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## Review

# A review of Bayesian belief network models as decision-support tools for wetland conservation: Are water birds potential umbrella taxa?

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## ABSTRACT

Creative approaches to identifying umbrella species hold promise for devising effective surrogates of ecological communities or ecosystems. However, mechanistic niche models that predict range or habitat overlap among species may yet lack development. We reviewed literature on taxon-centered Bayesian belief network (BBN) models to explore a novel approach to identify umbrella taxa identifying taxonomic groups that share the largest proportion of habitat requirements (i.e., states of important habitat variables) with other wetland-dependent taxa. We reviewed and compiled published literature to provide a comprehensive and reproducible account of the current understanding of habitat requirements for freshwater, wetland-dependent taxa using BBNs. We found that wetland birds had the highest degree of shared habitat requirements with other taxa, and consequently may be suitable umbrella taxa in freshwater wetlands. Comparing habitat requirements using a BBN approach to build species distribution models, this review also identified taxa that may not benefit from conservation actions targeted at umbrella taxa by identifying taxa with unique habitat requirements not shared with umbrellas. Using a standard node set that accurately and comprehensively represents the ecosystem in question, BBNs could be designed to improve identification of umbrella taxa. In wetlands, expert knowledge about hydrology, geomorphology and soils could add important information regarding physical landscape characteristics relevant to species. Thus, a systems-oriented framework may improve overarching inferences from BBNs and subsequent utility to conservation planning and management.

## 1. Introduction

Biological conservation relies on identifying and connecting species with the habitat requirements important for the successful completion of life cycles. Species distribution models (SDMs) are increasingly relied upon to identify habitat elements important for conservation (Dibner et al., 2017; Phillips et al., 2017). Predictive SDMs are particularly needed for understanding how species will respond to ongoing environmental change (Wood et al., 2018). Increased access to, and advances in technology have improved our ability to understand associations between species and their habitats (Elith and Leathwick, 2009). Technological advances include Geographic Information Systems (GIS) and remote sensing technology, paired with increased computing power and the development of spatial statistical models (e.g., Guisan and Thuiller, 2005). Examples of this approach include Gap Analysis Program (GAP) models mapping land cover and predicted distributions

of species, bioclimatic envelopes, habitat suitability indices, maximum entropy models (MAXENT), and genetic algorithm for rule-set prediction (GARP; Elith et al., 2006; Guisan and Zimmermann, 2000; Sowa et al., 2007). The results of SDMs are commonly used to build species-specific Habitat Suitability Indices (HSIs) that estimate the probability of species presence across a landscape and have been used extensively in conservation planning (Zajac et al., 2015). Thus, identifying the key elements of habitat for species of conservation concern is important for informing conservation actions (Lin et al., 2018).

Bayesian belief networks (BBNs) represent one form of SDM that offer a unique modeling approach by identifying explicit causal relationships among organisms and their habitats, as well as incorporating measures of uncertainty. In the ecological literature, BBNs go beyond species-habitat correlations because they explicitly consider discrete processes that influence occupancy across space and time (i.e., access and selection; Jones, 2001). BBNs consist of input, intermediate and output nodes that are linked together via conditional probability tables

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(CPTs) according to hypothesized causal relationships (Fig. 1; Drew and Collazo, 2014). As graphically based probabilistic models (i.e., influence diagrams), BBNs may incorporate information gleaned from literature reviews, expert opinions and monitoring efforts to examine how all possible values of environmental variables may influence the occurrence or distribution of individuals. Bayesian belief networks approach SDMs by exhaustively exploring potential ecological variables defining a species' niche while simultaneously incorporating metrics of uncertainty surrounding estimates of habitat requirements (Marcot et al., 2006; Usitalo et al., 2015). The inclusion of measures of uncertainty is important as many conservation decisions must be made in the absence of complete information. Thus, a BBN modeling approach can be used to inform decisions made using an adaptive management approach to reduce uncertainty (Drew and Collazo, 2014).

