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Review

# The usefulness of surrogates in biodiversity conservation: A synthesis

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ABSTRACT

Preserving biodiversity requires extensive information on species distributions and effectiveness of conservation actions. A surrogate approach, where a small number of species act as surrogates for broader groups of species, can simplify this task. Types of surrogates include indicator, umbrella, keystone and flagship species, and using diversity of higher taxonomic levels to represent species diversity. An overview of the empirical evidence of the usefulness of surrogates as a conservation tool is missing. We synthesised knowledge on if and when surrogate species are useful by systematically searching for meta-analyses and literature reviews assessing this. Results from 34 reviews revealed weak correlations between diversity of indicator species and other species and that umbrella species were not consistently useful for prioritising conservation actions. However, diversity of higher taxonomic levels can be representative of species diversity. No reviews have assessed the usefulness of keystone or flagship species. Thus, surrogate taxa often do not represent biodiversity or threatened species, and conservation actions aimed at surrogates might not necessarily benefit other species. However, surrogates are more likely to be useful when using a higher-taxon approach, when strong ecological similarities exists between a surrogate and other species, when surrogates are used at regional or landscape rather than local scales, and when using sets of multiple species as surrogates. As some use of surrogate species will always be necessary, surrogates should be carefully selected and their usefulness and cost-effectiveness should be assessed, including the risk that conservation actions aimed at that surrogate have unintended effects on other species.

## 1. Introduction

Conservation of biodiversity requires knowledge on the distribution and trends of a large number of species, many of which might be poorly known (Caro and O'Doherty, 1999; Landres et al., 1988). There is also a need for information on the effectiveness of conservation actions to alleviate threats to these species. As it is impossible to survey all species, or obtain knowledge on the requirements of all species affected by conservation actions, there is a need to reduce the complexity of obtaining relevant information (Lindenmayer and Likens, 2011). The most commonly used option to achieve this is the surrogate approach, where one or a small number of well-known species or taxonomic groups act as surrogates for lesser-known species (Moreno et al., 2007; Wiens et al., 2008). The rationale is that the diversity of certain species, and their response to threats or conservation actions, are representative of other species (Caro and O'Doherty, 1999; Landres et al., 1988). Thus, surrogate taxa can be used to estimate the status of biodiversity, including threatened or difficult-to-survey species (Pearson, 2006; Spector, 2006), assess effects of threatening environmental changes or conservation actions (Dalerum et al., 2008), and prioritise conservation actions (Reid, 1998; Sætersdal and Gjerde, 2011).

There are five commonly applied types of surrogate approaches (Table 1) (Caro and O'Doherty, 1999; Cottee-Jones and Whittaker, 2012). There is a range of **indicator** approaches, including bio-indicators, i.e. using certain species to monitor environmental quality (Markert et al., 2003) and structural indicators, i.e. using the presence of certain habitat structures that benefits biodiversity as an indicator (Lindenmayer et al., 2000). Here, the focus is on indicator species, where the presence or richness of a specific species or taxonomic group is assumed to indicate the presence or richness of other species, with conservation actions aimed at indicator species often assumed to benefit other species (de Bello et al., 2010; Gregory et al., 2005; Lindenmayer, 1999; Moreno et al., 2007; Zhang et al., 2020). With a **higher-taxon** approach, richness of higher taxonomic levels is assumed to indicate the richness of lower taxonomic levels. For example, areas with a high number of insect orders are assumed to also contain many families, genera, and species of these insect groups (Caro and O'Doherty, 1999; Gaston and Williams, 1993). With an **umbrella** approach, conservation

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**Table 1**
Definitions and examples for the most commonly used types of surrogates.

| Surrogate type | Definition | Examples |
|---|---|---|
| Indicator species | The presence, abundance, or persistence of species, or the species richness of a taxonomic group, is used as an indicator of target species, overall biodiversity, environmental conditions, or environmental change (de Bello et al., 2010; Gregory et al., 2005; Lindenmayer, 1999; Moreno et al., 2007; Zhang et al., 2020). | The occurrence of the epiphytic lichen *Lobaria pulmonaria* is used to identify forest areas of high conservation value (Nilsson et al., 1995). |
| Higher-taxon approach | Information on higher taxonomic levels is used to indicate lower taxonomic levels. For instance, an area with a high number of insect genera is assumed to have a high number of insect species. This approach can help make monitoring more time and cost efficient (Caro and O'Doherty, 1999; Gaston and Williams, 1993). | Surveying the richness of bryophyte genera can be an effective method for rapidly assessing the species richness bryophytes (Alves et al., 2016). |
| Umbrella species | Conservation actions aimed at a species with certain habitat requirements are assumed to preserve the habitat of co-occurring species with less demanding requirements. Such requirements include large area requirements, and requirements for connectivity (Caro, 2003; Caro and O'Doherty, 1999; Roberge and Angelstam, 2004; Yamaura et al., 2018; Zhang et al., 2020). | Protection of areas to preserve the tiger (*Panthera tigris*) is assumed to also preserve co-occurring species within the tiger's large home range (Vasudeva et al., 2022). |
| Keystone species | Keystone species have disproportionally large ecological impact on species communities or ecosystem functioning relative to their abundance or biomass. Declines of a keystone species is likely to be reflected in the performance of other species, so ensuring persistence of a keystone preserves other species (Cottee-Jones and Whittaker, 2012; Menge et al., 2013; Paine, 1969; Zhang et al., 2020). | The habitats created, transformed and maintained by the Eurasian beaver (*Castor fiber*) support a variety of plant and animal species, meaning preservation of beavers will help maintain these species communities (Janiszewski et al., 2014). |
| Flagship species | Often large and charismatic vertebrates, used to attract public interest, awareness and support towards conservation actions aimed at a flagship species, which in turn will benefit less charismatic taxa. Flagship species are often chosen to appeal to the target audience, so this approach does not necessarily rely on an established relationship between the flagship and target species (Caro and O'Doherty, 1999; Verissimo et al., 2011; Yamaura et al., 2018; Zhang et al., 2020). | The giant panda (*Ailuropoda melanoleuca*) is used by the World Wide Fund for Nature (WWF) to gather funds for conservation actions aimed at preserving habitat for the giant panda and other species (World Wide Fund for Nature, 2023). |

