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ARTICLE

Can morphological traits explain species-specific differences in meta-analyses? A case study of forest beetles

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Abstract

Meta-analyses have become a valuable tool with which to synthesize effects across studies, but in ecology and evolution, they are often characterized by high heterogeneity, where effect sizes vary between studies. Much of this heterogeneity can be attributed to species-specific differences in responses to predictor variables. Here, we aimed to incorporate a novel trait-based approach to explain species-specific differences in a meta-analysis by testing the ability of morphological traits to explain why the effectiveness of flight-intercept trap design varies according to beetle species, a critical issue in forest pest management. An existing morphological trait database for forest beetles was supplemented, providing trait data for 97 species, while data from a previous meta-analysis on capture rates of bark or woodboring beetles according to different trap designs were updated. We combined these sources by including nine morphological traits as moderators in meta-analysis models, for five different components of trap design. Traits were selected based on theoretical hypotheses relating to beetle movement, maneuverability, and sensory perception. We compared the performance of morphological traits as moderators versus guild, taxonomic family, and null meta-analysis models. Morphological traits for the effect of trap type (panel vs. multiple-funnel) on beetle capture rates improved model fit (AIC_c), reduced within-study variance (σ^2), and explained more variation (McFadden's pseudo-R^2) compared with null, guild, and taxonomic family models. For example, morphological trait models explained 10% more of the variance (pseudo-R^2) when compared with a null model. However, using traits was less informative to explain how detailed elements of trap design such as surface treatment and color influence capture rates. The reduction of within-study variance when accounting for morphological traits demonstrates their potential value for explaining species-specific differences. Morphological traits associated with flight efficiency, maneuverability, and eye size were particularly informative for explaining the effectiveness of trap type. This could lead to improved predictability of optimal trap design according to species. Therefore, morphological

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traits could be a valuable tool for understanding species-specific differences in community ecology, but other causes of heterogeneity across studies, such as forest type and structure, require further investigation.

KEYWORDS
bark beetle, Coleoptera, forest pest management, intercept trap, invasive species, woodborer

INTRODUCTION

Meta-analyses have become increasingly popular in ecological research over the past 30 years, but they are often characterized by inconsistency in effect sizes between studies (Gurevitch et al., 2018; Senior et al., 2016). This phenomenon is termed "heterogeneity" (Higgins et al., 2003). For example, in meta-analyses in ecology and evolution, the average proportion of variance attributed to heterogeneity rather than to sampling error or chance has been estimated at 84.67% to 91.69% (Senior et al., 2016). These figures are well in excess of the widely adopted threshold of 75% for "high" heterogeneity (Higgins et al., 2003). Much of the heterogeneity in ecological research is assumed to be attributable to species-specific differences. For example, heterogeneity shows a significant positive correlation with number of species (Senior et al., 2016).

Species-specific differences pose a challenge to ecological research because if the effect of a given predictor variable depends on species identity, then this might imply that each species must be separately investigated to determine its response. Trait-based approaches offer a potential solution to this problem, on the premise that differing responses of species can be explained in terms of their traits (Brousseau et al., 2018; Wong et al., 2019). Accordingly, the application of trait-based approaches has the potential to improve the predictability of individual species' responses and inform hypotheses that explain why and how species differ in their response. Trait-based approaches have been extensively applied for some taxonomic groups, such as plants (e.g., Garnier & Navas, 2012). While their application to terrestrial entomology is more embryonic, successful applications in original research include responses of insect communities to land use and management (e.g., Martin et al., 2019; Roquer-Beni et al., 2021; Staton et al., 2021) and to sampling methodology (Hutchinson et al., 2021; Knapp et al., 2020; Thompson et al., 2021).

One example that typifies heterogeneity in ecological data is the effect of flight-intercept trap design on beetle capture rates in forest habitats. This is an important area of research because beetles and other insect pests are a major contributor to forest disturbances (van Lierop et al., 2015), which can result in severe impacts on biodiversity, timber production, and other ecosystem services (Dhar et al., 2016; Valenta et al., 2017). These impacts are predicted to worsen under a changing climate (Jactel et al., 2019; Ramsfield et al., 2016). Thus, early detection of insect pest outbreaks is critical in facilitating successful outbreak management (Epanchin-Niell et al., 2014). Early detection and monitoring in national plant protection schemes often involves the use of baited flight-intercept traps (Allison et al., 2021; Poland & Rassati, 2018; Rabaglia et al., 2019). To evaluate the most effective design of these traps, a recent meta-analysis compared bark and woodboring beetle capture rates between different trap design features, such as multiple-funnel versus panel traps, surface lubrication treatment, wet versus dry collection cups, and trap color (Allison & Redak, 2017). Substantial variation was reported in the effects of trap design on capture rates, for which guild and taxonomic family had only a limited influence. As such, new research that improves our mechanistic understanding of how and why the effectiveness of trap design varies according to target taxa is needed. In the absence of such advances, the authors of the meta-analysis concluded that monitoring, survey, and detection programs will remain "operationally and conceptually inadequate," a problem apparently caused by species-specific differences (Allison & Redak, 2017).

Adopting a trait-based approach could help to explain some of this heterogeneity, particularly with respect to species-specific differences. Ultimately, this could have implications for understanding heterogeneity in community ecology data more broadly. Although trait-based research is hindered by the scarcity of published trait values with standardized definitions and measurement protocols (Schneider et al., 2019), the recent publication of a standardized morphological trait database for European forest saproxylic beetles presents opportunities for further applications relating to this guild (Hagge et al., 2021b). A suite of morphological traits could provide insights into how a species of beetle interacts with a baited flight-intercept trap. For example, given that downwind odor plume structures vary according to intercept trap design (Bouwer et al., 2020), the distance at which an insect detects the plume might be influenced by its antennal size and configuration. The likelihood of successful oriented flight to the trap could be influenced by the insect's flight speed and maneuverability, as determined by the size and shape of its body, wings, and elytra (Fountain-Jones et al., 2015; Jones et al., 2019). In the near field of a trap, the likelihood of an insect approaching and contacting a trap can be affected by visual cues associated with the trap silhouette (Campbell et al., 2009; McIntosh et al., 2001; Strom et al., 1999), indicating a possible role of eye morphology. At the stage of contact with the trap, the likelihood of capture might depend on maneuverability and landing technique, which might be determined by the morphology of wings, elytra, legs, and body shape (De Souza & Alexander, 1997; Li et al., 2017). Of the various trap design features tested in a previous meta-analysis (Allison & Redak, 2017), trap type (e.g., panel vs. multiple-funnel) is relevant to all of these aspects and is therefore predicted to interact with a wide range of morphological traits. Surface treatment and wet versus dry collection cups are only likely to influence the later stages of the insect–trap interaction, and therefore morphological traits are expected to be of more limited relevance to these features. Morphological traits are also unlikely to explain any differences in capture rates between traps of different colors.

