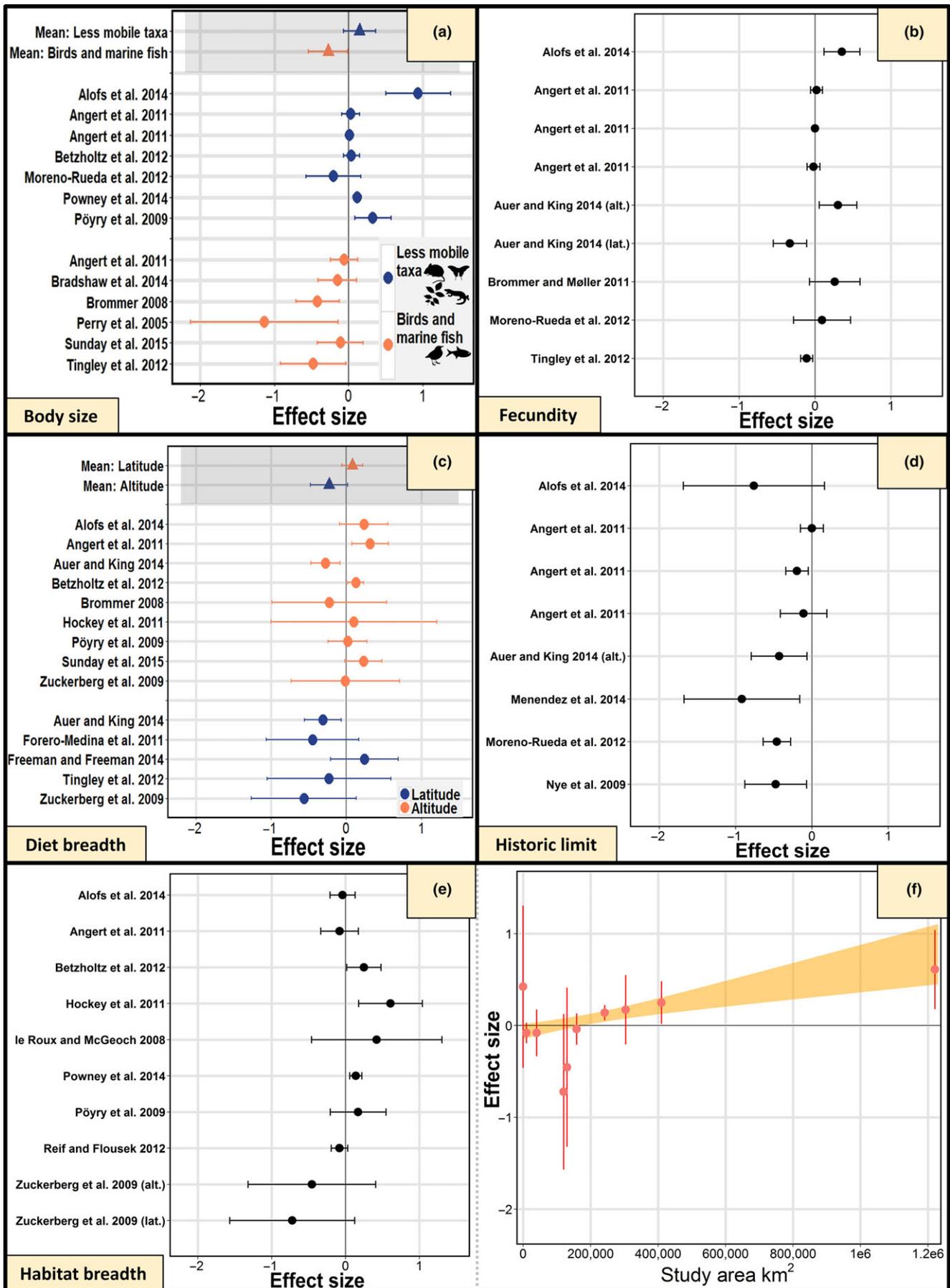
FIGURE 2 Raw and mean effect sizes for the relationship between species' traits and range shifts as a function of study-level covariates, according to the top model for each trait: (a) effects of body size on range shifts, differentiating between more mobile taxa (birds and marine fish) and less mobile taxa (plants, small mammals, invertebrates, reptiles, and freshwater fish); (b) raw effect sizes for fecundity, with no significant effects of covariates; (c) effect sizes for diet breadth, differentiating between studies of latitudinal vs. altitudinal range shifts; (d) raw effect sizes for historic range limit, with no significant effects of covariates; (e) raw effect sizes for habitat breadth without covariates; and (f) effect sizes of habitat breadth as a function of study area size. Error bars and orange-shaded regions indicate 95% confidence intervals.