actions aimed at one species is assumed to benefit co-occurring species. Often, umbrella species have large habitat requirements (Caro, 2003; Caro and O'Doherty, 1999; Roberge and Angelstam, 2004; Yamaura et al., 2018; Zhang et al., 2020). **Keystone species** have a larger impact on the ecosystem than is expected just based on their abundance or biomass. Therefore, the conservation of the keystone is assumed to lead to the preservation of linked species (Cottee-Jones and Whittaker, 2012; Menge et al., 2013; Paine, 1969; Zhang et al., 2020). With a **flagship** approach, a species is used to attract financial support for conservation actions that are assumed to also benefit other species (Caro and O'Doherty, 1999; Verissimo et al., 2011; Yamaura et al., 2018; Zhang et al., 2020). In practice, different types of surrogates are sometimes used interchangeably, and the definitions might overlap. For example, indicator species can be used to identify areas with high biodiversity that can be targeted for conservation actions, which has similarities with the role of umbrella species. Moreover, flagship species are commonly expected to both be effective at attracting financial support and useful as umbrella species, as conservation actions aimed flagship species are often assumed to benefit co-occurring species (Caro and O'Doherty, 1999).

Several criteria for when species are suitable as surrogates have been suggested in the scientific literature. It is important that they are well-known in terms of taxonomy, biology, and ecology (Caro and O'Doherty, 1999; Griffith, 1997; Heink and Kowarik, 2010; Moreno et al., 2007), and they should be cost-effective to detect, sample, and monitor (Carignan and Villard, 2002; Caro and O'Doherty, 1999; Moreno et al., 2007; Wiens et al., 2008). Obviously it is also important that surrogates represent other species, and that conservation actions aimed at surrogates will benefit other species (Barton et al., 2015; Caro et al., 2005; Lindenmayer and Likens, 2011). This is more likely when species share life-history characteristics, habitat associations, or other ecological requirements (Wiens et al., 2008), but this may vary across different habitat attributes and other environmental conditions (Eglington et al., 2012; Landres, 1992; Landres et al., 1988; Lewandowski et al., 2010).

It has been suggested that surrogates with certain traits are more likely to represent other species. For instance, it has been suggested that indicator and umbrella species should be large-bodied, as large species with a large home range and broad geographic distribution represent more species than small-bodied species (Caro and O'Doherty, 1999; Yamaura et al., 2018). Additionally, it has been suggested that keystone species should play a critical part in important ecological processes in order to fulfil their role as a keystone (Büchs, 2003; Griffith, 1997), and that flagship species should be charismatic in order to appeal to target audiences (Bowen-Jones and Entwistle, 2002). However, it remains largely unexplored if species possessing these traits actually perform better as surrogates than others.

The use of surrogate taxa should be motivated by evidence that they are useful as a conservation tool, i.e. that the presence or diversity of surrogate taxa are representative of other species, and that conservation actions aimed at surrogates benefit other species. Several reviews have discussed the usefulness of surrogates or tested certain types of surrogates in specific contexts (e.g., Branton and Richardson, 2011; Caro et al., 2005; de Oliveira et al., 2020; Eglington et al., 2012; Gao et al., 2015; Landres et al., 1988; Westgate et al., 2014). Some of them question the usefulness of surrogates in biodiversity conservation (e.g., de Morais et al., 2018; Favreau et al., 2006; Roberge and Angelstam, 2004; Westgate et al., 2014). However, given the lack of feasible alternatives, the widespread usage of surrogates is unlikely to stop (Caro et al., 2005; Lindenmayer and Likens, 2011; Zhang et al., 2020). To ensure that the use of surrogates does not lead to poor conservation decisions, there is a need for a comprehensive overview of whether surrogate taxa are useful as a conservation tool, and under which conditions surrogates are likely to be more or less useful. Thus, the aim of this study was to summarise the information from previous reviews to determine if and when surrogate taxa will be useful as a conservation tool.

## 2. Methods

We systematically searched for review papers that assess how well surrogate taxa represent the status of lesser-known species, species of conservation concern or overall biodiversity, or if conservation actions aimed at surrogate taxa benefits other species. Searches were undertaken in January 2022, using the databases Scopus, Web of Science Core Collection, Agris, and CAB Abstracts. We used search terms related to different types of surrogates or the correlation or congruence between species, and combined these with search terms related to reviews, which resulted in the following search string:

(((congruence OR surrogate) AND (species OR taxa OR biodiversity)) OR cross-tax* OR “indicator species” OR “indicator tax*” OR “umbrella species” OR “umbrella tax*” OR “keystone species” OR “keystone tax*” OR “flagship species” OR “flagship tax*” OR (proxy w/5 species) OR (proxy w/5 taxa) OR (proxy w/5 biodiversity) OR (correlat* w/5 richness) OR (correlat* w/5 taxa) OR (correlat* w/5 biodiversity)) AND (review* OR meta-analys* OR synthes*).

The resulting articles were screened based on title, abstract, and the full text. All papers eligible for inclusion had to i) use empirical evidence to assess one or more types of surrogate taxa, by using meta-analysis to investigate the relationship between surrogates and other species or whether conservation actions benefit both surrogates and other species, or by using literature reviews to synthesise the evidence supporting or opposing the use of surrogates in conservation; ii) focus on terrestrial species and habitats; and iii) focus on the status at a certain point in time rather than temporal trends of relationships. The reference lists of articles remaining after full text-screening were used to identify potentially relevant reviews missed during initial searches. These were then screened using the same eligibility criteria.

All included reviews were categorized into two types, meta-analyses and literature reviews. Meta-analyses used systematic methods to find relevant primary studies, and analysed the results from these studies using meta-analysis. Literature reviews included both those who used systematic and non-systematic methods to find relevant primary studies.

For all included reviews, we read the methods, results and conclusions to answer the following questions:

1. What is the evidence that the investigated surrogate species is useful as a conservation tool, i.e. do the surrogate species represent other species and does conservation actions aimed at the surrogate benefit other species?
2. Is the usefulness of the surrogate as a conservation tool consistent across different geographical regions, biomes, spatial extents, spatial grains, and across species?
3. Which methods were used to assess the surrogate species?
4. Are the species traits suggested for selecting surrogates valid?

For meta-analyses testing the correlation between indicator species and other species, we also extracted information on the percentage of diversity of target species that was explained by the diversity of indicator species. We then calculated a weighted mean across all meta-analyses, with the weight based on the number of correlations included in each meta-analysis.

