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RESEARCH ARTICLE

The capacity of sentinel species to detect changes in environmental conditions and ecosystem structure

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Abstract

1. A major obstacle to preventing and reversing biodiversity loss in the Anthropocene lies in the scarcity of tools and data for monitoring the health and trajectory of ecosystems. Sentinel species can provide insight into unobserved ecosystem change, but it is unclear how effective sentinels are due to the local, context-dependent nature of past research.
2. Here, we present the first global evaluation on the effectiveness of sentinel species as indicators of ecosystem change. We conducted a meta-analysis on 372 case studies to identify the ecological and methodological factors that correlate with the most effective sentinel species.
3. Sentinel performance did not vary consistently across taxa or system; instead, sentinels that were more directly linked to ecosystem change due to their trophic role as predators were more effective. In addition, sentinel responses that were measured on a shorter timescale were more effective at indicating ecosystem change.
4. *Policy Implications*. These results contribute to the longstanding debate on "what makes a good sentinel" and demonstrate the importance of both ecological and methodological factors when selecting sentinels to detect ecosystem change. For example, sentinel species which are trophically linked and measured on short timescales may be more effective for managers seeking to monitor ecosystem change than other species. By identifying effective traits for the use of sentinel species, scientists and policymakers will be able to develop rapid and adaptable management plans in response to global change.

KEYWORDS
biodiversity conservation, ecosystem sentinels, environmental change, flagship species, indicator species, keystone species, surrogate species, umbrella species

1 | INTRODUCTION

Anthropogenic change is causing the collapse of organismal populations and global biodiversity (Dirzo et al., 2014; Johnson et al., 2017; Urban, 2015). The loss of flora and fauna degrades ecosystem integrity and function, which cascades to threaten ecosystem, cultural, and economic services provided for humans (Díaz et al., 2006; Jarić et al., 2022). A shortage of measurable and relevant indicators to monitor the health and trajectory of ecosystems is a clear impediment to effective conservation (Juan-Jordá et al., 2022; Mace et al., 2018). Without indicators to help scientists and policymakers assess and track climate and ecosystem change, conservation goals set by global treaties like the Convention on Biological Diversity (CBD) may not be achieved (Mace et al., 2018).

Indicator species can allow scientists and managers to understand ecosystem status without devoting scarce resources to monitoring every biophysical process and organism in an ecosystem. One way to select indicators for management is by using sentinel species (hereafter, 'sentinels'), which are a subset of indicators that help provide information about components of the environment or ecosystems (Zacharias & Roff, 2001). Sentinels have been shown through extensive meta-analyses to detect pollution, disease, and other environmental and human health hazards (Kerby et al., 2010; Rabinowitz et al., 2005). For example, Kerby et al. (2010) found that amphibians are only moderately sensitive to water-borne toxins, suggesting that other taxa may be more useful for monitoring of environmental health hazards. These global meta-analyses are excellent tools for indicating which species are more or less sensitive to environmental changes, thereby aiding researchers and professionals in effectively guiding the selection and monitoring of sentinels.

While there is a rich literature and synthesis on such pollution and health sentinels, there is a lack of similar global analyses on another widely used sentinel type: ecosystem sentinels. Ecosystem sentinels are species that respond to changes in environmental variability in a timely and measurable way, and help to indicate ecosystem change (Hazen et al., 2019). Ecosystem sentinels differ from other related terms used in conservation biology like indicator, umbrella, keystone species, or conservation proxies (Caro, 2010), as they are specifically used to indicate the process of ecosystem change (Hazen et al., 2019). Ecosystem sentinel responses include a wide array of ecological traits that can be measured including demography, behaviour, and morphometrics, among others (Hazen et al., 2019). Selecting the most appropriate species can be subjective (Heink & Kowarik, 2010; Siddig et al., 2016), and includes multifaceted criteria such as species charisma, conspicuousness, ease of sampling, rarity, functional importance and ecological mechanism (Hazen et al., 2019; Heink & Kowarik, 2010; Marneweck et al., 2022; Natsukawa & Sergio, 2022; Siddig et al., 2016). For example, two recent reviews on sentinel species provided contrasting views on trophic position as a criteria for choosing ecosystem sentinels—one supported top predators (Natsukawa & Sergio, 2022), and another mesopredators (Marneweck et al., 2022). Part of these discrepancies likely stems from reliance on local, context-dependent research as opposed to global quantitative tests of the appropriateness of sentinel species (Sergio et al., 2008). In fact, there have been reviews on a multitude of ecosystem sentinel taxa, including: ants (Andersen & Majer, 2004), bats (Jones, Jacobs, et al., 2009), deer (Hanley, 1993), marine mammals (Moore, 2008), otters (Jessup et al., 2004), penguins (Boersma, 2008), sea snakes (Rasmussen et al., 2021), swamp rabbits (Hillard et al., 2017), and squirrels (Smith, 2012; Wheeler & Hik, 2013). Yet we still lack a general understanding of which sentinels and ecological factors can most strengthen our ability to detect environmental and ecosystem change, based on empirical evidence of responsive relationships with sentinel species (Hazen et al., 2019).