TABLE 1 Mean effect sizes and between-study variation (τ^2) modeled for each trait using random effects models without covariates. For each study trait, the number of studies of assemblages used for the meta-analysis, number of species per study (mean $\pm$ SD), and total number of species responses pooled across studies are summarized. Number of studies included in meta-analysis is lower than studies reported in vote counting (Figure 1) because effect sizes could not be obtained from all studies

Trait	Studies	Species per study	Total responses	Mean effect size	τ^2	SE	$p \leq$
Body size	13	164 $\pm$ 283	2131	−0.032	0.128	0.11	.77
Fecundity	9	67 $\pm$ 46	546	0.042	0.034	0.07	.55
Diet breadth	14	95 $\pm$ 77	1323	0.000	0.033	0.07	.99
Habitat breadth	10	187 $\pm$ 324	1863	0.068	0.049	0.09	.45
Historic range limit	8	52 $\pm$ 44	416	−0.300	0.037	0.09	.001

TABLE 2 Summary of covariates explaining variation in effect sizes of species traits as predictors of range shifts. For each model, we report τ^2 (variation not accounted for by covariates), ΔAIC_c, and w (AIC_c weight). Models with $\Delta AIC_c < 2$ for each trait are bolded

Covariates modeled	Body size τ^2	ΔAIC_c	w	Fecundity τ^2	ΔAIC_c	w	Diet breadth τ^2	ΔAIC_c	w
Exposure (Δ °C)	0.142	7.02	0.02	0.036	4.20	0.07	0.039	3.71	0.05
Number of species	0.144	7.24	0.02	0.039	4.86	0.05	**0.029**	**1.87**	**0.12**
Phylogenetic control	0.139	6.78	0.03	0.039	4.76	0.05	0.038	3.54	0.05
Range type	0.139	6.80	0.03	0.040	5.06	0.05	**0.021**	**0.00**	**0.32**
Study area	0.146	7.34	0.02	0.039	4.86	0.05	0.038	3.57	0.06
Study duration	0.145	7.30	0.02	0.034	3.85	0.09	0.038	3.50	0.06
Taxa mobility	**0.073**	**0.00**	**0.74**	0.038	4.53	0.06	0.031	2.33	0.10
No covariates	0.128	3.45	0.13	**0.034**	**0.00**	**0.58**	0.033	0.43	0.25

Covariates modeled	Habitat breadth τ^2	ΔAIC_c	w	Historic range limit τ^2	ΔAIC_c	w
Exposure (Δ °C)	0.052	13.67	0.00	0.043	5.31	0.03
Number of species	0.056	14.19	0.00	**0.015**	**1.13**	**0.26**
Phylogenetic control	0.041	12.35	0.00	n/a	n/a	n/a
Range type	0.036	11.60	0.00	0.022	2.46	0.29
Study area	**0.000**	**0.00**	**0.99**	0.029	3.54	0.08
Study duration	0.063	14.91	0.00	0.048	5.83	0.03
Taxa mobility	0.059	14.47	0.00	0.048	5.81	0.03
No covariates	0.049	10.04	0.01	**0.037**	**0.00**	**0.45**

shifts in long-distance migrants compared to short-distance migrants (Brommer, 2008; Brommer & Møller, 2010; Tingley, Koo, Moritz, Rush, & Beissinger, 2012) or to nonmigratory species (Tingley et al., 2012; Zuckerberg, Woods, & Porter, 2009). A potential problem with using migratory behavior (and other proxy traits discussed in this study) as a predictor of range shifts is that other traits associated with long-distance migration may have confounding effects. For

example, long-distant migrants often show high fidelity to breeding and overwintering sites (Bensch, 1999; Laube et al., 2013) and may be more likely to exhibit phenological shifts in response to climate change (Estrada et al., 2016; Parmesan & Yohe, 2003).

Some traits showed no consistent relationship with range shifts. Fecundity and longevity both had a relatively even mixture of significant positive, significant negative, and nonsignificant relationships

(Figure 1), and fecundity did not have a significant mean effect size in the meta-analysis. For diet breadth, relationships with range shifts were insignificant about as often as they were significant (Figure 1), and significant relationships were equally positive (Angert et al., 2011; Betzholtz, Pettersson, Ryrholm, Franzén, & Franze, 2013; Freeman & Class Freeman, 2014; Sunday et al., 2015) and negative (Auer & King, 2014; Brommer, 2008; Brommer & Møller, 2010). Given these contradictory results, it is unsurprising that our meta-analysis found a mean effect size of zero for diet breadth in models both with and without covariates (Tables 1 and 2). Although species with greater diet breadth are predicted to have larger range shifts, an alternative hypothesis is that specialist species may be more likely to shift their ranges as they track their required resources, whereas generalists can persist better in situ (Buckley & Kingsolver, 2012; Jarzyna, Porter, Maurer, Zuckerberg, & Finley, 2015).