We then synthesised the information across all included reviews, separate for each type of surrogate (i.e. indicator, umbrella, keystone and flagship species and the higher-taxon approach). Different types of surrogates were sometimes used interchangeably across the included reviews, but we used the definitions in Table 1 to categorise which type of surrogate(s) was assessed in each review.

## 3. Results

We identified 34 reviews assessing empirical evidence on whether surrogate taxa can represent the occurrence or diversity of other species or if conservation actions aimed at surrogate taxa will benefit other species (Table 2). Thirteen of these were meta-analyses, which included between 14 and 400 studies, and 21 were literature reviews. Seventeen reviews performed assessments of indicator species, four the higher-taxon approach, ten umbrella species, five keystone species and two flagship species. Three literature reviews did not assess a specific type of surrogate, but rather the general approach of using surrogates within conservation. Eighteen reviews focused on a single taxonomic or ecological group as a surrogate (e.g. mega-fauna, top predators), while the remaining sixteen compared multiple groups. A majority of reviews (23) had a global focus, while the remaining eleven had a limited geographical focus. Seven reviews considered multiple biomes, and twelve assessed effects on different spatial scales (spatial extent or spatial grain; Wiens, 1989).

### 3.1. Indicator approach

Nine meta-analyses and eight literature reviews assessed an indicator approach (Table 2). Meta-analyses usually tested the correlation between the species richness or diversity of indicator species and other species, but did not assess to what extent conservation actions aimed at indicator species benefit other species. The meta-analyses generally revealed weak correlations between indicator species and other species. Across the eight meta-analyses, the diversity of indicator species on average explained 13 % (min: 11 %, max: 26 %) of the diversity of other species (Castagneyrol and Jactel, 2012; de Araújo, 2013; de Morais et al., 2018; Eglington et al., 2012; Liu et al., 2020; Westgate et al., 2014; Westgate et al., 2017; Wolters et al., 2006). The variance in the diversity explained were low in individual meta-analyses (Table 2), which indicates that instances with a strong correlation between the diversity of indicator species and other species were rare. Weak correlations were evident both in meta-analyses of correlations for such indicator species that the authors expected were useful as indicator species for other species (Castagneyrol and Jactel, 2012; Eglington et al., 2012; Liu et al., 2020), and explorative studies testing correlations between several different taxonomic groups (de Morais et al., 2018; Westgate et al., 2014; Westgate et al., 2017; Wolters et al., 2006). One meta-analysis revealed that diversity hotspots for indicator species are unlikely to also be hotspots for other species (Lewandowski et al., 2010). The included literature reviews summarised conclusions of primary studies assessing correlations between species or discussed their potential usefulness as indicator species. These concluded that it is unlikely that the species richness of indicator species is associated with the species richness of other groups (Carignan and Villard, 2002). More specifically, they found it unlikely that plants are useful indicator species for bryophytes (Bagella, 2014), that birds and other forest species are indicator species of forest biodiversity (Gao et al., 2015; Humphrey and Watts, 2004; Nilsson et al., 2001), and that ants are useful indicator species of overall biodiversity (Alonso, 2000; but see Andersen and Majer, 2004).

Nine meta-analyses found that the strength of correlations between indicator species and other species varied dependent on the context. There was a clear pattern of stronger correlations between species at larger spatial extents and grains: six of the seven meta-analyses explicitly testing the impact of spatial extent on correlations, and the three meta-analyses testing the impact of spatial grain, found stronger relationships at larger spatial scales (Eglington et al., 2012; Lewandowski et al., 2010; Liu et al., 2020; Westgate et al., 2014; Westgate et al., 2017; Wolters et al., 2006). Three meta-analyses revealed stronger correlations between species that were more closely related or shared similar functions or traits, e.g. between different plant groups rather than between plants and animals, and between species with similar mobility and range size (de Araújo, 2013; de Morais et al., 2018; Eglington et al., 2012), and another meta-analysis found that sets of species (birds, vascular plants and mammals) was better for representing other species rather than using a single taxonomic group (Westgate et al., 2017). Several meta-analyses found different patterns in correlations with the geographical region or biome investigated (Eglington et al., 2012; Lewandowski et al., 2010; Liu et al., 2020; Westgate et al., 2014; Westgate et al., 2017; Wolters et al., 2006). For example, Wolters et al. (2006) found stronger correlations between various taxonomic groups in tropical compared to temperate areas, while in contrast, Westgate et al. (2014) found stronger cross-taxon correlations at higher latitudes, and separate meta-analyses found the strongest correlation in different habitat types (e.g., grasslands: Lewandowski et al., 2010; forests: Liu et al., 2020). No reviews assessed whether indicator species with certain traits were more likely to

**Table 2**

Overview of the 34 reviews (ordered according to surrogate approach) found through systematic searches, which assess the usefulness of a surrogate approach.