Here, we first introduce a conceptual diagram describing the concept of ecosystem sentinels (Figure 1) and provide examples of how such sentinel species can indicate environmental changes (i.e. "environmental change sentinels", which indicate changes in air and sea temperature, habitat, salinity, sea ice, etc.) and changes in ecosystem components (i.e. "ecosystem component sentinels", which indicate changes in prey availability, community composition, biodiversity, etc.). Therefore, ecosystem sentinels respond to and reflect different ecological relationships, including with the environment and with other species within an ecosystem (Figure 1). An example of an environmental change sentinel, Cassin's auklet (*Ptychoramphus aleuticus*) demography responds to changes in sea surface temperature and upwelling before other ecosystem components (Wolf et al., 2010; Figure 1b). Therefore, Cassin's auklets can indirectly detect when ecosystem components (i.e. salmon, see Wolf et al., 2010) may change in response to changing environments. An example of an ecosystem component sentinel, desert tortoise (*Gopherus agassizii*) presence serves as an indicator of changes in vertebrate biodiversity in the Mojave Desert (Boykin et al., 2021; Figure 1c). At last, an example of both an environmental change and ecosystem component sentinel, polar bear (*Ursus maritimus*) body condition may be indicative of both changing sea ice and seal body condition, because seals are an important prey of polar bears, and both polar bears and seals are strongly related to sea ice availability (Rode et al., 2021; Figure 1d).

Using this diagram, we next conducted a meta-analysis on the effectiveness of sentinel species at indicating changes in the environment and ecosystem components. Despite the increasing popularity of ecosystem sentinels in the literature (Hazen et al., 2019), there remains a need to conduct a quantitative, comprehensive analysis to identify the factors that improve the strength of sentinel responsiveness to ecosystem change and maximise the applicability and implementation of the sentinel species concept. This will help researchers and practitioners to develop management plans to better monitor ecosystems using reliable sentinel species. Following past research, we hypothesised that both ecological and methodological factors should modify whether sentinels are effective at indicating environmental change or ecosystem component change. Under ecological factors, we hypothesised that the sentinel relationship with an ecosystem component may affect its responsiveness, where sentinels that were trophically linked (e.g. predators) to ecosystem components would be more effective than other sentinels (Natsukawa

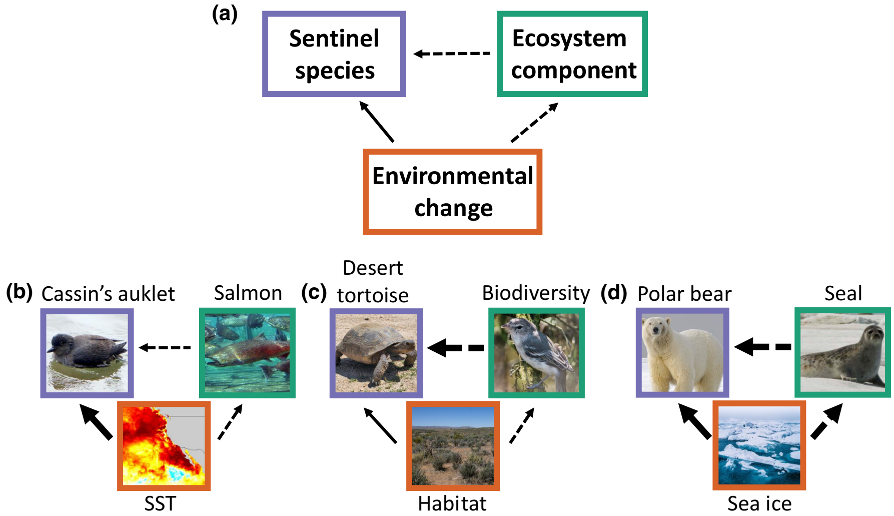

FIGURE 1 A conceptual diagram to describe how sentinel species indicate environmental and ecosystem change. (a) Sentinel species may respond directly to environmental change, such as habitat availability, or indirectly by responding to environmentally driven changes in ecosystem components, such as prey availability. Thus, sentinel species can be used to indicate both changes in the environment (i.e. "environmental change sentinel") and changes in broader ecosystem components (i.e. "ecosystem component sentinel). (b) An example of an environmental change sentinel, Cassin's auklet (*Ptychoramphus aleuticus*) demography is related to sea surface temperature (SST) and indirectly related to ecosystem components like salmon (Wolf et al., 2010). (c) An example of an ecosystem component sentinel, desert tortoise (*Gopherus agassizii*) presence is related to desert biodiversity, and linked via environmental change in habitat (Boykin et al., 2021). (d) An example of both an environmental change and ecosystem component sentinel, polar bear (*Ursus maritimus*) body condition is related to both sea ice and seal body condition (Rode et al., 2021). Bold lines indicate the direct pathway from environmental change to sentinel species, whereas dashed lines indicate the indirect pathway from environmental change to ecosystem component to sentinel species. In each example, the direction of the arrow indicates the direction of influence, and the width of the arrow indicates the strength of the relationship (i.e. the correlation between sentinel and environmental change or ecosystem component) established in the sentinel study. Environmental change sentinels are strongly, directly related to environmental change (b), ecosystem component sentinels are strongly, directly related to ecosystem components (c), and both environmental change and ecosystem component sentinels are strongly, directly related to both (d) as indicated by the width of the arrows in this diagram.