Body size also showed no significant mean effect size in relation to range shifts across studies of mammals, invertebrates, plants, reptiles, and freshwater fish, but smaller species of birds and marine fish tended to have greater range shifts than larger species (Figures 1 and 2). Larger-bodied organisms tend to disperse farther than smaller species (Dawideit et al., 2009; Jenkins et al., 2007; Sekar, 2012; Sutherland, Harestad, Price, & Lertzman, 2000), and fossil data suggest that larger species exhibited greater range shifts in response to glacial–interglacial cycles of the Pleistocene (Kaustuv, Jablonski, & Valentine, 2001; Lyons, Wagner, & Dzikiewicz, 2010). Therefore, larger species should show greater range shifts in response to contemporary climate change (Angert et al., 2011). However, body size is typically inversely correlated with reproductive potential and would therefore be expected to show a negative relationship with range shifts (Perry et al., 2005), creating confounding effects.

4.2 | Limitations of our meta-analysis

Our meta-analysis provides a glimpse of the potential to make important inferences by bringing together disparate studies of range shifts and traits, but was limited in several ways. Some traits have consistently supported the leading hypotheses, but have been tested by too few studies to enable a formal meta-analysis (Figure 1). For example, larger range shifts occurred in plant species with wind dispersed seeds compared to those with seeds dispersed by animals or gravity (Felde, Kapfer, & Grytnes, 2012; Holzinger, Hülber, Camenisch, & Grabherr, 2007; Parolo & Rossi, 2008), in specialist butterflies with more nitrogen-rich diets (Betzholtz et al., 2013), and in birds with larger brain mass (Brommer & Møller, 2010). Significant variation in range shifts has also been reported among species belonging to different diet guilds (Brommer, 2008; Freeman & Class Freeman, 2014; Reif & Flousek, 2012), or occupying different habitat niches (Angert et al., 2011; Hockey et al., 2011; Pöyry et al., 2009; Reif & Flousek, 2012), but methodological differences in defining these groups prohibited us from calculating effect sizes or making cross-study comparisons. While the current leading hypotheses relating species' traits to range shifts provide a good starting point, they

must be expanded to include additional traits as well as alternative competing hypotheses for the effects of traits.

Lack of strong mean effect sizes in our meta-analysis could be due to heterogeneity among studies that was not modeled, such as differences in species' detectability or barriers to movement. Detection probability varies among species, sites, and observers (Iknayan, Tingley, Furnas, & Beissinger, 2014; Jarzyna & Jetz, 2016; MacKenzie et al., 2002), and studies that do not control for detection probability may produce biased estimates of range shifts or have little power to detect them (Tingley & Beissinger, 2009). However, few studies of range shifts have explicitly modeled the detection process (Moritz et al., 2008; Tingley et al., 2009, 2012). The presence of anthropogenic land-use change in the study area may introduce additional bias in measures of range shifts, particularly if land-use change limits the areas where species can expand to track favorable climate (Hof, Araújo, Jetz, & Rahbek, 2011; Jetz, Wilcove, & Dobson, 2007; Nuñez et al., 2013). Species interactions may provide additional biotic barriers to movement through dependence on concomitant shifts in symbiotic species (Araújo & Luoto, 2007; Schweiger, Settele, Kudrna, Klotz, & Kühn, 2008).

Heterogeneous effect sizes could also be due to methodological variation in the quantification of both traits and range shifts (Brown et al., 2016). Our meta-analysis included studies of both range margins and range centers, and the small sample size of the latter group precluded using range type as a covariate for comparisons of mean effect sizes. It is possible that some traits may better explain shifts at the range margin vs. center (Angert et al., 2011), or in portions of the range where shifts are more probable due to heterogeneous climate change velocities (Loarie et al., 2009), but these relationships require further testing. Range shifts were measured in a variety of ways (magnitude of shift, rate of shift, or shift vs. no shift) and methods to standardize measurements of range shifts have been proposed (Angert et al., 2011; Brommer & Møller, 2010). To our knowledge, there have been no studies that have evaluated which range response variable is most suitable for testing against species' traits. Finally, choice of traits, measurement, and categorization varied greatly across studies. For example, none of the six studies of diet guild in birds used the same set of guilds, making cross-study comparison difficult. Moreover, studies investigating the influence of migratory distance failed to find a significant difference in range shifts between migratory and nonmigratory bird species (Angert et al., 2011), but significant results emerged when short- vs. long-distance migrants were compared (Brommer, 2008; Tingley et al., 2012; Zuckerberg et al., 2009). The growing coverage of global trait databases, such as TraitNet (traitnet.ecoinformatics.org), Elton Traits (Wilman et al., 2014), and the TRYplant trait database (www.try-db.org), will facilitate standardization of trait data, but future analyses should also include trait sets that are comparable to other studies. Further complications in quantifying traits may arise due to trait variation within a population, particularly if individuals at an expanding range edge have different traits than individuals in the range center (Bowler & Benton, 2005; Chuang & Peterson, 2016; Krause et al., 2016).