| Study | Study type | Surrogate approach | Surrogate taxa | Target taxa | Geographic region | Biome | Spatial scale | Assessment | Main conclusion |
|---|---|---|---|---|---|---|---|---|---|
| Alonso (2000) | Literature review | Indicator | Ants | No specific target taxa considered | No specific region considered | No specific biome considered | No specific spatial scales considered | Review of studies testing correlations in species richness or diversity between ants and other taxa | Few studies find positive correlations between ant species richness and richness of other taxa |
| Andersen and Majer (2004) | Literature review | Indicator | Ants | No specific target taxa considered | Australia | No specific biome considered | No specific spatial scales considered | Review of studies assessing the role of ants as indicators | Ants are effective as indicators |
| Bagella (2014) | Systematic literature review | Indicator | Vascular plants | Bryophytes | Tropical, temperate, boreal | Forest, mountainous, disturbed areas | No specific spatial scales considered | Review of studies testing the co-variation in species richness between vascular plants and bryophytes | Half of the comparisons find positive co-variation in the richness of plants and bryophytes |
| Carignan and Villard (2002) | Literature review | Indicator | No specific surrogate taxa considered | No specific target taxa considered | No specific region considered | No specific biome considered | No specific spatial scales considered | Review of studies assessing the indicator approach | There is little support that species richness of indicators is associated with the richness of other taxa |
| Castagneyrol and Jactel (2012) | Systematic review and meta-analysis | Indicator | Plants | Arthropods, birds, herpetofauna, mammals | No specific region considered | Forest, grassland | Spatial extent treated as continuous variable | Meta-analysis of studies testing the correlation in species richness between plants and animal taxa | There are significant positive, but weak, correlations in the species richness between plants and animal taxa. On average, plant richness account for 20 % ± 4 % ($CI_{95\%}$) of variability in richness of animals. |
| de Araújo (2013) | Systematic review and meta-analysis | Indicator | Plants | Herbivorous insects | Tropical, temperate | Forest | No specific spatial scales considered | Meta-analysis of studies testing the correlation in species richness between plants and herbivorous insects | There are significant positive, but weak, correlations in the species richness between plants and herbivorous insects. On average, plant richness account for 26 % ± 4 % ($CI_{95\%}$) of variability in richness of herbivorous insects. |
| de Morais et al. (2018) | Systematic review and meta-analysis | Indicator | Animals, microorganisms, plants | Animals, microorganisms, plants | No specific region considered | No specific biome considered | No specific spatial scales considered | Meta-analysis of studies testing the correlation in species richness, abundance or composition between taxa | There are significant positive, but weak, correlations in species richness, abundance and composition between taxa. E.g., on average species richness of one taxa account for 18 % ± 19 % (SD) of variability in richness of other taxa |
| Eglington et al. (2012) | Systematic review and meta-analysis | Indicator | Birds | Herpetofauna, invertebrates, mammals, plants | Global, Asia, Australasia, Europe, N. America | Agricultural, forest, grassland, | Spatial extent: global, continental, national, regional, landscape. Spatial grain: <0.001–>1000 $km^2$ | Meta-analysis of studies testing the correlation in species richness between birds and other taxa | There are significant positive, but weak, correlations in species richness between birds and other taxa. On average, species richness of birds account for 18 % ($CI_{95\%}$: 13–26) of variability in richness of other taxa. |
| Gao et al. (2015) | Systematic literature review | Indicator | Birds, bryophytes, fungi, invertebrates, lichens, mammals, plants, reptiles | No specific target taxa considered | Europe | Forest | Spatial extent: landscape, local (forest stand) | Review of studies testing the correlation in species richness between indicators and other taxa | There is only weak evidence that biodiversity indicators are effective |
| Humphrey and Watts (2004) | Literature review | Indicator | No specific target taxa considered | No specific target taxa considered | United Kingdom | Forest | No specific spatial scales considered | Review of studies assessing the indicator approach | It is difficult to identify indicators that are uniformly effective |
| Lewandowski et al. (2010) | Systematic review and | Indicator, Umbrella | Arthropods, birds, fungi, herpetofauna, | Arthropods, birds, fungi, herpetofauna, | Tropical, temperate, boreal | Chaparral, desert, forest, grassland | Spatial extent: continental, regional, local | Meta-analysis of studies testing if sites with high richness of indicators are | A biodiversity hotspot (indicator) approach is effective in 25 % of tests, while a complementarity |

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**Table 2** (*continued*)

| Study | Study type | Surrogate approach | Surrogate taxa | Target taxa | Geographic region | Biome | Spatial scale | Assessment | Main conclusion |
|---|---|---|---|---|---|---|---|---|---|
| | meta-analysis | | lichens, mammals, plants, molluscs | lichens, mammals, plants, molluscs | | | | biodiversity hotspots, or testing if sites with umbrellas have a high biodiversity | (umbrella) approach is effective in 50 % of tests |
| Liu et al. (2020) | Systematic review and meta-analysis | Indicator | Plants | Soil microbes | Tropical, subtropical, temperate, boreal | Forest, grasslands, shrubland | Spatial extent: divided into six classes based on latitudinal cover range (<0.05°–>20°) | Meta-analysis of studies testing the correlation in diversity between plants and soil microbes | There are significant positive, but weak, correlations in species richness between plants and soil microbes. On average, species richness of plants account for 11 % ($CI_{95\%}$: 5–19 %) of variability in richness of soil microbes. |
| Nilsson et al. (2001) | Literature review | Indicator | No specific surrogate taxa considered | No specific target taxa considered | Europe | Forest | No specific spatial scales considered | Review of studies testing the correlation in species richness between indicators and other taxa | All correlations between indicators and other taxa were weak |
| Sergio et al. (2008) | Literature review | Indicator, umbrella, keystone, flagship | Top predators | No specific target taxa considered | No specific region considered | No specific biome considered | No specific spatial scales considered | Review of studies assessing the role of top predators as indicators, umbrellas, keystone and flagships | The effectiveness of top predators as indicators, umbrellas, keystones, and flagships is limited, and highly context dependent |
| Westgate et al. (2014) | Systematic review and meta-analysis | Indicator | Amphibians, arthropods, birds, fungi, insects, mammals, molluscs, plants, reptiles | Amphibians, arthropods, birds, fungi, insects, mammals, molluscs, plants, reptiles | No specific region considered | No specific biome considered | Spatial extent treated as continuous variable | Meta-analysis of studies testing the correlation in species richness and composition between taxa | There are positive, but weak, correlations in species richness and composition between taxa. E.g., on average, the richness of one taxon account for 12 % ± 13 % (SD) of variability in richness of other taxa |
| Westgate et al. (2017) | Systematic review and meta-analysis | Indicator | Amphibians, birds, bryophytes, insects, mammals, plants, reptiles | Amphibians, birds, bryophytes, insects, mammals, plants, reptiles | No specific region considered | No specific biome considered | Spatial extent and grain treated as continuous variable | Meta-analysis of studies testing the correlation in species richness and composition between taxa | There are positive, but weak, correlations in species richness and composition between taxa. E.g., on average, the richness of one taxon account for 12 % (max = 37 %) of variability in richness of other taxa |
| Wolters et al. (2006) | Systematic review and meta-analysis | Indicator | Birds, beetles, butterflies, mammals, plants | Birds, beetles, butterflies, mammals, plants | Tropical, temperate | No specific biome considered | Spatial extent divided into five classes (<0.001–>1000 $km^2$) | Meta-analysis of studies testing the correlation in species richness between taxa | There are significant positive, but weak, correlations in species richness between taxa. On average, the richness of one taxon account for 14 % ± 0.5 % ($CI_{95\%}$) of variability in richness of another taxon. |
| Bertrand et al. (2006) | Literature review | Higher-taxon | No specific surrogate taxa considered | No specific target taxa considered | No specific region considered | No specific biome considered | No specific spatial scales considered | Review of studies assessing the higher-taxon approach | A higher-taxon approach cannot be expected to be effective. |
| de Oliveira et al. (2020) | Systematic review and meta-analysis | Higher-taxon | Invertebrates, microorganisms, plants, vertebrates | Invertebrates, microorganisms, plants, vertebrates | No specific region considered | No specific biome considered | Spatial extent treated as continuous variable | Meta-analysis of studies testing the correlation between richness of higher and lower taxonomic levels | There are significant positive correlations in richness between higher and lower taxonomic levels. On average richness of higher taxonomic levels account for 84 % ± 2 % ($CI_{95\%}$) of variability in richness of lower taxonomic levels |
| Gaston and Williams (1993) | Literature review | Higher-taxon | No specific surrogate taxa considered | No specific target taxa considered | No specific region considered | No specific biome considered | No specific spatial scales considered | Review of studies assessing the higher-taxon approach | There are several limitations to the higher-taxon approach, which makes it less likely to be effective |