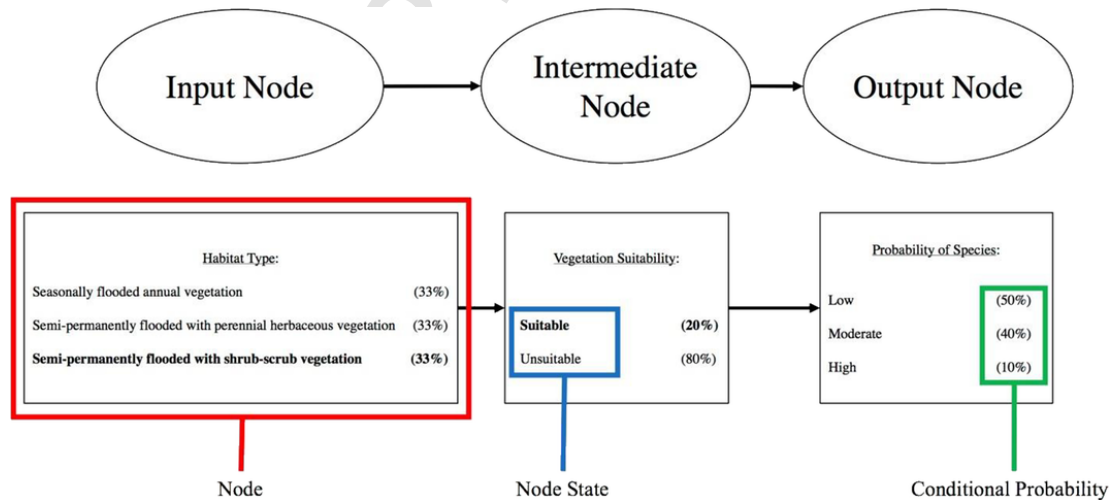
The umbrella species concept (Wilcox, 1984) can enhance conservation for suites of species with similar habitat requirements by countering incomplete biodiversity surveys that lack time, financial support, or adequate methods. The umbrella species concept provides a framework to improve the effectiveness of conservation action while reducing the complexity of quantifying species-specific outcomes. Umbrella species are unique in that they represent an ecologically-defined role in conservation as managing for their life history needs is expected to serve other species that co-occur or rely on the same set of resources (Roberge and Agelstam, 2004). As such, umbrella species are habitat specialists with large ranges sizes, and that are often sensitive to environmental disturbance (Kalinkat et al., 2017). Creative approaches to identifying umbrella species hold promise for devising effective surrogates of ecological communities or ecosystems (Sattler et al., 2014), but mechanistic niche modeling for predicting overlap of species' ranges and habitat requirements can be developed by narrowing gaps in our understanding of species ecology (Kearney and Porter, 2009).

Efforts to quantitatively identify umbrella species from among multiple candidate taxa (Caro and O'Doherty, 1999; Fleishman et al., 2000; Maslo et al., 2016; Stewart et al., 2017) often focus solely on contrasting spatial overlap identified using potentially incomplete sets of environmental predictors (Andelman and Fagan, 2000; Seddon and Leech, 2008). Despite past mixed success of using umbrella species for conservation planning (e.g., successful: Fleishman et al., 2000; Roth and

Weber, 2007; Suter et al., 2002, unsuccessful: Launer and Murphy, 1994; Ozaki et al., 2006), the concept continues to improve by broadening to encompass both taxonomic and functional diversity (Sattler et al., 2014). Typical approaches to identifying umbrella species have used SDMs that lacked explicit mechanistic reasoning to identify spatial ranges (i.e., beyond spatial overlap to encompass responses to similar environmental conditions) (Cayuela et al., 2009; Elith and Leathwick, 2009). As the umbrella approach to wider species conservation holds promise for identifying effective surrogate taxa (Sattler et al., 2014), we present a method to identify umbrella taxa informed by suites of BBN models that represent spatial ranges with causal reasoning.