& Sergio, 2022). Moreover, we hypothesised that trophic position would affect sentinel effect size as consumers more directly linked to environmental change (i.e. primary consumers) should be more sensitive compared to consumers with extra trophic levels between it and environmental change (i.e. omnivores and secondary consumers) (Marneweck et al., 2022). In addition, we hypothesised that ectotherms would be more sensitive to environmental change than endotherms because of their sensitivity to external environmental temperature, and that body mass of the sentinel would alter the strength of the sentinel (Natsukawa & Sergio, 2022). We also hypothesised that methodological factors, like faster-scale sampling methods (e.g. diet assays) and shorter timescale measurements (e.g. daily) would be more sensitive to underlying environmental or ecosystem change (Hazen et al., 2019).

Via a systematic literature review, we collected 206 studies between 1978 and 2022 from which we documented 372 examples of ecosystem sentinels to evaluate these hypotheses and quantify the relationship between measured sentinel responses, environmental change, and ecosystem components. By conducting a global meta-analysis of the strength of different taxa as sentinels, we identified key ecological and methodological factors which correlate with sentinels that are the most effective at indicating environmental change and alteration in ecosystem components. Following these findings, we highlighted examples of sentinels used in management and delineate future directions to help achieve ecosystem management goals.

2 | MATERIALS AND METHODS

2.1 | Literature review

We collected data using Web of Science and Google Scholar as tools, searching for relevant articles online using combinations of the following keywords: sentinel species, focal species, keystone species, indicator species, predictor species, and umbrella species, in combination with ("AND") the following taxonomic keywords: amphibians, annelids, arthropods, bats, birds, bivalves, carnivores, cetaceans, crustaceans, fish, frogs, insects, invertebrates, pinnipeds, raptors, reptiles, rodents, salamanders, seabirds, songbirds, snakes, turtles and ungulates. We also checked the references cited in these papers and reviews to locate more articles. This literature search was conducted from June 10 to October 1 2022. This initial screening of papers resulted in 326 potential studies from 1978 to 2022. See Figure S1 in Supporting Information for a PRISMA flow diagram of the review process.

We then screened these studies under the criteria that they must at minimum explicitly discuss that the species in reference are sentinels of environmental change or ecosystem component change (Figure 1). For example, a hypothetical study could state, "We measured seabird diet as a sentinel of prey community structure, through the link of sea surface temperature affecting both seabirds and prey". We narrowed the screening this way to focus only on studies that tested the sentinel species concept (as defined in the Introduction), as opposed to studies that tested the relationship between environmental and/or ecosystem change on a species, for which there are likely thousands of examples. For this reason, we also did not include review articles in our final screening. This final screening resulted in 206 studies spanning from 1978 to 2022.

2.2 | Data collection

After screening, we collected quantitative and qualitative data from these studies using the following set of criteria (see Figures S2 and S3 for a more detailed workflow of our data collection process). For each study, a new data point was created for each unique relationship between sentinel/environmental change or sentinel/ecosystem component (Figure 1). In many cases, studies quantified multiple relationships across multiple taxa or sentinel measurements (e.g. diet, population size, etc.). In studies that did not quantitatively measure this relationship or for which we could not collect an effect size, we recorded one data row for qualitative analysis. Some studies conducted analyses of multiple measurements of the same or very similar variables (e.g. multiple measurements of habitat quality; different time lags). To minimise oversampling, we used a reductionist meta-analytic approach to include one effect size per distinct, quantified relationship (López-López et al., 2018). We used a decision rule to choose the strongest effect size that researchers or managers would use in their evaluation of the sentinel being studied, representing the best-case scenario of sentinel performance. Through this process, we collected 606 unique data rows from these studies.

For each of these studies, we recorded information on the location, taxa, sentinel relationship and system. In each data row for which the sentinel relationship was quantified, we recorded the Pearson correlation coefficient, *r*, as a measure of effect size (Koricheva et al., 2013) as it was the most prevalent way of measuring the sentinel relationship in the literature. Indeed, correlation coefficients are often used as measures of effect size in meta-analyses when data are continuous and/or from non-experimental research (Nakagawa & Cuthill, 2007), however it is important to note that they may not adequately describe nonlinear relationships between variables. These data were recorded from the manuscript text or extracted from figures using Web Plot Digitizer (Rohatgi, 2012). In some cases, we calculated correlation coefficients from other effect sizes (e.g. Chi-squares, Spearman's correlation, ANOVA) using methods described in Koricheva et al. (2013; Box 13.3). We also recorded the sample size of the correlation coefficient. In addition, we conducted a "vote-counting analysis" (Koricheva et al., 2013; Natsukawa & Sergio, 2022), where each study was either classified as "1", when it indicated support for a taxa as a sentinel, or "0", when it indicated no such support to illustrate summary statistics. Finally, we also recorded two types of predictor variables: ecological variables, and methodological variables, which we hypothesised would modify the strength of relationships between sentinels and environmental change or ecosystem components.

2.2.1 | Ecological and methodological variables

First, we collected predictor variables that described the sentinel, which may affect the strength of the effect size. We recorded the taxonomy of the sentinel species, which we binned into the broader taxonomic categories of amphibian, bird, fish, invertebrate, mammal and reptile. We also recorded the system where the sentinel was studied: freshwater, marine, and terrestrial. Finally, we recorded whether there was a relationship studied between the sentinel and an ecosystem component and/or environmental change (Figure 1).