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**Table 2** (*continued*)

| Study | Study type | Surrogate approach | Surrogate taxa | Target taxa | Geographic region | Biome | Spatial scale | Assessment | Main conclusion |
|---|---|---|---|---|---|---|---|---|---|
| Zou et al. (2020) | Systematic review and meta-analysis | Higher-taxon | Amphibians, arthropods, birds, insects, mammals, reptiles | Amphibians, arthropods, birds, insects, mammals, reptiles | Tropical, temperate, boreal | Forest, grassland | No specific spatial scales considered | Meta-analysis of studies testing the correlation between richness and diversity of higher and lower taxonomic levels | There are significant positive correlations in richness between higher and lower taxonomic levels. On average, Shannon diversity of higher taxonomic levels account for 56 % ± 17 % (SD) of variability in diversity of lower taxonomic levels |
| Branton and Richardson (2011) | Systematic review and meta-analysis | Umbrella | Birds, insects, mammals | Amphibians, birds, fungi, insects, lichens, mammals, molluscs, plants | No specific region considered | No specific biome considered | No specific spatial scales considered | Meta-analysis of studies testing if species richness and abundance is higher in sites with umbrellas | Species richness and abundance of co-occurring taxa is significantly higher in sites where umbrella taxa occur. E.g., on average 6 ($CI_{95\%}$: 3.4–9.1) more species were present in sites with an umbrella taxa compared to control sites |
| Caro (2003) | Literature review | Umbrella | Mammals | No specific target taxa considered | No specific region considered | No specific biome considered | No specific spatial scales considered | Review of studies assessing the umbrella approach | There is little evidence that an umbrella approach is generally effective, but it can be effective in some specific cases |
| Lindenmayer and Westgate (2020) | Systematic literature review | Umbrella, keystone, flagship | No specific surrogate taxa considered | No specific target taxa considered | No specific region considered | No specific biome considered | No specific spatial scales considered | Review of studies assessing the umbrella, keystone or flagship approach | Tests of an umbrella approach reveal varying results, and few studies have tested a keystone and flagship approach. Thus, it is difficult to predict when and where a surrogate approach will be effective. |
| Pérez-Espona (2021) | Literature review | Umbrella | Army ants (*Eciton*) | Arthropods, birds, microbes, vertebrates | Neotropics | Forest | No specific spatial scales considered | Review of studies assessing the role of *Eciton* army ants as umbrellas | Army ants are effective as umbrellas |
| Roberge and Angelstam (2004) | Literature review | Umbrella | Birds, butterflies, mammals, plants | Amphibians, birds, invertebrates, mammals, plants, reptiles | No specific region considered | No specific biome considered | No specific spatial scales considered | Review of studies testing if protection of umbrellas will benefit other taxa | Single taxon are unlikely to be effective umbrellas, but a multi-taxa umbrella approach is more likely to be effective |
| Rodrigues and Brooks (2007) | Systematic review and meta-analysis | Umbrella | Arthropods, birds, bryophytes, fungi, herpetofauna, insects, mammals, molluscs, plants | Arthropods, birds, bryophytes, fungi, herpetofauna, insects, lichens, mammals, molluscs, plants | No specific region considered | No specific biome considered | No specific spatial scales considered | Analysis of studies testing to what extent protecting umbrellas protects other taxa | There is only weak evidence that conserving umbrellas will conserve other taxa. On average, the surrogacy value of umbrellas is 0.12 ($CI_{95\%}$: 0.03–0.28) (perfect surrogacy = 1) |
| Rogers et al. (2012) | Literature review | Umbrella | No specific surrogate taxa considered | No specific target taxa considered | Australia | Wetland | No specific spatial scales considered | Review of studies assessing the role of wetland taxa as umbrellas | An assemblage of wetland taxa can act as umbrellas for a broader assemblage of wetland taxa |
| Yamaura et al. (2018) | Literature review | Umbrella | Megafauna | No specific target taxa considered | No specific region considered | No specific biome considered | No specific spatial scales considered | Review of studies assessing the role of megafauna as umbrellas | Megafauna is unlikely to be effective as an umbrella |
| Janiszewski et al. (2014) | Literature review | Keystone | Eurasian beaver (*Castor fiber*) | Amphibians, birds, invertebrates, mammals, reptiles | No specific region considered | Wetland | No specific spatial scales considered | Review of studies assessing the role of the Eurasian beaver as a keystone | The Eurasian beaver is a keystone taxon |
| Kotliar et al. (1999) | Literature review | Keystone | Prairie dogs (*Cynomys* spp.) | Vertebrates | N. America | Prairie | No specific spatial scales considered | Review of studies assessing the role of Prairie dogs as a keystone | Prairie dogs are a keystone taxon |

(*continued on next page*)

**Table 2** (*continued*)

| Study | Study type | Surrogate approach | Surrogate taxa | Target taxa | Geographic region | Biome | Spatial scale | Assessment | Main conclusion |
|---|---|---|---|---|---|---|---|---|---|
| Spector (2006) | Literature review | Keystone | Dung beetles (*Scarabaeidae*) | No specific target taxa considered | No specific region considered | No specific biome considered | No specific spatial scales considered | Review of studies assessing the role of *Scarabaeinae* dung beetles as keystones | Dung beetles are a keystone taxon |
| Favreau et al. (2006) | Literature review | Surrogate | No specific surrogate taxa considered | No specific target taxa considered | No specific region considered | No specific biome considered | No specific spatial scales considered | Review of studies testing if presence of surrogates overlaps with other taxa | There are no general rules for when and where a surrogate approach is effective |
| Sætersdal and Gjerde (2011) | Literature review | Surrogate | No specific surrogate taxa considered | No specific target taxa considered | No specific region considered | No specific biome considered | No specific spatial scales considered | Review of studies assessing the surrogate approach | The effectiveness of a surrogate approach varies unpredictably, and the assumption underlying the effectiveness of surrogates is not supported by ecological theory |

be representative of other taxa.