Given the ability of BBNs to generate spatially-explicit predictions based on functionally-defined species-habitat relationships, they represent a potentially valuable approach to evaluate a species' expected performance as an umbrella species. Therefore, we took a case study and literature review approach to identify potential umbrella taxa within an ecosystem using BBN models. Restricting our research to freshwater wetland ecosystems, we undertook a systematic literature review to quantify the categorical overlap of habitat requirements for freshwater wetland-dependent species among existing BBNs. We reviewed existing taxon-centered BBN models to: 1) assess how BBNs were constructed, 2) describe how BBNs were used to inform biological conservation and identify the extent BBNs appeared to be used by those making biological conservation decisions, and 3) identify candidate umbrella taxa.

We chose freshwater wetlands because of the important role they play for a large number of species and the widespread concern for their conservation (Dudgeon et al., 2006). Despite the numerous ecosystem services provided by wetlands, greater than 50% of wetland area in the contiguous United States (US) has been converted to agricultural and urban land use (Horvath et al., 2017). There is a growing recognition of the difficulties of wetland restoration to renew lost biodiversity and ecosystem function (Meli et al., 2014; Zedler, 2000). Multiple factors including habitat fragmentation, hydrological changes, the introduction of exotic species, and overpopulation of other native species combined with wetland loss are correlated with declines in wetland flora and fauna (Adams, 1999; Bunn and Arthington, 2002; Findlay and Houlihan, 1997; Kerbes et al., 1990; Knutson et al., 1999; Quesnelle et



**Fig. 1.** An illustration of a simple Bayesian Belief Network (BBN). The links between input, intermediate and output nodes (ellipses) indicate a mechanistic relationship in the direction of the arrow (i.e., the state of the input node variable drives the state of the intermediate node variable etc.). Input nodes are defined by marginal (unconditional) probability distributions defined by the range of states found in nature. Intermediate and output nodes are defined by conditional probability tables, with the probability for the node being in a specific state given by the configuration of the states of "parent" nodes. In the bottom part of the figure we demonstrate a hypothetical landscape with equal probabilities of encountering each type of habitat. In bold we represent that where there is semi-permanently flooded habitat with shrub-scrub vegetation, there is a 20% probability of finding suitable habitat (intermediate node) for an imaginary taxa. As the habitat is suitable, there is a 50% probability that the chances of encountering one individual of the species is low, a 40% probability that the chances of encountering one individual of the species is moderate, and a 10% probability that the chances of encountering one individual of the species is high. In this simplistic example, we show that the range of the probability of encountering the species (output node) changes based on the state at the input node.

al., 2013; Wettstein and Schmid, 1999). Substantial wetland loss (Ramsar Convention Secretariat, 2013) and a paucity of restoration studies conducted in freshwater wetlands (Brudvig, 2011) further drive an urgency to identify conservation and restoration strategies that provide habitat for the breadth of wetland-dependent species (Galat et al., 1998; Lehtinen and Galatowitsch, 2001). Thus, approaching wetland conservation using a bottom-up framework to identify umbrella taxa in freshwater wetland ecosystems may creatively provide restoration targets (i.e., shared habitat requirements) to maximize the restoration of biodiversity in wetlands.

## 2. Methods

We systematically searched for and reviewed published literature to provide a comprehensive and reproducible overview of habitat requirements for freshwater wetland-dependent taxa using BBNs. We evaluated the scope of available peer-reviewed literature concerning habitat needs of freshwater wetland-dependent taxa, including identifying the presence of overlapping habitat requirements among taxa as well as collective sources of uncertainty. To do so, we searched the Google Scholar literature database using an ‘abstract’ search and with the publication date criteria set to ‘anytime’ (search undertaken in January 2018). We initially examined all English-language literature pertaining to freshwater wetland-dependent taxa, using the phrase “(wetland species AND Bayesian Belief Network AND species distribution model AND conditional probability table AND node)” (460 articles), to identify articles with published network models which we could compare. We then refined the search by including only publications that explored the distributions of species, rather than ecosystem or landscape-feature approaches. Our synthesis of the resulting publications consisted of four steps.