Second, we collected predictor variables related to the ecology of the sentinel and its relation to the environment or ecosystem that may describe the strength of the effect size, which we binned into the categories of air temperature, ocean habitat, ocean temperature, precipitation, sea ice and terrestrial/freshwater habitat. We also collected data on nature of relationship with ecosystem component (i.e. trophic relationship or co-occurring). We did not place the few examples of competing or parasitising species in either category due to insufficiently small sample size ($N=4$). We also collected data on trophic position (i.e. primary consumer, secondary consumer, or omnivore). We collected body mass (kg) from the databases Amniote (Myhrvold et al., 2015), AmphiBIO (Oliveira et al., 2017), AVONET (Tobias et al., 2022), PanTHERIA (Jones, Bielby, et al., 2009) and SeaLifeBase (Palomares & Pauly, 2024). We also collected data on whether the sentinel species was an ectotherm or endotherm.

Third, we collected methodological predictor variables related to the sampling of the sentinel that may influence its effectiveness (Hazen et al., 2019). We also collected the sampling method of the sentinel (biodiversity, diet, morphometrics, population size, reproduction, space-use and survival). To clarify, "biodiversity" sampling methods use sentinels to indicate biodiversity measurements like species richness, alpha and beta diversity, and so forth. We also collected the sampling scale (e.g. daily, monthly, yearly, decadal and spatial). We included "spatial" sampling scale as some studies measured sentinel responses over space (e.g. woodpecker biodiversity in forested vs. un-forested plots) instead of over time (e.g. seabird demography over years).

2.3 | Meta-analysis

We calculated effect sizes using the absolute value of the Pearson correlation coefficients, *r*, as we were only concerned with the strength, and not the direction, of the relationship with the sentinel species. We calculated sampling variances of the effect size using an adjusted method for the large-sample equation for the sampling variance of a Pearson correlation coefficient (Koricheva et al., 2013): $\mathrm{Var}(r) = (1 - r)^2/(n - 1)$. In our analysis, we weighted studies using the natural log of the sample sizes, to downweigh some studies which had inordinately high sample sizes. We found that log weighting the effect sizes did not change the effect size and variance of our intercept-only meta-analysis, compared to removing outliers with extremely high sample sizes. We included the random effect of study ID to account for similarities in multiple data rows collected from the same study. Our intercept-only meta-analysis, which we fit to understand the overall mean effect size before including predictor variables, had significant heterogeneity ($Q = 1032.52$, $df = 368$, $p < 0.0001$) as measured using Cochran's Q test (Koricheva et al., 2013). In addition, we tested for publication bias using funnel plots (Koricheva et al., 2013) of the standard error of the results versus their residual values. We did not find any evidence of publication bias, with a "funnel" shape shown where studies with larger precision had less variation in effect size (Figure S4).

We accounted for heterogeneity between studies using weighted generalised linear mixed-effects models (function: *rma.mv*) in the R package "metafor" (Viechtbauer, 2010). For this meta-analysis, we included the following predictor variables in the full model: taxonomy, system, trophic position, thermoregulation, ecosystem component/environmental change–sentinel connection, sampling method, body size, sampling scale, environmental change category and ecosystem component category. Due to collinearity between taxonomy and thermoregulation, we left out taxonomy from our meta-analysis but note that preliminary analyses indicate that taxonomy was not a significant predictor. We conducted backwards stepwise selection until we reached the lowest AIC (Burnham & Anderson, 2003). During the model selection process, we preliminarily tested for significant interactions but did not find any between our predictors. Additionally, due to differences in methodology between sentinel/environmental change and sentinel/ecosystem component studies, we further conducted model selection by splitting the sample dataset by connection and running backwards stepwise selection until we reached the lowest AIC. We found that this did not significantly change the predictors kept after model selection compared to our model which did not split up the data (Tables S1, S3 and S5). Final estimates of effect size and confidence intervals were calculated using these final meta-analytic models.

3 | RESULTS

3.1 | How are ecosystem sentinels used around the world?

We documented sentinels in seven continents, five oceans, and across terrestrial, marine and freshwater systems (Figure 2a; Figure S1). The majority of research was carried out in Europe and North America (70.9%), with much research concentrated along the California coast where marine birds, mammals, and fish have been documented as sentinels of ocean change in the California Current ecosystem. In contrast, sentinels were understudied in Asia and Africa (12.6%), likely reflecting a bias in research effort. Most sentinels occurred in marine systems (56.4%), followed by terrestrial (36.1%), and freshwater systems (7.4%). Sentinels represented all six major taxa (amphibians, birds, fish, invertebrates, mammals and reptiles), ranging from species as small as grey treefrogs (*Dryophytes versicolor*) (0.007 kg) to species as large as blue whales (*Balaenoptera musculus*) (154,321 kg). Birds were the most common sentinel taxa (59.4%), ranging from seabirds to raptors to grassland passerines.

Sentinels were almost equally used to measure changes in environment (52.5%) and ecosystem components (47.5%). However, about one-third of studies (38.2%) also quantified the relationship between environmental change and the ecosystem component (see Figure 2). Quantifying changes in space-use was the most popular method to measure sentinel responses (30.6%), such as measuring changes in site occupancy or habitat use (Figure 2b). Many studies also used multi-annual measurements (59.2%), like reproduction or population change. For example, American alligators (*Alligator mississippiensis*) were reported as being sentinels of Florida Everglades ecosystems because their population size is sensitive to hydrologic conditions (Waddle et al., 2015). Other studies of sentinels used finer timescale measurements (3.0%), such as daily diet. For example, puffin diet is sensitive to prey fish biomass and has been used as a sentinel for indicating fisheries stocks (Sydeman et al., 2022).