### 3.2. Higher-taxon approach

Two meta-analyses and two literature reviews assessed the higher-taxon approach (Table 2). The meta-analyses tested the correlation between the diversity of higher and lower taxonomic levels, finding that the richness or diversity of higher taxonomic levels on average explained 70 % (min: 56 %, max: 84 %) of richness or diversity of lower taxonomic levels. The strength of correlations decreased at higher taxonomic levels, but increased with increasing spatial extent (de Oliveira et al., 2020; Zou et al., 2020). The two literature reviews concluded that the higher-taxon approach should not be used when classifications of taxonomic groups are not based on phylogenetic relationships, but rather on subjective divisions of species based on tradition or species characteristics (Bertrand et al., 2006; Gaston and Williams, 1993).

### 3.3. Umbrella approach

Three meta-analyses and seven literature reviews assessed the umbrella approach (Table 2). The meta-analyses of the umbrella approach tested the overlap in spatial distribution, or habitat or resource requirements between umbrella species and other species, in such a way that hypothetical or actual conservation schemes based on the umbrella encompass other species. These meta-analyses were all performed in a variety of biomes and geographical regions, and included a range of different umbrella species. Two of the meta-analyses revealed that conservation actions aimed at umbrella species can be beneficial for other species, as sites occupied by various umbrella species often encompass other species, or have a higher abundance and richness of target species (Branton and Richardson, 2011; Lewandowski et al., 2010). However, a meta-analysis by Rodrigues and Brooks (2007) revealed that it is unlikely that selecting conservation areas based on the presence of an umbrella will encompass other species. All three meta-analyses included both umbrella species that are used in practice such as large mammal species, and randomly selected umbrella species. However, no meta-analysis assessed if one type of umbrella species performed better than the other. Literature reviews of the umbrella approach generally either summarised the evidence supporting the role of certain species as an umbrella, or summarised results from studies testing if protection of umbrella species benefit other species. These concluded that certain species groups could be used as an umbrella species in several cases: ants in the neotropics, large mammals in east Africa, and wetland plants in Australian wetlands (Caro, 2003; Pérez-Espona, 2021; Rogers et al., 2012). Others concluded that a single species, mega-fauna, or top predators should not be used as umbrella species (Lindenmayer and Westgate, 2020; Roberge and Angelstam, 2004; Sergio et al., 2008; Yamaura et al., 2018).

The extent of overlap in the distribution of umbrella species and other species varied depending on the context. One meta-analysis assessed if the overlap varied across spatial extents, geographical regions and biomes, finding most overlap between species at larger spatial extents and in the boreal zone, tropical forests, and grasslands (Lewandowski et al., 2010). In addition, the overlap differed between taxonomic groups, with birds, mammals, and plants performing better as umbrella species than arthropods, fungi, herpetofauna, lichens and molluscs in one study (Lewandowski et al., 2010), and birds performing better than mammals in another (Branton and Richardson, 2011).

Two of the meta-analyses tested if species with certain traits were better umbrella species than other species. Lewandowski et al. (2010) concluded that taxonomic groups with many habitat specialists were better umbrella species than other groups, as these were more likely to encompass a wider range of habitat types. On the other hand, Branton and Richardson (2011) concluded that there was no difference between resource generalists versus specialists as umbrella species. This study also concluded that small-bodied species were better as umbrella species than large-bodied species, and that omnivorous birds were better as umbrella species compared to carnivorous birds.

### *3.4. Keystone approach*

Five literature reviews assessed the keystone approach (Table 2), but none of these tested whether keystone species have a large impact on species communities or ecosystem functioning, if the loss of a keystone will affect species communities, or if conservation actions aimed at a keystone also benefit other species. In fact, a systematic literature review concluded that about 75 % of primary studies that claim that a species is a keystone do not support this with any empirical evidence (Lindenmayer and Westgate, 2020). Instead, the included literature reviews suggested that beavers, prairie dogs, dung beetles, and top predators are keystone species because their presence is thought to benefit many other species, and they provide unique functions in ecosystems (Janiszewski et al., 2014; Kotliar et al., 1999; Sergio et al., 2008; Spector, 2006).

### *3.5. Flagship approach*

Two literature reviews assessed a flagship approach (Table 2), by assessing if they fulfil their role as a marketing tool to raise public awareness and collect funds for conservation actions (Lindenmayer and Westgate, 2020; Sergio et al., 2008). However, no reviews have assessed to what extent the funds collected through flagship species are used effectively to preserve other species.

## 4. Discussion

The three reviews assessing the general approach of using surrogates in biodiversity conservation concluded that there is low predictability for if and when this approach will be useful (Favreau et al., 2006; Lindenmayer and Westgate, 2020; Sætersdal and Gjerde, 2011). Reviews on indicator species revealed that many suggested indicators are of limited use for representing other species, since the average correlation between the diversity of indicator species and other species were generally weak, with few instances of strong correlations between species. Reviews focusing on umbrella species revealed varied results; two meta-analyses found that sites occupied by umbrella species often encompass other species, while another found that umbrella species were unlikely to be effective surrogates for other species. Literature reviews also revealed that some, but not all, species groups were useful umbrella species. Thus, using umbrella species to, e.g., prioritise sites for conservation actions is unlikely to uniformly lead to the preservation of other species. It is more difficult to draw general conclusions regarding the use of keystone and flagship species, as no reviews assessed if conservation actions aimed at keystone or flagship species benefit other species. In contrast, the strong correlations between the diversity of higher and lower taxonomic levels means that the diversity of genera of families can be used to represent species diversity. Additionally, the strength of relationships between surrogates and other species were stronger in some specific contexts (see Section 4.2).