First, we summarized how BBNs were constructed. We compiled information on model type which included alpha-level (i.e., based on a literature review), beta-level (i.e., incorporated expert opinion), and gamma-level BBNs (i.e., included fieldwork to validate model predictions). We also compared model features including the number of nodes (i.e., BBN complexity), the sources and amount of uncertainty. Finally, we classified each BBN as either a process model (species-habitat relationships estimated for a single season or generalized across a life cycle) or dynamic model (relationships could vary from one time-period to another).

Then, we describe how BBNs were used to inform biological conservation and identified the extent to which BBNs appeared to be used by those making biological conservation decisions. There has been a recent call for translational science; translating what is learned from empirical research on species-habitat relationships into conservation action by developing tools accessible to decision makers such as resource managers (Littell et al., 2017). Given the emphasis on translational science and the promotion of BBNs as easy to understand models, one might expect use of BBN models in natural resource management to be common. To determine if this was the case, we compiled data for each publication on: publication type (journal vs report), journal category (applied or method development), and funding source. If BBNs are easily comprehensible due to their graphical nature, (Douglas and Newton, 2014), we expected to find evidence of their use as decision-support tools. By collecting these general criteria, we sought to identify potential gaps in the translation (i.e., from development to deployment) of the BBN approach in conservation.

Lastly, we examined the potential to identify umbrella species using BBNs. To do so, we identified important states of nodes (i.e., habitat requirements) shared across models to help identify potential umbrella taxa. Then, we summarized the BBN models that captured species-specific, mechanistically derived habitat requirements (sensu O’Hagan, 2012) to identify taxonomic groups that shared the largest proportion

of habitat requirements. The taxonomic group that had the largest amount of overlap with the other taxonomic groups was considered a candidate umbrella taxa.

## 3. Theory

The taxon-centered BBN models used to inform our umbrella taxa investigation mechanistically identify specific habitat requirements across taxa in a given ecosystem. This approach supports future research to quantitatively distinguish priority habitat for the focus of conservation planning, as well as identifies taxa with unique habitat requirements or unique habitat types that may not benefit from conservation actions targeted at umbrella taxa.

## 4. Results

### 4.1. BBN model construction

We identified a total of 53 articles with ecological BBNs for freshwater wetland-dependent taxa; consisting of 33 peer-reviewed articles, 9 reports or conference proceedings, 10 master of science theses or doctoral dissertations, and 1 book chapter (Appendix 1). The majority of studies followed the same three-step trajectory. The first step created an alpha-level BBN through a literature review, although few studies provided details on their literature review ( $n = 5$  studies provided literature review details). Next, all but one study elicited expert knowledge in a two-step process to refine and modify the alpha structures and build beta-level models. For the third step, over half of studies ( $n = 26$ ) validated their beta-level models with field data, completing the study with a published gamma-level model. The primary output nodes (i.e., response variable) for these studies were either abundance of the taxa in question or habitat suitability for the taxa in question. Nearly all studies used process models; only a single study used a dynamic model. The one temporally dynamic model (Chee et al., 2016) was also the only study to use any type of spatial statistical framework (geospatially explicit resampling between time periods). A habitat suitability response was typically represented as a binary categorical variable of suitable versus not suitable.

Few articles ( $n = 7$ ) discussed sources or levels of uncertainty. Articles that did estimate uncertainty surrounding the nodes that contributed the highest uncertainty in species outcomes identified the following sources: amount of flooded area, connectivity of different wetland patches, flood duration, maximum water temperature, interspecific competition, predation, and blood mercury measurements. Despite low reporting on any estimates of uncertainty (due to either data uncertainty or structural uncertainty), authors emphasized refining variable definitions if they could be interpreted in different ways by experts (i.e., structural uncertainty). Some examples of poorly defined variables included ‘water quality’ variables, determining the state of an individual plant or animal when two states are very similar, and the precise definition of outcomes following restoration.

### 4.2. BBNs as tools for biological conservation of freshwater wetlands

The sources of peer-review articles were primarily ecological journals (e.g., *Ecological Indicators*), the modeling journal, *Environmental Modeling & Software* ( $n = 6$ ), and conservation journals such as *Biological Conservation* ( $n = 2$ ) and *Conservation Biology* ( $n = 1$ ). Lead authorship on peer-reviewed articles and reports was rarely by graduate students or early-career scientists such as postdoctoral researchers (26%), and more commonly by research fellows or senior researchers at the time of publication (Appendix 2).