In this study, we investigated whether morphological traits could improve our understanding of how and why optimal trap design for forest beetles varies according to species, using a trait-based meta-analysis approach. This is the first exploratory attempt to explain some of the mechanistic causes of heterogeneity in trap design effects on forest insects, which could have implications for understanding heterogeneity in community ecology data more broadly. Specifically, we addressed the following research questions: (1) Does the inclusion of morphological traits in meta-analytic models of the effects of trap design on capture rates of forest beetles improve model fit and explain more variability compared with guild- or taxonomic-based models? (ii) For which trap design features (i.e., trap type, surface treatment, wet/dry cup, white/black and transparent/black) are morphological traits as a whole most informative? (3) Which specific morphological traits are most informative when investigating the effect of trap design on capture rates? To answer these questions, our general approach was to first develop a morphological trait database based on an existing European database and protocols (Hagge et al., 2021b), then incorporate this into trait-based meta-analysis models for comparison with a previous meta-analysis (Allison & Redak, 2017).

MATERIALS AND METHODS

Development of morphological trait database

A total of 22 morphological traits were selected for inclusion in a new morphological trait database, based on their hypothesized relevance to the types of interactions a flying beetle species could have with a trap and its odor plume (Table 1). Traits were selected to represent body size and shape, hairiness, body mass, and the morphology of eyes, antennae, leg parts, wings, and elytra. Our approach to the number of specimens measured per species depended on whether the species was separated by sex in the studies included in the meta-analysis. For those species separated by sex in at least one study, we aimed to measure 10 specimens of each sex for each species. For species not separated by sex in any study, we aimed to measure 10 specimens for each species, but each specimen was still sexed where possible with the aim of measuring equal numbers of each sex. In species where wing presence was dimorphic (e.g., Xyleborini), only the winged sex was included in the database (because only winged insects are relevant to flight-intercept trap design). For some species, the number of specimens measured was constrained due to a lack of available specimens. As such, the number of specimens measured per species ranged from three to 20 (mean 12.93). Specimens were primarily sourced from internal private collections held by a coauthor (Jeremy D. Allison) at the Great Lakes Forestry Centre (Ontario, Canada), with additional specimens donated on request by other noncatalogued private collections mainly in North America plus some from Europe (see *Acknowledgments* for details). Freeze-dried specimens were preferentially selected but were not always available, and the storage medium was recorded in the trait database.

All length and area measurements were carried out using a digital microscope with an in-built camera (Nikon SMZ1500/Nikon DS-Ri1), in Nikon NIS Elements software (version 4.00.08), calibrated using a microscale. All trait values were visually sense-checked for obvious outliers during the development of the trait database, and any potential outliers were remeasured using the original specimen. Further descriptions of the measurement protocols are provided in Table 1.

Analysis overview and literature search

Our aim was to update and reanalyze a previous meta-analysis (Allison & Redak, 2017) to compare the performance of our new trait-based models to the previous approach based on guild (bark beetle, predator, woodborer) and taxonomic family, using R software version 4.0.5 (R Core Team, 2020). We investigated five of the six trap design features included in the previous meta-analysis (Table 2). The only design feature we did not repeat in the analysis was green versus purple color traps because of the small number of studies and difficulties in obtaining specimens for sufficient species.

TABLE 1 Trait selection and measurement protocol: justification for inclusion of the 22 morphological traits in the database, and measurement procedures.

Trait	Potential functional relevance to flight-intercept trap design	Measurement protocol
General fundamental traits		
Body length	Microhabitat use, dispersal ability, movement, and maneuverability (Fountain-Jones et al., 2015; Pérez-Sánchez et al., 2020)	Maximum length of body (head to abdomen), excluding mandibles or wings, in dorsal view
Body height	Movement of elytra (Forsythe, 1987) and microhabitat use (Barton et al., 2011)	Maximum body height, in lateral view
Body width		Maximum body width, in dorsal view
Body roundness		Body height divided by body width
Head width	Microhabitat use (Fountain-Jones et al., 2015)	Maximum width of head in lateral or frontal view, including eyes
Mass	Microhabitat use, dispersal ability (Fountain-Jones et al., 2015)	Weighed using Sartorius A210P with a resolution of 0.0001 g. Frozen specimens were defrosted for 1 h on absorbent paper; storage medium also recorded
Sensory traits (potentially relevant to detection of baited traps)		
Hairiness (pronotum)	Can support sensilla (Hallberg & Hansson, 1999)	Coded according to following categories: 0 = more or less glabrous; 1 = short sparse hairs (<50/mm^2, 0.5 to 1 times minimum diameter of hind tibia); 2 = dense short hairs (>50/mm^2); 3 = dense, mix of short and long hairs; 4 = dense long hairs (>1 times diameter of hind tibia)
Hairiness (head)		
Antenna type	Antennae play primary role in volatile recognition (Conchou et al., 2019; Elgar et al., 2018; Renou & Anton, 2020)	Structure of antenna (e.g., filiform, serrate, capitate)
Antenna length		Total length of antenna, including scape
Antenna width		Maximum width of antenna, excluding scape
Eye length	Habitat preference (Fountain-Jones et al., 2015), response to visual cues, for example, trap silhouette (Campbell et al., 2009; McIntosh et al., 2001; Strom et al., 1999)	Maximum length of eye in lateral view, with divided eyes (e.g., Trypodendron) accounting for total length of each segment on one side of head
Eye area		Area occupied by one eye in lateral view (including each section of divided eyes)
Mobility and maneuverability (potentially relevant to movement towards, and interaction with, flight-intercept traps)		
Elytra length	Maneuverability, lift, flight efficiency (De Souza & Alexander, 1997; Fountain-Jones et al., 2015)	Maximum length of elytra in dorsal view
Wing length	Dispersal ability, flight efficiency, maneuverability (Gibb et al., 2006; Fountain-Jones et al., 2015)	Maximum length of fully extended wing
Wing width		Maximum width of fully extended wing
Wing area		Total area of fully extended wing
Wing load		Mass divided by wing area
Wing aspect ratio		Wing length divided by wing width
Front femur length	Maneuverability in flight, landing technique (Li et al., 2017)	Length of front femur
Tarsus length	Adhesion to surfaces (Betz, 2002)	Length of front tarsus, excluding claws
Tarsus width		Maximum width of front tarsus, excluding hairs