### *4.1. The usefulness of surrogates as a conservation tool is limited*

Together, the evidence suggest some cases when surrogate taxa can be useful as a conservation tool, but generally, surrogates will often not be representative of overall biodiversity or species of conservation concern. Therefore, conservation actions aimed at surrogates will not necessarily benefit other species. However, one striking exception to the generally weak relationships between surrogates and other species was the higher-taxon approach (de Oliveira et al., 2020; Zou et al., 2020). The diversity of families, genera, or other higher taxonomic levels often worked well as a surrogate for the diversity of lower taxonomic levels, for example species. This is probably because many ecological characteristics are shared among closely related species, meaning that they respond similarly to environmental conditions (Rosser, 2017; Wiens and Graham, 2005). While the strength of correlations decreased with increasing taxonomic levels, using family-level diversity may still be more useful, as less identification effort is saved when using the diversity of genera instead of species (Zou et al., 2020).

One reason why other types of surrogates are of limited use as conservation tools can be that some of the assumptions underlying the ability of surrogates to represent other species (nested species assemblages, cross-taxon correlations, and spatio-temporal consistency) are not supported by ecological theory related to community assembly (Sætersdal and Gjerde, 2011). For instance, species are likely to share some but not all niche dimensions, since large niche overlap results in interspecific competition (Landres et al., 1988; Lindenmayer, 1999; Verner, 1984). Furthermore, factors such as diseases or stochastic variation influence species differently, which may also result in weakened correlations between species (Carignan and Villard, 2002). Thus, conservation actions aimed at surrogates are rarely equally beneficial for other species. Another reason is that for surrogates to fulfil their role in the long-term, they should be unlikely to go locally extinct (Caro and O'Doherty, 1999). This means that they are not the most sensitive species, and thus they are not necessarily representative of more sensitive species. Therefore, multiple surrogate taxa, with different requirements, may better represent a larger number of species than using only one. This approach was suggested in several reviews (Branton and Richardson, 2011; Carignan and Villard, 2002; Lindenmayer and Westgate, 2020; Roberge and Angelstam, 2004; Westgate et al., 2017). One meta-analysis study found that using birds, plants and mammals as indicator species was better for representing other species, rather than using only one of these species groups (Westgate et al., 2017).

That few reviews assessed keystone and flagship approaches is most likely due to the low numbers of primary studies testing these approaches. While there are primary studies investigating if the presence of keystone species such as the Eurasian beaver or three-toed woodpecker benefit other species (Fedyń et al., 2022; Pakkala et al., 2018), Lindenmayer and Westgate (2020) concluded that most studies claiming that a species is a keystone does not support this with empirical evidence. One reason for this can be the difficulty in testing to what extent a species is a keystone. Most primary studies of the flagship approach assess if flagship species are effective marketing tools, and not if they are useful for preserving other species. However, there are primary studies showing that funds collected for the conservation of a flagship species lead to preservation of other species (McGowan et al., 2020; Williams et al., 2000). These studies test if a species is useful both as a flagship and an umbrella, and this seems to be the case in at least some studies (McGowan et al., 2020). Consequently, there is some evidence that both keystone and flagship species can be useful as a conservation tool, but there is a need for more meta-analyses testing these approaches in a wider context, as none of the included reviews on the keystone and flagship approaches actually tested if they are useful as conservation tools.

### *4.2. The usefulness of surrogate taxa varies across regions, biomes and spatial scales*

The strength of the relationship between surrogates and other species differed across geographical regions, biomes, and spatial scales. Correlations were more likely to be stronger at larger spatial scales. In most meta-analyses, the spatial scale was treated as a continuous variable, but some treated scales as a categorical variable. These reviews concluded that correlations were generally strongest on global scales, but also stronger on continental, national and regional (>1000 km2) compared to local scales (<1000 km2). One possible reason for this is that at larger spatial scales, patterns of species richness are a product of few environmental factors, while at smaller scales, these patterns are affected by several factors that are not necessarily shared among species (Eglington et al., 2012). However, this is complicated by the fact that for implementation of conservation actions, regional and landscape scales are more likely to be relevant compared to global, continental or national scales. Thus, the surrogate approach may be most useful at intermediate scales, but only as long as both the surrogate and other species respond to threats and conservation actions at this scale. The strength of correlations varied inconclusively across different geographical regions and biomes. Lewandowski et al. (2010) suggest that this can be because in certain regions, species may be strongly affected by the same processes, while in others, species are affected by separate processes. That the strength of relationships between species varied between geographical regions, biomes, and scales means that it is less likely that a surrogate is useful outside the context for which it was established. Thus, a different context may demand that the time-consuming process of identifying appropriate surrogates has to be restarted, thereby limiting the usefulness surrogate taxa as a conservation tool (Lindenmayer and Likens, 2011).

The species identified as the best surrogates varied across the included reviews, making it impossible to conclude that specific taxonomic groups generally perform better as surrogates than other. However, some meta-analyses concluded that species that are similar to the target species are generally more useful as surrogates (Branton and Richardson, 2011; de Oliveira et al., 2020; Eglington et al., 2012; Rodrigues and Brooks, 2007). This can be species that are closely related or species sharing similar functions or traits, as these species are more likely to share similar resources or be similarly affected by threats.

### *4.3. All aspects of the usefulness of surrogate taxa have not been assessed*

Evaluating the usefulness of surrogate taxa as a conservation tool requires assessing whether surrogate taxa represent other species, and to what extent conservation actions aimed at surrogates benefit other species. Evaluating the representativeness of surrogates requires specific assessments. For indicator species, this involves testing the strength of the correlation between the presence or species richness of indicator species and other species (de Bello et al., 2010; Moreno et al., 2007) and for the higher-taxon approach testing the correlation between higher and lower taxonomic levels (Gaston and Williams, 1993). For umbrella species it involves assessing the degree of spatial overlap or overlap in requirements between an umbrella and other species (Caro, 2003; Roberge and Angelstam, 2004). For keystone species, it involves testing the impact of the presence (or loss) of a keystone on species communities (Cottee-Jones and Whittaker, 2012; Menge et al., 2013; Mills et al., 1993), and for flagship species assessing to what extent a flagship is successful at collecting funds for conservation actions and if these funds can be used effectively to preserve other species (Verissimo et al., 2011). The included meta-analyses generally tested these aspects for indicator and umbrella species and the higher-taxon approach, while no reviews tested this for keystone species, and reviews on flagship species only assessed if they are effective for collecting conservation funds.