We found that sentinels measured a wide variety of environmental changes to ecosystems, ranging from changes in ocean and air temperature to sea ice to terrestrial habitat characteristics (Figure 2c). In marine systems, ocean temperature was the most prominent environmental category (62.3% of marine) measured by sentinels, whereas in terrestrial systems, habitat metrics were most often measured (80.6% of terrestrial). A majority of sentinels were trophically connected (61.9%), measuring a direct trophic relationship with ecosystem components. In contrast, a significant portion of sentinels (38.1%) co-occur with ecosystem components without direct trophic links (Figure 2d). Marine sentinels commonly measured a trophic relationship with their prey species (92.7% of marine), whereas terrestrial sentinels mainly measured co-occurring, non-trophic relationships with species (78.4% of terrestrial). This latter finding is best explained by the predominance of terrestrial species as indicators of biodiversity metrics (68.4% of biodiversity metrics; e.g. (Drever et al., 2008)). Given the prevalence of sentinels across diverse taxa and systems, our review indicates a need for identifying the factors that enable sentinels to be most effective as indicators of change.

3.2 | How effective are sentinel species at detecting change?

We conducted a meta-analysis of our data synthesis using weighted generalised linear mixed-effects models to determine the contexts

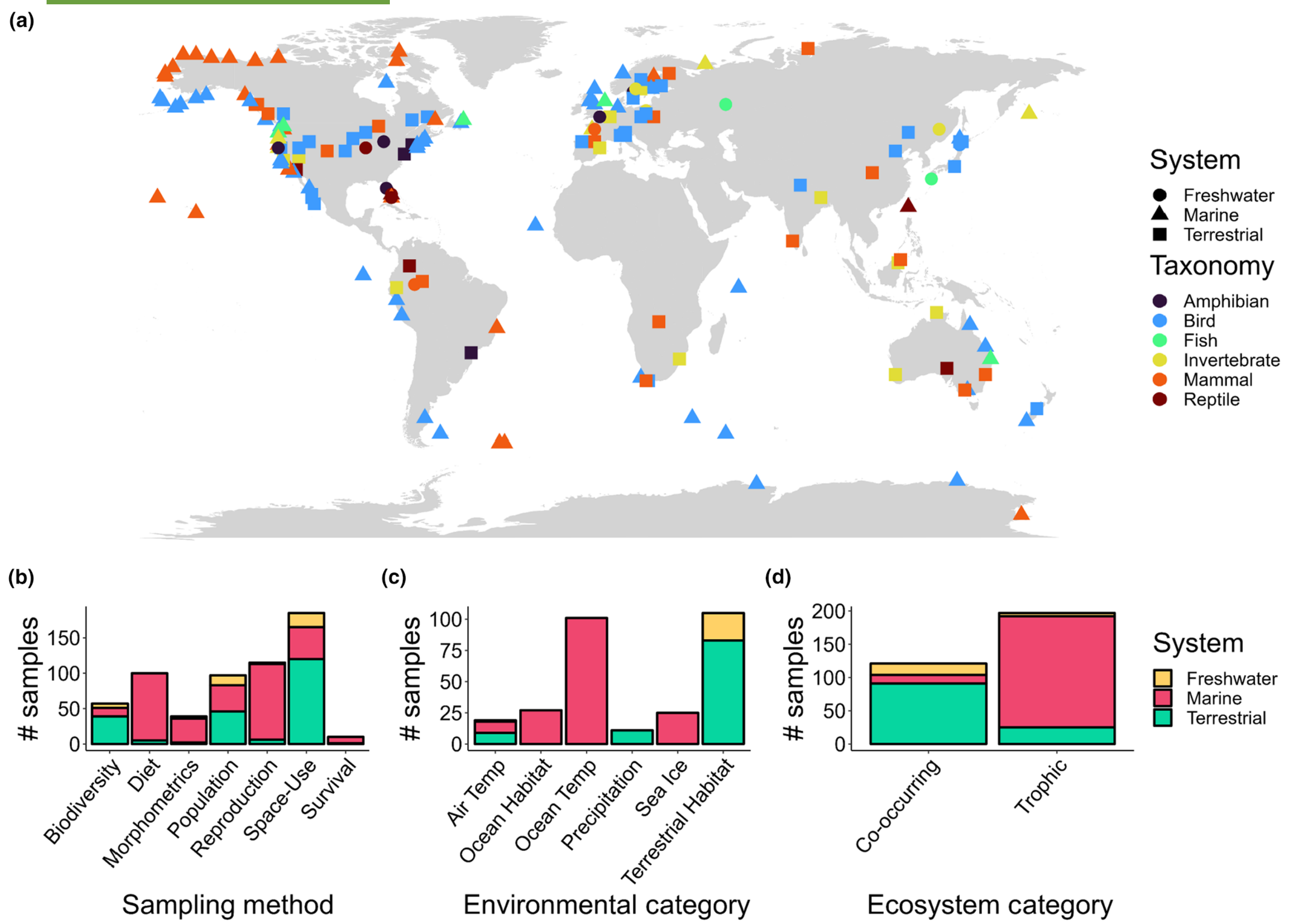

FIGURE 2 A global synthesis of sentinel species. (a) Geographic location of sentinel studies. Colours indicate the general taxonomy of the sentinel species, whereas shape indicates the system where the sentinel was located. (b) Number of samples collected for each sampling method to detect changes in the sentinel species. (c) Number of samples collected for each sentinel-environmental change relationship. (d) Number of samples collected for each sentinel-ecosystem component relationship. (b–d) are coloured by the system where the sentinel was located.