The earliest evidence we found of BBNs being used to model habitat requirements of freshwater wetland species was from 2003, with an ac-

celerated rate of increase in peer-reviewed literature using BBNs to explore habitat relationships of wetland taxa as years have gone on (Fig. 2). The majority of articles focused on Australasian wetlands (including Australia, Tasmania, Papua New Guinea, and New Zealand; 42%), but wetlands from all continental regions (excepting Antarctica) have been represented by BBNs in the peer-reviewed literature (Appendix 1).

The most common taxonomic subjects were fish (Actinopterygii; n = 15 models), followed by macroinvertebrates (e.g., Amphipoda, Coleoptera, Gryllidae, Lepidoptera, etc.; n = 10 models) and birds (e.g., Ardeidae, *Aythya affinis*, *Bucephala islandica*, *Dolichonyx oryzivorus*, *Grus canadensis*, *Hydrophasianus chirurgus*, *Megasceryle alcyon*, *Rallus elegans*, *Tympanuchus cupido*, *Tympanuchus phasianellus*, *Thryothorus ludovicianus*; n = 10 models). In order of abundance, articles also included wetland plants (e.g., *Galaxiella pusilla*, *Pilularia globulifera*, *Salicaceae*, etc.; n = 9 models), bacteria (e.g., *Escherichia coli*; n = 5 models), fungi (e.g., *Batrachochytrium dendrobatidis*, *Bridgeoporus nobilissimus*, and *Poronia punctata*; n = 3 models), mammals (e.g., *Corynorhinus townsendii*, Lutrinae, *Sus scrofa* etc.; n = 3 models), amphibians (i.e., Anura; n = 2 models), reptiles (i.e., Testudines etc.; n = 2 models), and viruses (e.g., West Nile, malaria, etc.; n = 2 models). Four additional studies modeled habitat requirements for invasive species found in wetlands. Articles took the form of either single- or multi-species BBNs of predominantly data-poor species, with multi-species models developed if the environmental drivers of occupancy were shared across taxa.

Articles failed to identify a specific wetland type in 43% (21/49 studies) of the literature we reviewed, instead simply referring to ‘wetlands’. Ten out of 49 studies identified the modeled system as floodplain wetlands. In all these cases, the primary source of floodwaters was natural river connections rather than intentionally inundated through pumped water or other irrigation systems. Emergent wetlands were identified in 4/49 studies, and riparian wetlands were referred to in 3/49 studies. Other descriptive terminology used to classify wetlands included slackwater, claypan, forested (including seeps), wet meadows, polders, artificial and temporary (2% or one article, each). We found no patterns between taxonomic group and the distinction of wetland types. That is, none of the taxonomic groups had BBNs built in

single wetland types that could potentially have led to the identification of an overabundance of unique habitat requirements.

Based on information in the acknowledgements sections, the majority of peer-reviewed articles were funded through government agencies with a primary mission to support applied research to improve natural resource management, such as the National Climate Change Adaptation Research Facility (Australia), the United States Fish and Wildlife Service (USA), and the United States Geological Survey (USA) (Appendix 2). There were fewer instances of funding from government agencies with a primary mission to advance science theory, such as the National Science Foundation (USA), the National Science Council (China) or the Natural Sciences and Engineering Research Council (Canada). Very few articles cited funding from nongovernmental organizations concerned with ecological restoration or biological conservation.