To identify relevant studies published since the previous meta-analysis (Allison & Redak, 2017), we repeated the literature search in Web of Science for publications dated between January 2017 and August 2021 using the same search term ("trap AND forest AND Coleoptera") and inclusion criteria (i.e., studies that reported the necessary summary statistics required for meta-analysis, for bark and woodboring beetles). Studies were only included where the experimental design precluded any correlations between different trap design features or confounding

TABLE 2 Numbers of coleopteran species (within our new database and the existing European database [Hagge et al., 2021b]), observations of effect sizes, and studies for each trap design feature.

Trap design feature	No. species (see Appendix S3)	No. observations	No. studies	Total sample size and range per observation (per treatment)
Trap type	54	163	13	390 (5–36)
Surface treatment	24	79	6	136 (7–15)
Wet versus dry cup	35	72	7	116 (5–18)
White versus black	20	157	9	456 (4–21)
Transparent versus black	17	33	4	46 (10–14)

Note: Total sample size is summed across all observations for each trap design feature, per treatment (e.g., multiple-funnel). Sample size was equal between both treatments for each trap design feature, except for white versus black color, where the lowest sample size treatment is reported.

variables such as habitat type. Data from figures was extracted using GetData Graph Digitizer version 2.2.6 (http://www.getdata-graph-digitizer.com).

Trait selection as moderators

We combined our new morphological trait database with an existing trait database for European saproxylic beetles (Hagge et al., 2021a, 2021b). Of the 22 morphological traits in our new trait database, six were not included in the existing European database (head hairiness, pronotum hairiness, antenna type, antenna width, tarsus length, tarsus width). An exploratory analysis indicated that these six traits were either highly correlated with other variables or, in the case of hairiness, were not significant variables in trait moderator meta-analysis models. Therefore, they were not included in the final analysis, and we were able to use the complete existing European database (and the additional species contained therein). An additional two traits, mass and wing load, were also excluded from the final analysis because approaches to specimen storage were inconsistent, which precluded a standardized measure of mass.

Correlations among the resultant 14 traits were then explored to further refine the final trait selection. Although correlated moderators (i.e., traits) can be accommodated by meta-analysis models (Cinar et al., 2021), very high correlations could lead to problems associated with overfitting, while some of the traits represented similar morphological features (e.g., eye size metrics). Therefore, mirroring the approach of Hagge et al. (2021b), we fitted phylogenetic generalized least squares (PGLS) regression models for each trait, with body length as the fixed effect. Both body length and the response trait were log-transformed (except for body roundness because the distribution was not skewed). PGLS models account for the nonindependence of species by specifying a phylogenetic tree in the random effects structure, which was approximated based on the taxonomic classification of each species using the ape package in R (Paradis & Schliep, 2019). The phylogenetic signal was assumed to correspond to Brownian motion ($\lambda = 1$ [Pagel, 1999]). Residual values were then derived for each trait and a correlation matrix of residuals calculated using Pearson's coefficient (see Appendix S1). This allowed us to inspect the correlation of traits, after accounting for body size. Three strong correlations ($r > 0.75$) were found between wing size traits, while moderate correlations were found for two eye size traits ($r = 0.655$) and four traits relating to body or head shape (e.g., $r = 0.631$, 0.640, 0.653, 0.688, 0.693). Therefore, to represent these trait groups, we selected wing area, eye area, body roundness, and head width, on the basis that they contained the most information (for example, wing area is related to both wing length and wing width). This led to the selection of nine traits in the final analysis (e.g., Figure 1c).

Data for the nine selected traits in the new database were merged with the same nine traits in the existing European database (Hagge et al., 2021b). Four trait values for specific species were missing from the European trait database (antenna length for *Dendroctonus brevicomis* and *D. frontalis*, and wing width and wing size for *Monochamus galloprovincialis*). Therefore, these were imputed by predicting values from the linear relationship between the missing trait and body length for congeneric species. After merging, mean trait values were calculated for all specimens of each species (and sex, where separate effect sizes were provided by at least one study in the meta-analysis).

Meta-analysis

Our meta-analysis approach broadly comprised two stages. First, we repeated the previous meta-analysis by Allison and Redak (2017), which used mixed meta-analytic models to evaluate the effect of trap design