enabling sentinels to best indicate changes in the environment and/or ecosystem components. Across all sentinels, we found that the correlation between sentinel responses and their environment or ecosystem component was moderate (effect size [ES] = 0.47; 95% CI = 0.436 to 0.511), but with significant heterogeneity between studies (Cochran's $Q = 1032.52$, df = 368, $p < 0.0001$). The relationship between sentinels and environmental change (ES = 0.49; 95% CI = 0.392 to 0.568) was slightly stronger than that of sentinels and changes in ecosystem components (ES = 0.47; 95% CI = 0.361 to 0.574; Tables S1 and S2). Importantly, most studies qualitatively self-reported that their sentinel was effective (79.0%), despite many of these studies quantitatively finding non-significant or weakly significant relationships. For example, 54.7% of studies with a Pearson correlation coefficient ($r < 0.5$) self-reported that their sentinel was effective (Figure S5). We follow by identifying the ecological and methodological contexts that explain this heterogeneity in sentinel performance.

To examine context-dependence, we assessed sentinel performance as a function of taxa, system, trophic position, thermoregulation, body size, sampling method, sampling scale, and environmental change and ecosystem component categories. As a result of preliminary analyses and model selection, we found little evidence that any single taxa or system is a more effective sentinel than another, as these predictors were not retained in our final meta-analytical model (Table S1). Instead, we found that ecological and methodological factors best explained sentinel performance, with the final model including trophic position, thermoregulation, environmental change category and sampling scale.

Among sentinels of ecosystem change, ecosystem component category was important, with taxa that were trophically connected to ecosystem components (i.e. predator or prey) being on average 28.0% more responsive than taxa that only co-occurred with ecosystem components (ES = 0.51; 95% CI = 0.416 to 0.605; ES = 0.39; 95% CI = 0.296 to 0.501; respectively; Figure 3a). Across both sentinel types (indicators of environmental or ecosystem change), primary consumers were on average 24.4% more sensitive to environmental or ecosystem change than secondary consumers or omnivores (ES = 0.58; 95% CI = 0.496 to 0.705; ES = 0.46; 95% CI = 0.412 to 0.514; ES = 0.46; 95% CI = 0.231 to 0.706; respectively; Figure 3b).

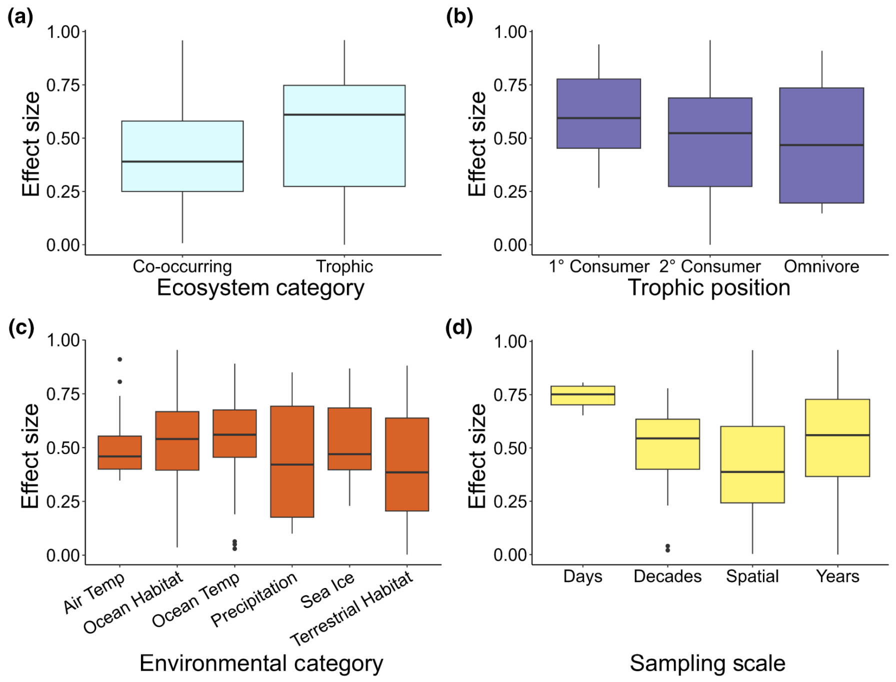

FIGURE 3 Effectiveness of sentinel ability by ecological and methodological predictors. Boxplots show the spread of the effect sizes (ES) in the data in our meta-analysis by: co-occurring vs. trophically-connected ecosystem components (a), trophic position (b), environmental change category (c), and sampling scale (d). In (d), only one observation was on the "monthly" scale (ES = 0.78), so we removed it from the graph. In boxplots: center line = median; box limits = upper and lower quartiles; whiskers = 1.5x interquartile range; dots = outliers.