### 4.3. Using BBNs to identify candidate umbrella taxa

We found 38 habitat requirements reported for wetland-dependent taxa in our literature review (Table 1). The most frequent habitat requirement was presence of or persistence of water. Persistent water during the study period was identified as an important variable driving occurrence/abundance patterns in 24% of models (n = 12 models), spanning various taxonomic groups including amphibians, birds, fish, macroinvertebrates, mammals, and plants. The next most common habitat requirement was the appropriate timing (or “regularity”) of seasonal flooding, by river inundation, rainfall or by irrigation (n = 10 models). Appropriate timing of seasonal flooding was required by amphibians, bacteria, fish, macroinvertebrates, plants, and viruses, although was not included in models of birds, fungi, mammals or reptiles. Other common habitat requirements (each found in n = 8 models) included deferment of effluent irrigation or pollution, total flooded area available, predictability of flood timing, extent, duration and frequency, and presence of a wooded border around wetlands. Less frequent habitat variables are listed in Table 1, along with those mentioned above.

The responses of bird species to environmental variables were the most complex, being sensitive to the broadest set of habitat variables (n = 20/38 habitat requirements were identified for bird species; Fig.

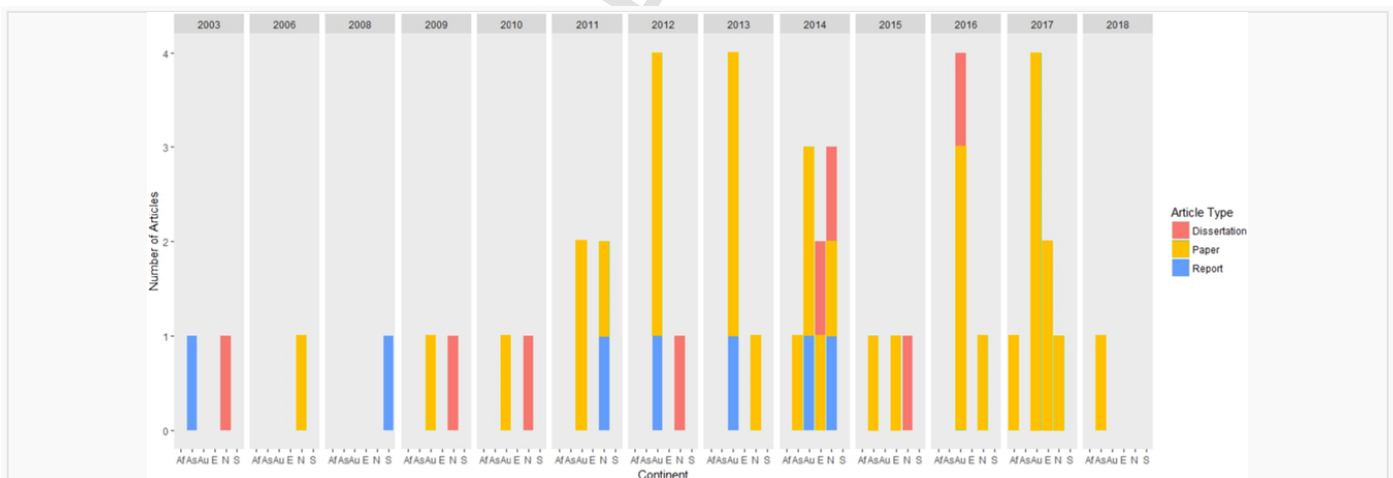


Fig. 2. Distribution of article frequency, publication date, article type, and continent that BBNs were modeling based on our literature review. A book chapter published in 2008 which was theoretical in nature, and thus not affiliated with any continent, was omitted from this figure (see Appendix 1). Contributions from member countries to BBNs from each continent are as follows: Africa (Af) constituted a paper with research throughout sub-Saharan Africa; Asia (As) from Burma (Myanmar), Cambodia, China, the Lao PDR, Taiwan, Thailand, and Vietnam; Australia (Au) from Australia, Papua New Guinea, and Tasmania; Europe (E) from Belgium, England, France, Norway, Romania, Scotland, and Spain; North America (N) from Canada and the USA; and South America (S) from Chile. Distribution of article frequency, publication date, article type, and continent that BBNs were modeling based on our literature review. A book chapter published in 2008 which was theoretical in nature, and thus not affiliated with any continent, was omitted from this figure (see Appendix 1). Contributions from member countries to BBNs from each continent are as follows: Africa (Af) constituted a paper with research throughout sub-Saharan Africa; Asia (As) from Burma (Myanmar), Cambodia, China, the Lao PDR, Taiwan, Thailand, and Vietnam; Australia (Au) from Australia, Papua New Guinea, and Tasmania; Europe (E) from Belgium, England, France, Norway, Romania, Scotland, and Spain; North America (N) from Canada and the USA; and South America (S) from Chile.