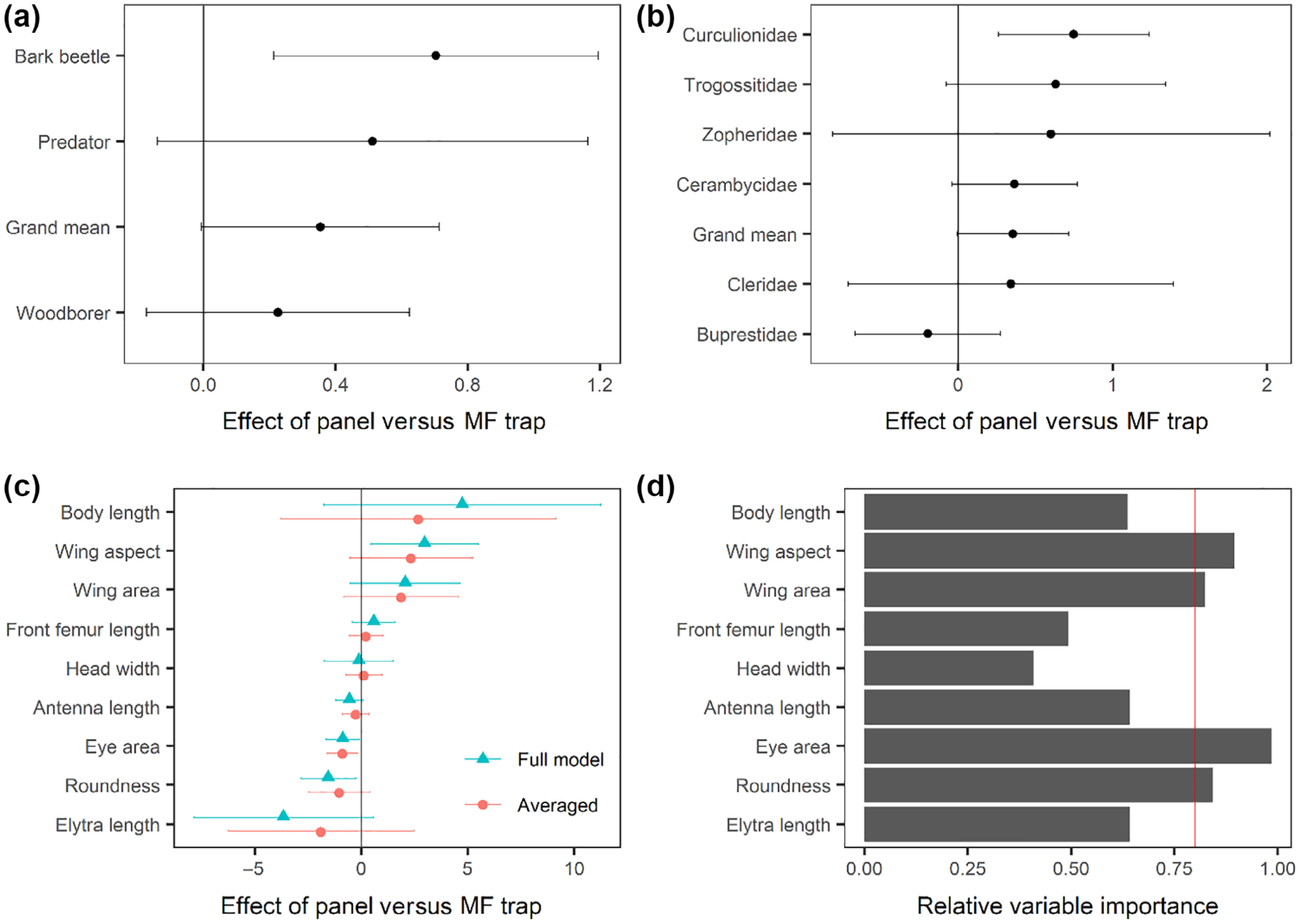

FIGURE 1 Mean effects with 95% CIs of trap type (panel vs. multiple-funnel [MF]) on (a) coleopteran guilds, (b) taxonomic families, and (c) morphological traits (averaged across models using an information theoretic (IT) approach or according to a full model with all traits) of forest Coleoptera, while (d), relative variable importance, represents the probability that the trait appears in the best-fitting model according to an IT approach, where a value >0.8 is considered "important." In panels (a–c), the *x*-axis >0 represents higher captures in panel versus MF traps.

features on insect capture rates according to taxa and guild. For this reanalysis, the only modification we made to the previous meta-analysis was that we used a reduced data set that only included those species represented in the trait database we generated for the current study (*Trait selection as moderators*). For the second stage, we compared these results to equivalent meta-analysis models using the nine selected morphological traits as moderators, rather than taxa or guild.

The metafor package in R was used to calculate effect sizes and run meta-analysis models (Viechtbauer, 2010). As in the previous meta-analysis (Allison & Redak, 2017), effect sizes were calculated as the standardized mean difference (Hedges, 1981). Separate meta-analysis models were built for each of the five trap design features (Table 2) and for each of three moderator categories: guild (bark beetle, predator, woodborer), taxonomic family, and morphological traits, plus a null model without moderators. As such, a total of 20 meta-analysis models were developed (in addition to information theoretic trait models, described below), while additional trait models were developed for subsets of the two major guilds for trap type. All models comprised a hierarchical random-effects structure using the "rma.mv" function, where random effects comprised row number (i.e., each effect size) nested within study ID. Intercepts were removed from categorical meta-analysis models (guild and family) to present the results, for consistency with the previous meta-analysis (Allison & Redak, 2017), but were included to calculate the statistics in Table 3. Because we could not source specimens for every species in the previous meta-analysis (Allison & Redak, 2017), the data set was filtered to only include those species included in our new trait database or in the existing European database (Hagge et al., 2021b) (Table 2). This filtered data set, which only comprised Coleoptera, was used for all aspects of the analysis so that the various moderator and null models could be directly compared.

TABLE 3 Comparison of meta-analysis models using coleopteran guild (bark beetle, predator, woodborer), taxonomic family, or morphological traits as moderators.

Dependent variable	Moderators	AIC_c value (Δ)	Pseudo-R^2 (adjusted)	σ^2 between-study + within-study	Omnibus test p-value
Trap type (panel versus MF)	Null	410.59	0 (0)	0.358 + 0.289	...
	Guild	405.58 (−4.62)	0.0219 (0.0071)	0.418 + 0.262	0.0653
	Family	397.09 (−12.52)	0.0577 (0.0281)	0.420 + 0.235	**0.0050**
	All traits	389.06 (−21.52)	0.1029 (0.0534)	0.381 + 0.207	**0.0003**
	Best trait model	387.88 (−22.71)	0.1000 (0.0555)	0.378 + 0.203	**0.0001**
Surface treatment	Null	165.00	0 (0)	0.567 + 0.133	...
	Guild	164.74 (−0.26)	0.0301 (−0.0077)	0.495 + 0.140	0.5347
	Family	161.46 (−3.54)	0.0809 (0.0179)	0.609 + 0.118	0.1222
	All traits	165.66 (0.66)	0.1379 (0.0119)	0.371 + 0.136	0.2985
	Best trait model	159.64 (−5.36)	0.0924 (0.0269)	0.231 + 0.124	**0.0297**
Wet versus dry cup	Null	180.91	0 (0)	0.290 + 0.210	...
	Guild	177.27 (−3.64)	0.0606 (0.0148)	0.469 + 0.189	0.2008
	Family	175.72 (−5.19)	0.0981 (0.0293)	0.476 + 0.171	0.0989
	All traits	179.43 (−1.48)	0.1399 (0.0253)	0.309 + 0.218	0.2139
	Best trait model	174.77 (−6.13)	0.0612 (0.0377)	0.288 + 0.180	**0.0207**
White versus black trap color	Null	287.84	0 (0)	2.666 + 0.101	...
	Guild	285.74 (−2.10)	0.0304 (0.0020)	3.375 + 0.103	0.8324
	Family	285.85 (−1.98)	0.0300 (0.0016)	2.646 + 0.094	0.1631
	All traits	284.81 (−3.03)	0.0832 (0.0122)	2.378 + 0.099	0.2437
	Best trait model	282.70 (−5.13)	0.0572 (0.0146)	2.739 + 0.093	0.0845
Transparent versus black trap color	Null	56.12	0 (0)	0.024 + 0.058	...
	Guild	64.30 (8.19)	0.0703 (−0.1326)	0.100 + 0.076	0.8812
	Family	78.20 (22.08)	0.2169 (−0.1889)	<0.001 + 0.118	0.7093
	All traits	78.27 (22.15)	0.2155 (−0.1903)	0.235 + 0.091	0.7866
	Best trait model	55.72 (−0.40)	0.0609 (−0.0203)	0.018 + 0.052	0.1084