We found that sentinels were more closely linked to changes in temperature compared to other variables (air temperature ES = 0.49; 95% CI = 0.269 to 0.717; ocean temperature ES = 0.54; 95% CI = 0.447 to 0.630; respectively) (Figure 3c). We also found that ectotherms were slightly 4.7% more sensitive sentinels than endotherms (ES = 0.49; 95% CI = 0.400 to 0.583; ES = 0.46; 95% CI = 0.416 to 0.524; respectively; Figure S6). Although the specific sampling method (e.g. biodiversity, diet, space-use) was not retained in our final model, sentinel responses that were sampled at shorter timescales were more responsive to changes in the environment or ecosystem than those sampled at longer timescales (Figure 3d). For example, sampling on the daily scale (ES = 0.75; 95% CI = 0.471 to 1.026) was 44.0% more sensitive than sampling on the yearly scale (ES = 0.52; 95% CI = 0.462 to 0.577). In addition, sampling on any temporal scale performed on average 65.7% better than sampling across space (ES = 0.38; 95% CI = 0.312 to 0.459) as a measurement of the environment or ecosystem change (Figure 3d). Given the heterogeneity in sentinel performance, the choice of sentinel species or scale of study may not simply correlate with the best sentinel of environmental or ecosystem processes.

4 | DISCUSSION

Our meta-analysis quantitatively shows that sentinel species can be promising ecosystem indicators and highlights the factors that help determine which sentinels are best suited to detect changes in environmental conditions and ecosystem structure. While the value of sentinel species will be highly dependent on system-specific contexts and objectives, we found several important generalisable patterns across our meta-analysis. Specifically, contrary to other taxa-specific reviews of smaller scope, we found that the efficacy of the sentinel was not strongly related to type of taxa or system. Instead, our results revealed that the ability of sentinels to detect environmental and ecosystem changes depended on certain biological and ecological factors. For example, sentinels were more sensitive to changes in abiotic conditions than habitat (Figure 3c). This highlights the importance of choosing sentinels that have close and mechanistic relationships with environmental and ecosystem change to help guide future management applications.

The importance of ecological factors in explaining sentinel ability may be best explained by trophic position—among ecosystem component sentinels, trophically linked taxa were more effective than taxa that were co-occurring (Figure 3a). As others have argued, ecologically-linked sentinels, rather than species that simply co-occur with one another, appear to be more effective at indicating ecosystem change (Hazen et al., 2019; Marneweck et al., 2022; Natsukawa & Sergio, 2022; Sergio et al., 2008). In addition, we found that sentinels more directly linked to bottom-up changes in the environment or ecosystem (e.g. primary consumers) were more sensitive than those indirectly linked to such changes (secondary consumers, omnivores; Figure 3b). However, upper-trophic level species were still effective sentinels on average in our meta-analysis, and have been shown to be effective in multiple species-specific cases, even when the relationship is not quantified (Boersma, 2008; Hazen et al., 2019; Natsukawa & Sergio, 2022). Thus, we recommend that sentinels that are more directly linked to the environment or ecosystem variables of interest will perform the best (Marneweck et al., 2022; Natsukawa & Sergio, 2022). Following this, we recommend that exploring other understudied ecological interactions in sentinels, such as competition or even parasitism, could be promising (Møller et al., 2017; Sobocinski et al., 2020; Sydeman et al., 2017; Tryjanowski & Morelli, 2015). For example, kittiwake (*Rissa tridactyla* and *R. brevirostris*) breeding success is considered a sentinel of reduced pink salmon (*Oncorhynchus gorbuscha*) abundance through competition for resources (Sydeman et al., 2017). Similarly in parasitism, the common cuckoo (*Cuculus canorus*), a brood parasite, has been found to be a sentinel of host bird biodiversity (Tryjanowski & Morelli, 2015). It is also an important caveat to note that sentinels are often selected for other reasons, such as ease of sampling or likelihood of surviving with potentially expensive tag equipment that may complicate the choice of sentinel species based on ecological criteria.

Our finding that sentinels of co-occurring species were not as effective as more directly linked sentinels supports past critiques of species that are not directly ecologically connected to ecosystem components (Linnell et al., 2000; Williams et al., 2000; Zacharias & Roff, 2001). We found many studies on terrestrial sentinels of co-occurring species with only weak, indirect links to ecosystem component taxa. Many of these co-occurring sentinels were generalists with broad habitat ranges, like raptors and carnivores, where direct links between sentinels and ecosystem components were difficult to establish (Estrada & Rodríguez-Estrella, 2016; Linnell et al., 2000; Natsukawa & Sergio, 2022; Ozaki et al., 2006; Santangeli et al., 2015). For example, raptors in Baja California were poor sentinels of biodiversity for ecosystem components that were distantly related to raptors, like plants (Estrada & Rodríguez-Estrella, 2016). Still, within certain contexts, sentinels of co-occurring species can be effective indicators of ecosystem or environmental change. Moreover, ecologically important species can be more useful sentinels for ecosystem management planning. For example, large carnivores like wolves (*Canis lupus*) and grizzly bears (*Ursus arctos horribilis*) have been found to be effective sentinels of mammal species richness because of their significant ecological role as top predators (Steenweg et al., 2023).