**Table 1**

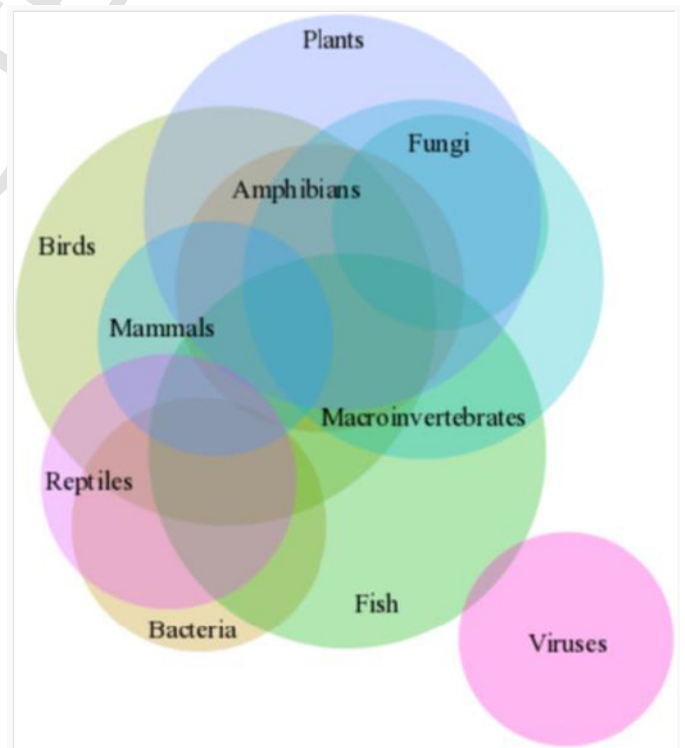
Habitat features that were the most important in determining occupancy or abundance of wetland-dependent taxa in our literature review. Features were determined as being important through sensitivity/percent entropy reduction analyses within the literature.

	Significant habitat feature	Number of studies	Dependent taxa
1	Persistent water	12	Amphibians, birds, fish, macroinvertebrates, mammals, plants
2	Regular flooding or irrigation	10	Amphibians, bacteria, fish, macroinvertebrates, plants, viruses
3	Deferring effluent irrigation or pollution	8	Amphibians, bacteria, birds, fish, macroinvertebrates, plants
4	Total area flooded	8	Birds, fish, mammals, plants
5	Predictable timing, extent, duration and frequency of flooding	8	Amphibians, bacteria, birds, fish, fungi, macroinvertebrates, plants, viruses
6	Woody border to wetland (woody shrub, forest or riparian border)	8	Amphibians, bacteria, birds, fish, fungi, macroinvertebrates, plants, reptiles
7	Burn history	5	Amphibians, birds, fish, fungi, macroinvertebrates, plants
8	Thermal tolerance	5	Amphibians, birds, fish, macroinvertebrates, plants
9	Grazing or trampling	4	Birds, fungi, macroinvertebrates, plants
10	Specific location of habitat	4	Birds, fish, mammals, reptiles
11	Disturbance	3	Bacteria, birds, fish, reptiles
12	Erosion control/aggradation	3	Fish, macroinvertebrates
13	Food availability	3	Birds, mammals, reptiles
14	Availability of specific habitat type	3	Amphibians, birds, fish, mammals, plants
15	Connectivity between habitats	2	Amphibians, birds, macroinvertebrates, plants
16	Interspecific competition	2	Bacteria
17	Amount of surrounding agriculture	2	Birds, plants
18	Distance to roads or density of roads	2	Birds, mammals
19	Mosquito breeding ability	2	Viruses
20	Symbiotic relationships with another species	2	Birds, plants
21	Precise timing of management regime	2	Birds, fish
22	Air temperature	1	Viruses
23	Control of non-native plants	1	Macroinvertebrates, reptiles
24	Dissolved oxygen content of water	1	Macroinvertebrates
25	Groundwater depth	1	Plants
26	Surrounding human population density	1	Viruses
27	Urban development	1	Birds
28	Natural plain banking wetland	1	Fish
29	Parasites/pathogens	1	Reptiles