Note: The following metrics were used to test the performance of moderators: AIC_c (a relative measure of model fit that penalizes overfitting, where a negative change (Δ) relative to the null model represents a better fit), McFadden's pseudo-R^2 (represents percentage explained variability relative to the null model), adjusted pseudo-R^2 (which penalizes overfitting and can therefore be negative), σ^2 (estimates of variance between and within studies), and omnibus moderator test (Q_M), which tests whether all of the moderator coefficients equal 0. The "best" trait model comprised the combination of traits that achieved the lowest AIC_c value using an IT approach.
Abbreviation: MF, multiple funnel.

In the meta-analysis models, trait values were log-transformed (except body roundness) and then scaled (but not centered) using the "scale" function. To test the robustness of the influence of trait moderators, we used two approaches for the trait models: a "full" model using all nine traits as moderators and an information theoretic (IT) approach to test models with all possible combinations of the nine traits (excluding interactions) plus the null model, using the glmulti package (Calcagno, 2020). The latter approach allows calculation of averaged model coefficients for each trait across all combinations of models. In addition, the relative variable importance (RVI) of each trait is calculated as the sum of Akaike weights in which the trait appears, where Akaike weight represents the probability that the model is the best-fitting model out of all possible combinations. Simulations indicate that these two approaches outperform univariate models (i.e., separate models with individual moderators) when evaluating the importance of multiple moderators in meta-analysis (Cinar et al., 2021).

Heterogeneity of the null models, that is, variation in the effect of trap design feature, was initially tested using a Q-test. Model performance of each moderator category (null, guild, family, and trait) was then compared using four metrics: (1) small-sample corrected Akaike's information criterion (AIC_c) to indicate relative model fit; (2) McFadden's pseudo-R^2 as a measure of explained variability (McFadden, 1973), which is intended to mimic R^2 values commonly used in linear regression by providing a percentage output but tends to produce lower values (Smith & Mckenna, 2013); we also calculated McFadden's adjusted pseudo-R^2, which applies a deduction for the number of moderators in the model to penalize overfitting, which means it can have a negative value; (3) σ^2, comprising two values that estimate residual variance between studies and within studies; and (4) omnibus moderator test (Q_M), which tests the null hypothesis that the coefficients of all moderators equal zero.

The influence of outliers on the full trait models was evaluated by removing data points with the highest Cook's distance (up to four). In all cases, the removal of outliers decreased AIC_c values and increased adjusted pseudo-R^2 values, indicating our full models were conservative. Only two trait moderators that were statistically significant under the full model were no longer significant when outliers were removed (antenna length for trap type, and head width for surface treatment), neither of which was significant according to the model-averaged estimates calculated using the IT approach.

We also investigated the role of intraspecific trait variation in explaining heterogeneity by building two linear models, both with variance of body length within species and sex as the predictor variable and variance in trap type effect sizes among or within observations as response variables. We then repeated this for the other eight traits.

RESULTS

Our morphological trait database comprised 866 specimens belonging to 67 species of Coleoptera. Trait values for an additional 27 coleopteran species were sourced from an existing European database (Hagge et al., 2021b). The updated literature search produced five additional studies that fulfilled the selection criteria and contained data for species in our trait database (Appendix S2). Of the five trap design features included in our meta-analysis, trap type (panel vs. multiple-funnel) was best represented in the literature, with a total of 163 observations from 13 studies, represented by 54 species within the trait databases (Table 2; Appendix S3). Most studies were undertaken in the United States and Canada, with five undertaken in Europe and one in New Zealand (Appendix S2).

Null meta-analysis models without moderators exhibited significant heterogeneity for all trap design features ($p < 0.001$), except transparent versus black color ($p = 0.053$). Morphological trait moderators were most informative for trap type (panel vs. multiple-funnel). For this trap design feature, the model with all nine morphological traits as moderators had lower AIC_c and higher adjusted pseudo-R^2 values compared with a null model without moderators, and with moderator models based on guild or taxonomic family (Table 3). This indicates that traits improved model fit and increased the amount of explained variability for trap type. Furthermore, the trait moderator model had improved statistical significance (Table 3: $Q_M = 0.0003$) compared with guild or taxonomic family moderators for trap type. Traits were particularly effective at reducing variance within studies of trap type, rather than variance between studies (Table 3).

For the trap type analysis, one of the three guilds and one of six taxonomic families were significantly associated with panel rather than multiple-funnel traps (Figure 1a,b). Of the nine morphological traits included as moderators in the full trait model, wing aspect was significantly associated with panel traps, while eye area and body roundness were significantly associated with multiple-funnel traps (Figure 1c). These three traits also had a RVI of at least 0.8 (Figure 1d), indicating a high probability that they appear in the best-fitting model according to an IT approach. Furthermore, two of these three traits (wing aspect and body roundness) showed consistent effects between the two major guilds, though they were not consistently significant (Figure 2).

The pseudo-R^2 value for the full trait model and the best-fitting trait model for trap type (Table 3: 0.1029 and 0.1000, respectively) exceeded those of the null, guild, or family models but fell short of the range of 0.2–0.4 that indicates an "excellent" model fit (McFadden, 1977). This remaining heterogeneity can be visualized in the comparison of predicted effect sizes using the "best" trait model against actual effect sizes (Figure 3).