Few included reviews evaluated to what extent conservation actions aimed at preserving indicator species, higher taxonomic groups, or keystone species also lead to the preservation of target species, or if funds collected using a flagship also benefit other species. The only exception was meta-analyses testing if protected areas selected based on the occurrence of an umbrella also protected co-occurring species. Furthermore, none of the included reviews related the conservation outcome of using surrogate taxa to the cost, time and effort saved compared to other alternatives, or evaluated if using a specific species as a surrogate was more effective than using another species (Cabeza et al., 2008), meaning it is unknown to what extent the use of surrogates helps streamline conservation. Together, this means that it is not fully known whether or not surrogate taxa are a useful conservation tool.

### *4.4. It is unclear if surrogate taxa can be selected based on species traits*

It has been suggested that certain species traits increase the probability that a species is useful as a surrogate (e.g., Caro and O'Doherty, 1999; Landres et al., 1988; Yamaura et al., 2018). Two meta-analyses tested if species with some of these traits performed better as umbrella species compared to other species, e.g., if umbrella taxa with certain traits had a higher degree of spatial overlap with other species. One concluded that specialist species are better umbrella species compared to generalists (Lewandowski et al., 2010), and the other that generalist species, and small-bodied species are better umbrella species than specialist or large-bodied species (Branton and Richardson, 2011). Some meta-analyses revealed that surrogate taxa were more likely to be useful if there were ecological similarities between a surrogate and other species, for instance if species shared similar traits. Thus, while there is currently no evidence that species with specific traits will generally be useful as surrogates, it can be relevant to select surrogate taxa based on shared traits with target species. There was also no clear evidence that the relationships between species were stronger for indicator or umbrella species that were selected based on expert knowledge rather than at random, e.g., because experts expect that the response of specific species to threats or conservation actions are representative of other species. Given the lack of evidence, we caution against using certain traits as a shortcut to identify surrogate taxa, without confirming that there is a correlation between the surrogate and target species.

## 5. Conclusions

Several knowledge gaps remain regarding the usefulness of surrogate taxa as a conservation tool. There is a need for meta-analyses testing the usefulness of keystone and flagship species, as well as studies evaluating whether conservation actions aimed at surrogates benefit other species. It is also largely unknown if species with certain traits are better surrogates than other species.

The results from a large number of meta-analyses and literature reviews revealed that surrogate taxa are, in general, of limited use for representing species of conservation concern, predicting general biodiversity patterns across different contexts, or for prioritising conservation actions. However, based on the evidence we suggest some situations when surrogates are more likely to be a useful conservation tool:

1. **When using the higher-taxon approach**, i.e. using the richness of higher taxonomic levels as a surrogate for richness of lower taxonomic levels. This is likely to be most useful in a monitoring context, to make surveys more time and cost-efficient.
2. **When there are strong ecological similarities between a surrogate and the target species within a specific context**. The similarities can be regarding taxonomy, functions, traits, habitat associations, or other ecological requirements.
3. **On regional and landscape scales rather than local scales.** The strength of correlations generally increased with increasing spatial scales, but if the aim of surrogates is to facilitate effective implementation of conservation actions, regional and landscape scales are more likely to be relevant compared to global, continental or national scales.
4. **When sets of multiple species are used as surrogates**. A set of species represents a broader range of habitats, possess a wider variety of requirements, depend on a wider variety of ecological processes, and display a wider range of sensitivities to, e.g., habitat modification and disturbances, especially if they represent different taxonomic groups (Carignan and Villard, 2002; Heink and Kowarik, 2010). For example, Westgate et al. (2017) suggest that a combination of birds, vascular plants and mammals could be effective as surrogates, and Roberge and Angelstam (2004) suggest that a focal taxa approach is more effective, i.e. when several species sensitive to different threatening processes are used as surrogates. However, using a set of multiple surrogate species require careful consideration of the trade-off between better representing target species or

biodiversity, and the increased cost for monitoring a larger number of species.

### 5.1. Practical implications

While most types of surrogate taxa have limited use in representing other species and are often not useful for prioritising conservation actions, there are few feasible alternatives to using surrogates in conservation. It is impossible to survey all or most species during monitoring, or obtain knowledge on the requirements of all species affected by potential conservation actions (Lindenmayer and Likens, 2011). One alternative is using technological advancements to organise fully automated large-scale monitoring aimed at capturing the occurrence of a large number of different species, through the use of, e.g., environmental DNA, but such monitoring methods have yet to reach their full potential (Besson et al., 2022; Huo et al., 2023). Thus, surrogate taxa will be needed also in the future.

To avoid that the use of surrogate taxa leads to poor conservation decisions, there is in each situation a need for careful consideration of the selection of surrogate taxa (Barton et al., 2015). There is a need to weigh the potential benefits of using surrogate taxa against the risks of proposed conservation actions being inefficient or having unintended effects. It is also important that the selection of a surrogate is built on knowledge on which types of surrogates are more likely to be useful at representing other species, e.g., higher-taxa as surrogates for lower taxa, or species sharing ecological requirements (de Morais et al., 2018). The selection of a prospective surrogate should be followed by assessment to confirm that the surrogate share co-occurrence patterns with the species they are supposed to act as a surrogate for, and that it is affected by the threat of concern (Barton et al., 2015; Caro and O'Doherty, 1999). A surrogate taxon is only useful if it is easy and not too expensive to evaluate and use. It is therefore important to assess the cost and ease of using a specific surrogate, and to consider the potential trade-offs of choosing the least expensive and easily monitored surrogate, with the risk that the surrogate is a poor representative for other species (Lindenmayer et al., 2015; Lindenmayer and Westgate, 2020). In each new situation, the process of identifying appropriate surrogates will likely need to be repeated, as surrogates that are useful in one situation may be less useful in other contexts (Lindenmayer and Likens, 2011).

A way for conservation biologists to increase the likelihood of a surrogate approach being useful is to use sets of species as composite surrogates (de Morais et al., 2018). Another type of composite surrogate that have been found to be useful is obtained by combining information on multiple surrogate taxa with information on structural indicators that positively affect species, such as amount of certain vegetation types or substrates, habitat heterogeneity, patch size, or connectivity (Hekkala et al., 2023; Lawrence et al., 2018; Sverdrup-Thygeson et al., 2017).

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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