Our review showed the popularity of local, context-dependent examples of sentinel research, even in some cases if quantitative evidence did not provide support for the focal species as effective sentinels (Figure S5). Many studies quantified the link between sentinels and environmental change, even if they were ultimately interested in indicating change in ecosystem components. Moreover, some studies did not provide strong evidence for a causative link between the environment and ecosystem components, which would maximise the effectiveness of ecosystem sentinels in management. This is problematic when relationships have not been quantified, as sentinel ability may become ineffective in the future, as nonlinear, complex relationships between sentinels and increasing anthropogenic change may give negligible, intuitive, and sometimes contradictory inferences on the true states of ecosystems (George et al., 2015; Reed et al., 2016; Versluijs et al., 2019). Some of the sentinels most effective at indicating ecosystem changes may simply be difficult to study or observe. We suggest that our conceptual diagram (Figure 1) in tandem with new tools for sampling species (e.g. biologging, remote-sensing, drones, automated passive monitoring) could allow for a better choice of sentinels. For example, we found that the timescale of sampling, rather than sampling method, was an important indicator of a sentinel's effectiveness (Figure 3d), suggesting that finer-scale measurements (e.g. diet on the daily scale) may be able to capture more adequately environmental or ecosystem change. Further research is needed at multiple timescales across the context-dependent, system boundaries that we found—such as conducting studies on terrestrial species as predator/prey sentinels (Marneweck et al., 2022; Natsukawa & Sergio, 2022) or marine species as biodiversity sentinels (Hazen et al., 2019). A lack of appropriate sampling scale may be obfuscating the potential effectiveness of some sentinels. Expanding quantitative sentinel research across these boundaries will help identify the scenarios and locations where sentinels will be most sensitive.

Finally, with an ecological understanding of how sentinels can be effective indicators, we recommend that future research invest in the capacity of sentinels to improve management decision making. Managers seeking to monitor ecosystem change may focus on sentinel species which are trophically linked and measured on shorter timescales. This could include measurements such as diet or foraging activity using GPS monitoring. For example, Peruvian booby (*Sula variegate*) foraging behaviour (i.e. range of daily trips and distances of dives on a daily scale) may be used as a sentinel of fishing activity on Peruvian anchovy (*Engraulis ringens*; Bertrand et al., 2012). In contrast, our results indicate that longer timescale, co-occurring (but not trophically linked) sentinels may be less effective for managers seeking to monitor ecosystem change. For example, capercaillie (*Tetrao urogallus*) population densities may only marginally correlate with forest-dwelling mammal and bird biodiversity (Pakkala et al., 2003). In addition, incorporating suites of sentinel species and measurements into monitoring programs is beginning to gain recognition; for example, the use of seabird diets for ecosystem-based marine management (Sydeman et al., 2022). Similarly, data on diet, reproduction, and population trends of penguins, fur seals, and albatrosses have been combined into consolidated indices to indicate Antarctic krill (*Euphausia superba*) abundance (Reid et al., 2005). Other ecosystem-based management programs, focusing in areas like the Everglades (Brandt et al., 2022), Yellowstone (Ray et al., 2019), and the Long Island Sound (Field et al., 2014), USA are using sentinel species in combination with abiotic, biotic and socioeconomic indicators to help develop management plans. We contend that incorporating sentinel species into these plans will allow for rapid and adaptable management in response to anthropogenic change, due to sentinels' sensitivity to environmental and ecosystem change. For example, an ecosystem-based management plan for a Pacific herring (*Clupea pallasii*) fishery in San Francisco Bay, USA used data from both sentinel predators of herring (e.g. salmon, whales, murres, sea lions) and alternative sentinel prey of those predators (e.g. anchovy, squid, krill) to suggest adjustments to harvest quotas (Thayer et al., 2020). Technological advances in a wide array of monitoring and analytical techniques (e.g. Hazen et al., 2019; Jachowski et al., 2023; Steenweg et al., 2023) may also allow for linked monitoring stations of suites of sentinel species to monitor ecosystem change responsively. In summary, by identifying the appropriate sentinels for management, scientists and policymakers can help capture ecosystem change to help reach biodiversity goals, such as those set by the Convention on Biological Diversity for 2030 (CBD, 2022).

AUTHOR CONTRIBUTIONS

All authors helped design the study. T.J. Clark-Wolf, Katie A. Holt, Erik Johansson, Anna C. Nisi, Kasim Rafiq, Leigh West and Briana Abrahms synthesised the data. T.J. Clark-Wolf performed the analyses. T.J. Clark-Wolf led the writing of the manuscript. All authors, including P. Dee Boersma, Elliott L. Hazen and Sue E. Moore, contributed critically to the manuscript drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The code and data needed to reproduce this analysis can be found on Github and is archived on Zenodo: https://doi.org/10.5281/zenodo.8101971 (Clark-Wolf, 2023).

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SUPPORTING INFORMATION

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

Figure S1. Prisma diagram detailing the systematic review process.

Figure S2. Workflow diagram detailing the process of extracting unique data points from papers in our meta-analysis.

Figure S3. Example workflow diagram detailing the process of extracting data points from (Wolf et al., 2010) for our meta-analysis.

Figure S4. Funnel plot for the final model of ecosystem sentinels (Table S1).

Figure S5. Histogram of the effect size of sentinels in our synthesis.

Figure S6. Boxplot of the effect size of sentinels by thermoregulation.

Table S1. Model selection results for the effect size of sentinels to environment or ecosystem component change data as a function of ecological or sampling predictor variables.

Table S2. Final model parameters for the effect size of sentinels to environmental change and ecosystem component data.

Table S3. Model selection results for the effect size of sentinels to only environmental change data as a function of ecological or sampling predictor variables.

Table S4. Final model parameters for the effect size of sentinels to only environmental change data.

Table S5. Model selection results for the effect size of sentinels to only ecosystem component change data as a function of ecological or sampling predictor variables.

Table S6. Final model parameters for the effect size of sentinels to only ecosystem component change data.

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