We found no evidence for a role of intraspecific trait variation in explaining heterogeneity or within-study variance; body length variance within species and sex was not significantly correlated with variance in trap type effect sizes among observations ($p = 0.962$) or variance within observations ($p = 0.626$). Variance in the remaining eight traits also had no significant effect, except for eye area variance, which was significantly associated with variance within observations ($p = 0.014$). This is likely a chance effect given that 18 separate models were run without any apparent theoretical explanation for a significant effect.

Of the other four trap design features, the full trait models for wet versus dry collection cup, surface treatment, and white versus black color performed more similarly to the null, guild, and family models. In addition, the omnibus moderator test was not significant for these full trait models (Table 3), indicating that traits were less informative for these comparisons than for trap type.

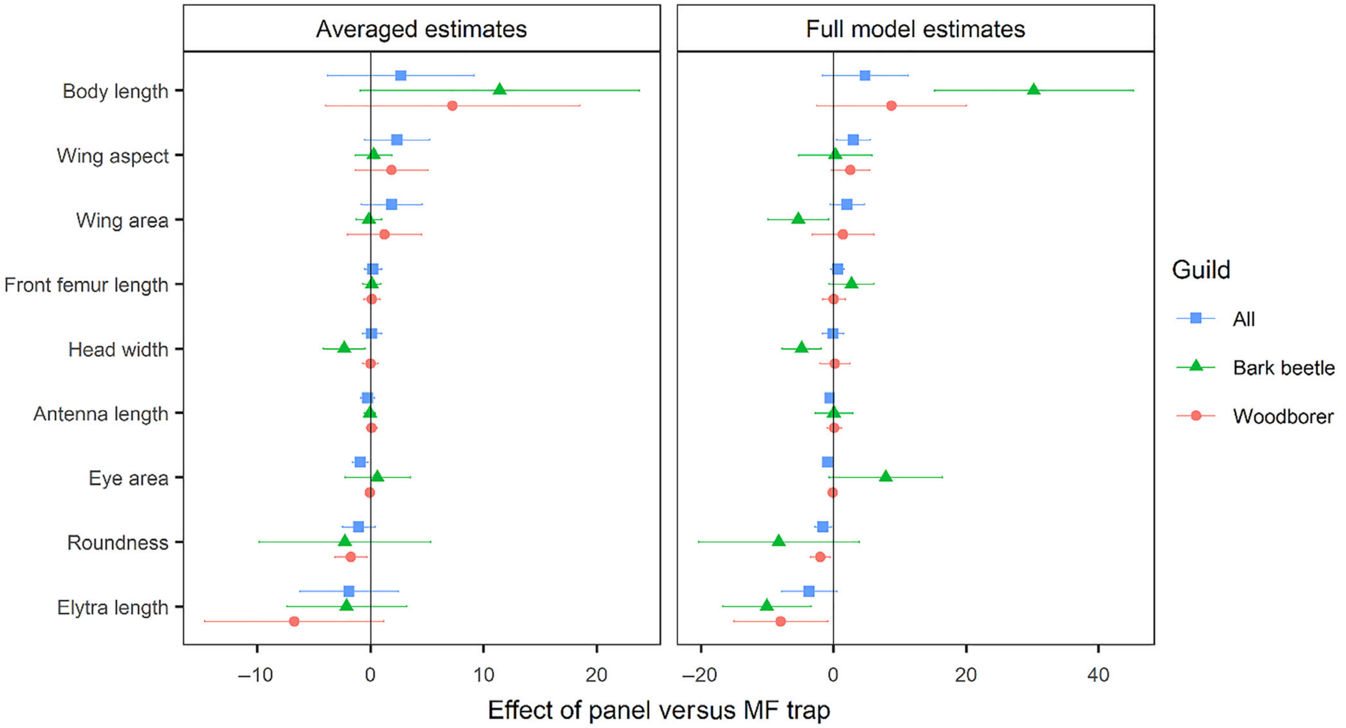

FIGURE 2 Influence of morphological traits on capture rates in panel versus multiple-funnel (MF) traps, separated by the two major coleopteran guilds, where *x*-axis values >0 represent higher capture rates in panel compared with MF traps. Points show mean effect sizes, with bars representing 95% CIs. Averaged estimates are derived from models with all possible combinations of traits using an information theoretic approach, whereas the full model includes all traits.

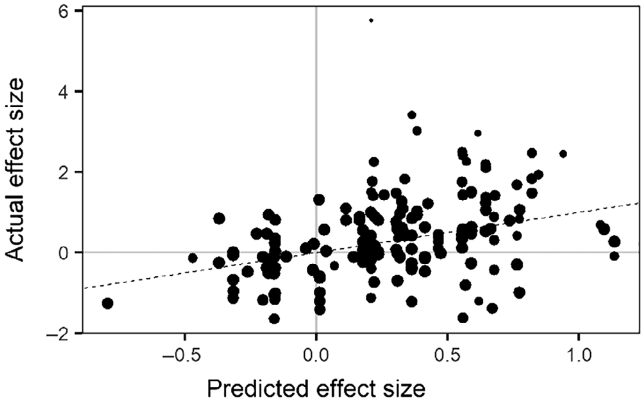

FIGURE 3 Comparison of predicted effect sizes based on "best" performing coleopteran morphological traits model (selected using an information theoretic approach) versus actual effect sizes, for trap type (panel vs. multiple funnel). The size of each point represents the inverse variance of the effect size, with larger points having less variance and, therefore, greater weighting in the models.

Nevertheless, one or two traits for each trap feature were significant in the full trait models and/or had a RVI of at least 0.8 (Table 3, Figure 4). The most important (RVI) trait associations were smaller body length in surface-treated traps, greater antenna length in wet collection cups, and smaller front femur length and greater wing area in white versus black traps (Figure 4). All moderator models performed poorly for transparent versus black traps (Table 3).