5 | CONCLUSIONS AND FUTURE DIRECTIONS

The diverse relationships between species' traits and range shifts that we found raise a key question: Are the species' traits that have been studied thus far useful predictors of variation in range shifts? Although some of our results support this assertion, most traits examined in the studies that we analyzed yielded no significant relationships (Figure 1; Table S1). Even for those relationships that were significant, little variation was explained by traits (3–6% in some studies), which led Angert et al. (2011) to conclude that the power of species' traits to predict range shifts is too low to be useful for conservation or management. Low predictive ability when regressing a trait or limited group of traits against range shifts is not necessarily surprising, given the complexity with which traits potentially influence shifts. Nevertheless, some studies have accounted for up to 40–60% of the variation in range shifts using species' traits (Alofs et al., 2014; Brommer, 2008). The well-documented importance of traits to other range shift processes, such as invasion or range expansion, provides a strong theoretical justification for their inclusion in studies of range shifts induced by contemporary climate change (Estrada et al., 2016).

We advocate a middle ground between these two views. It may be premature to conclude that species' traits do not have sufficient predictive power to be a useful proxy for range projections and management decisions. Our results suggest that at least two species' traits, habitat breadth and historic range limit, consistently described variation in range shifts across studies spanning diverse taxa and geographic locations, although considerable heterogeneity in effect sizes remains unexplained. However, our results also indicate that the evidence to date is equivocal or unsupported for the role of most leading traits—body size, migration strategy, movement ability, fecundity, longevity and diet breadth—as predictors of recent range shifts. Many more traits remain to be tested. Clearly, much work is still needed to identify the traits best suited to predicting variation in range shifts, and to better understand the influences of taxonomic, geographic, and methodological factors on trait effect sizes.

One approach that might better illuminate how species' traits modify range shifts is to investigate movements relative to niche tracking (Tingley et al., 2009). Our analysis considered only expansions in the poleward or upper elevational range margin, as analyses of other margins are comparatively sparse. However, heterogeneous change in climatic variables related to temperature and precipitation may cause some species to move in counterintuitive directions to track favorable climate (Crimmins, Dobrowski, Greenberg, Abatzoglou, & Mynsberge, 2011; Tingley et al., 2012; Wolf, Zimmerman, Anderegg, Busby, & Christensen, 2016). Species' traits may be stronger predictors of range shifts when investigated in the context of niche tracking and environmental matching (Sol et al., 2012; Wittmann, Barnes, Jerde, Jones, & Lodge, 2016; Wogan, 2016). For example, temperature and water flow preference of invertebrates in New South Wales explained whether range shifts occurred at warm vs. wet range edges (Chessman, 2012).

Phylogenetic context is also an important consideration when evaluating species' responses to global change (Jarzyna & Jetz, 2016), and strong phylogenetic biases have been documented for processes such as phenological shifts (Davis, Willis, Primack, & Miller-Rushing, 2010). More closely related species typically share more similar traits (Losos, 2008), so the relationship between traits and range shifts should have a phylogenetic signal (Angert et al., 2011; Pöyry et al., 2009). However, our meta-analysis found no differences in effect sizes between studies that did and did not control for phylogenetic relatedness. Within-study evaluation of phylogenetically corrected analyses has produced similar results, at least at the taxonomic level of order (Angert et al., 2011; Auer & King, 2014). The phylogenetic signal of range change remains unclear and will be an important area of future study as a control for, or alternative to, trait-based analysis of range shifts.

Finally, not all species will need to undergo range shifts in order to persist under changing climatic conditions. Numerous studies have documented species responding to changes in their environment through phenotypic plasticity, particularly shifts in phenology (Parmesan & Yohe, 2003). Traits such as ecological generalism may help species temporarily persist in situ under changing environmental conditions (Buckley & Kingsolver, 2012; Dawson et al., 2011). Relative to range shifts, phenological shifts can be predicted more strongly by traits (Buckley & Kingsolver, 2012). Despite the short time frame over which contemporary climate change has taken place, some populations have also shown genetic changes suggestive of evolutionary adaptation (Bradshaw & Holzapfel, 2006; Hoffmann & Sgrò, 2011). An ideal framework for predicting variation in range shifts should include the combined effects of niche tracking through space or time, plasticity or acclimation, evolution, and species' traits, with choice of traits based on a mechanistic framework such as that developed by Estrada et al. (2016).

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SUPPORTING INFORMATION

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