DISCUSSION

Our findings demonstrate that morphological traits can explain more variation than guild or taxonomic family when analyzing the effect of flight intercept trap design on beetle capture rates. In particular, morphological traits were more informative than guild or family in explaining the effect of trap type (panel vs. multiple-funnel) on beetle capture rates, in terms of improved model fit (AIC$_c$), significance of the omnibus moderator test, and explained variability (pseudo-R^2), even after penalizing for the number of traits included in the model (adjusted pseudo-R^2). Specifically, wing aspect, eye area, and body roundness were particularly important traits (significant in the full trait model and relative variable importance >0.8) and reduced variance within rather than between studies, revealing the value of morphological traits for explaining species-specific differences. However, and as expected, the use of morphological traits proved less informative for

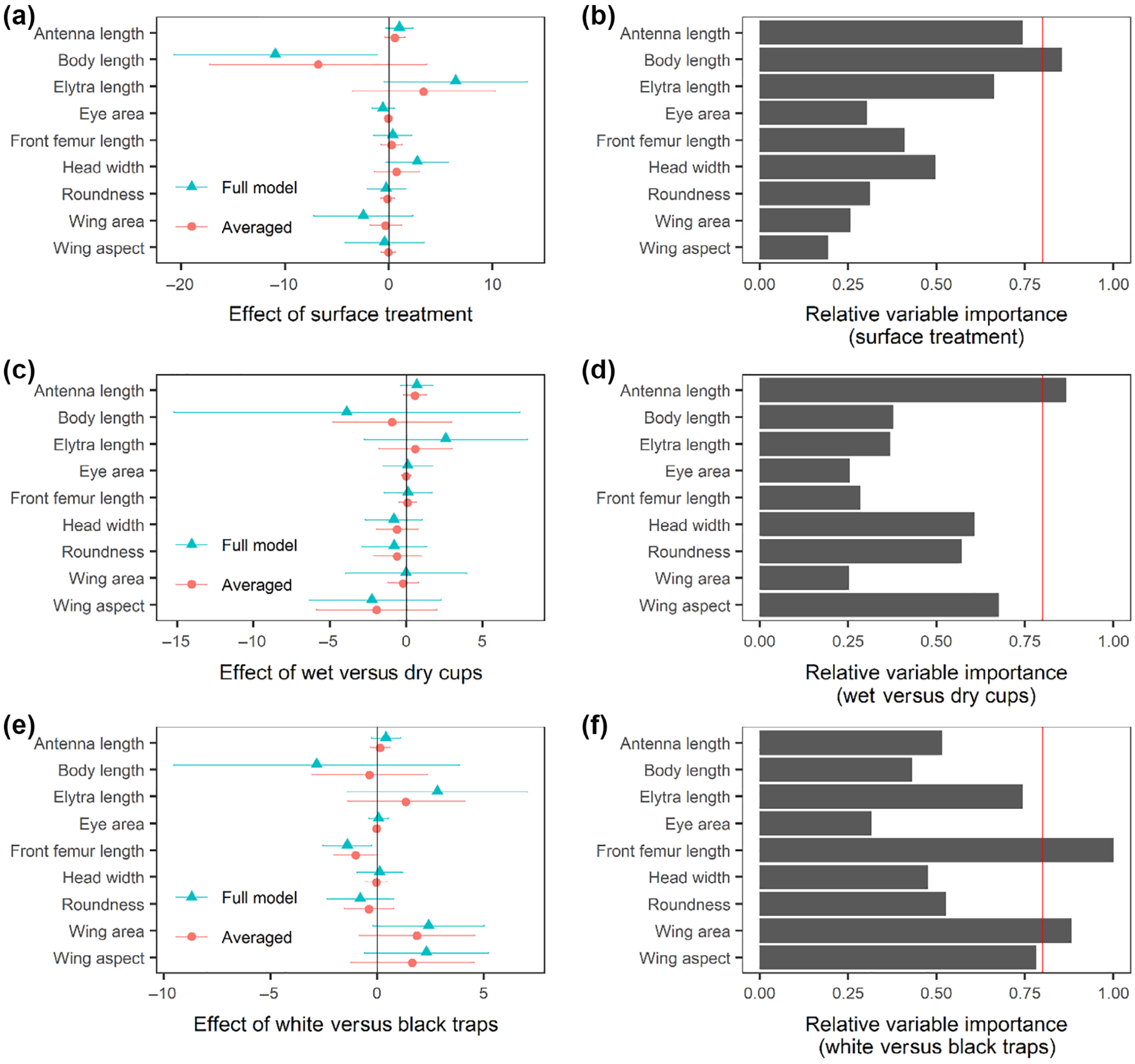

FIGURE 4 Influence of coleopteran morphological traits on capture rates according to surface treatment, wet/dry collection cup, and white versus black trap color. Plots (a), (c), and (e) show mean effect sizes with 95% CIs, where *x*-axis values >0 represent higher capture rates in surface treated versus nontreated (a), wet cups versus dry cups (c), and white versus black traps (e). Values are shown from models including all traits ("full model") and model-averaged values using an information theoretic (IT) approach. Plots (b), (d), and (f) show relative variable importance, which represents the probability that a trait appears in the best-fitting model according to an IT approach, where values >0.8 represent "important" traits.

other elements of trap design, including surface treatment, wet versus dry collection cup, and color, though some individual traits were significantly associated with one of these trap design features. This is consistent with our expectations that beetle morphology would be more relevant to trap type than other trap design elements, suggesting the findings for trap type are unlikely to be a false positive (Type I error).

Toward a mechanistic understanding of species-specific differences

A key advantage of the trait-based approach is an improved mechanistic understanding of how and why species-specific differences arise (Wong et al., 2019). Although there is currently a scarcity of studies examining the relationship between beetle morphology and trapping efficiency, our results raise a number of hypotheses that could explain how morphological traits could influence the effectiveness of trap design. For example, our analysis revealed the potentially important role of wing and body shape traits in determining the effect of trap type on beetle capture rates, which could be explained in terms of maneuverability. High aspect ratios (i.e., long narrow wings), which were associated with panel traps, suggest improved flight efficiency, whereas low aspect ratios suggest improved maneuverability (Aiello et al., 2021). Similarly, a more rounded body shape, which was associated with multiple-funnel traps, could improve movement of the elytra (Forsythe, 1987). Other traits that relate to flight power and efficiency, particularly larger wing area, body length, and reduced elytra length (Fountain-Jones et al., 2015), were also somewhat associated with panel traps with RVI > 0.6 (Figure 1d). As such, these five traits consistently point to higher capture rates of more flight-efficient beetles in panel versus multiple-funnel traps. Although the precise mechanism for this requires further research, more maneuverable and less flight-efficient beetles might be better equipped to escape after hitting flight-intercept panels or to avoid collision. In addition, given that beetles have been observed to fall out of multiple-funnel traps (Allison et al., 2014; McIntosh et al., 2001), more flight-efficient beetles might collide at greater speed than more maneuverable beetles, resulting in a greater probability of falling out of multiple-funnel traps.

Greater eye area was also associated with multiple-funnel traps. This may be because these traps have a less prominent vertical silhouette than panel traps, a feature that many woodboring and bark beetles use to detect suitable host trees (McIntosh et al., 2001). Therefore, beetles with larger eyes may be better adapted to detect these traps and be more attracted to them.

Although morphological traits were less informative for other trap design features (as expected), there was an association of smaller body length with surface lubrication treatment, possibly because smaller beetles are able to land on, and escape from, nontreated traps to a greater extent than larger beetles. Other associations included larger antenna length in wet versus dry collection cups, and smaller front femur length in white versus black traps, but these lack any apparent explanation. Morphological traits had no significant role in explaining trap catches between white or transparent versus black traps, probably because other traits, such as daily activity pattern, flower-visiting preference, and body color (given that males are attracted to the color of conspecific females in some species), may play a more important role (Cavaletto et al., 2020).

Trait-based predictions

Another important advantage of the trait-based approach is the potential to improve the predictability of species' responses to given predictor variables (Brousseau et al., 2018; Wong et al., 2019). By understanding how species respond based on their traits, it may be possible to predict the responses of previously untested species based on their traits. For example, our analysis could inform the development of a predictive tool to recommend an optimal trap design for a target beetle species.

Using the best-fitting model for trap type according to an IT approach, we can predict the effect size on species included in the European beetle trait database (Hagge et al., 2021b) but not included in our meta-analysis. According to this method, we would predict that *Agrilus* and *Anthaxia* species should be better captured by multiple-funnel rather than panel traps because their morphologies indicate that they are maneuverable flyers with good vision. On the other hand, the morphology of *Necydalis* species indicates flight efficiency but relatively poor vision, suggesting they would be more effectively captured by panel traps. Predictions for some species are strongly influenced by an extreme value for a single trait, which requires further testing. For example, the very short relative elytra length of many Staphylinidae and Nitidulidae led to high predicted associations with panel traps. Further testing of these predictions could facilitate the optimization of trapping programs for specific species.

When are morphological traits informative?

Although previous studies considered the role of traits in insect trapping (e.g., Hutchinson et al., 2021; Knapp et al., 2020; Thompson et al., 2021), to our knowledge our study is the first to demonstrate that a suite of numeric morphological traits can explain the effects of sampling method on the recorded insect community, indicating the relevance of morphology beyond body size. Our findings suggest that morphological traits are most relevant to the form and structure of trap design but were less informative for nonstructural details of trap design such as surface treatment and coloration. This has implications for the study of other trapping methodologies, while also demonstrating the importance of a hypothesis-driven approach to investigate potentially relevant traits in appropriate situations (Brousseau et al., 2018).

Our analysis provided no evidence for a role of intraspecific trait variation on capture rates according to trap type. Instead, species-specific differences relating to flight efficiency and maneuverability appeared to be more relevant. However, the importance of intraspecific variation has been demonstrated in other contexts, including invertebrate community responses to climatic gradients and environmental change (reviewed in Wong et al., 2019).

Limitations and future research

While our trait-based approach was informative for explaining some variation in effect sizes for trap type, substantial variation remained (Table 3), suggesting a limited understanding as to the relationship between traits and functioning (Fountain-Jones et al., 2015). More specifically, simple morphological traits seem to have a limited ability to explain complex processes such as active flight, maneuverability, and sensory detection of volatiles. For example, previous studies reported that flight performance was weakly explained by morphological traits such as body weight, wing size, and wing shape, and that the flight performance of some individuals was well below their apparent ability given their morphological traits (Javal et al., 2018; Shegelski et al., 2019). This can be attributed to both personality characteristics that are not explained by morphology, a phenomenon particularly relevant to intraspecific behavioral variation (Tremmel & Müller, 2013; Wong et al., 2019), and physical attributes that are more difficult to measure, such as flight muscle size and lipid content (Jones et al., 2019). Daily activity pattern (e.g., nocturnality) might be an important factor determining the importance of certain traits, such as eye size, but we were not able to investigate this because of a lack of information on many species. In addition, our analysis focused on directional trait responses, that is, mean trait values, whereas functional diversity metrics may be more relevant for studies of community effects on ecosystem services (Cadotte et al., 2011; Petchey & Gaston, 2006; Staton et al., 2022).

Unsurprisingly, trait-based approaches were not informative for explaining variation between studies. As such, further research is needed to test other major causes of heterogeneity, which in this case might include forest structure, forest type, climate, weather conditions, and experimental design (Burner et al., 2020).

CONCLUSIONS

Our study presents a novel approach to meta-analysis, using morphological traits to explain causes of variation. We found that, in some cases, morphological traits could be informative in explaining species-specific differences, leading to an improved mechanistic understanding of why species differ in their responses. This could facilitate a transition to a more predictive approach in forest entomology, with implications for explaining species-specific differences in community ecology more broadly. In our case study of trap design effects of beetle capture rates, morphological traits associated with flight efficiency and maneuverability were particularly informative for explaining species-specific differences between two flight-intercept trap types but were less informative for other more specific trap features, which conformed to our theoretical expectations. Therefore, morphological traits can be a valuable tool for understanding species-specific differences in community ecology, but other causes of heterogeneity require further investigation.

AUTHOR CONTRIBUTIONS

Tom Staton, Robbie D. Girling, Sandy M. Smith, and Jeremy D. Allison conceived the ideas and designed the methodology. Tom Staton, Jeremy D. Allison, and Richard A. Redak collected the data. Tom Staton analyzed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Hagge et al., 2021a) utilized for this research are available in Dryad at https://doi.org/10.5061/dryad.2fqz612p3. The trait database (Staton et al., 2023) described in this manuscript is available in Mendeley Data at: https://doi.org/10.17632/xv25b8y65h.2. The list of literature identified from our literature search is provided in Appendix S2. The search queries used to compile the literature for our meta-analysis are provided in the

Materials and Methods: *Analysis overview and literature search* section.

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SUPPORTING INFORMATION

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

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