**Table 1 (Continued)**

	Significant habitat feature	Number of studies	Dependent taxa
30	Meters of wetland perimeter habitat	1	Birds
31	Predation	1	Bacteria, reptiles
32	Rate of wetland drying	1	Plants
33	Salt-water intrusion	1	Macroinvertebrates
34	Season of year	1	Fish
35	Tree removal	1	Fungi, macroinvertebrates, plants
36	Type of local climate	1	Fish
37	Type of mining operation	1	Fish
38	Water depth	1	Plants

3). Both the variables themselves and the states associated with the highest/best response value overlapped with variables identified as important and their states as required for other taxa. The habitat requirements for birds (variable states) completely overlapped with those identified for mammals (n = 6), and almost entirely for amphibians (n = 8 in common out of 9 identified requirements for amphibians). While fish were the most common focus of BBNs in freshwater wetlands (i.e., floodplain wetlands, wet meadows, polders, and ponds), they were also the taxa with the greatest number of unique habitat requirements (n = 4 variables unidentified in studies of other taxa as important).



**Fig. 3.** Venn diagram showing the proportional overlap of habitat requirements among freshwater wetland taxonomic groups. Lists of important habitat requirements were compiled from our review of species-specific BBN model literature (n = 38 habitat features from 50 studies; Table 1; Appendix 1). Venn diagram showing the proportional overlap of habitat requirements among freshwater wetland taxonomic groups. Lists of important habitat requirements were compiled from our review of species-specific BBN model literature (n = 38 habitat features from 50 studies; Table 1; Appendix 1).

## 5. Discussion

### 5.1. Using BBNs to identify candidate umbrella taxa

The taxon-centered BBN models used to inform our umbrella taxa investigation for wetland conservation identified important habitat features (variables and states of variables) for freshwater wetland-dependent taxa. These shared habitat requirements across taxonomic groups can be used to leverage conservation choices that would benefit multiple species. For example, the models in our review indicated that maintaining appropriate hydrologic regimes and natural buffer areas surrounding wetlands would benefit multiple taxa. However, the top habitat features among taxon-centered BBNs were drawn from models built independently from one another to address specific local problems. The present lack of clarity in terminology and definitions makes it difficult to draw conclusions across taxa (e.g., Is the 'regular flooding or irrigation' node for one taxa equivalent to the 'predictable timing, extent, duration and frequency of flooding' node for another taxa?). Thus, to identify ecosystem-wide umbrella taxa, it would be beneficial to develop a standard node set with consistency of variable states that accurately represents the ecosystem in question.

In support of their use as umbrella taxa in freshwater wetland ecosystems, we found that birds had the greatest degree of overlap among habitat requirements shared with other species. Characteristics that indicate wetland birds make strong candidates for umbrella taxa representing wetland conservation include their status as habitat specialists with large ranges sizes, and that they are moderately sensitive to human disturbance (Caro, 2010; Green et al., 2002; Kalinkat et al., 2017; King et al., 2006; Roberge and Agelstam, 2004). For example, multiple bird species show sensitivity to human-caused disturbance that drives behavioral responses in vigilance, fleeing, habitat selection, mating displays and parental investment which can have population and community-wide impacts (Frid and Dill, 2002). As many wetland birds are migratory (e.g., Ma et al., 2009; Skagen, 1997), leveraging conservation efforts across entire annual ranges of wetland birds could maximize restoration of wetland biodiversity under an umbrella taxa approach.

The adoption of an umbrella taxa approach to conservation plans should, however, be made with caution as even under circumstances when umbrella taxa overlap spatially with rare or unique species, management decisions centered on umbrella taxa can cause unintended loss of non-target biodiversity (Severns and Moldenke, 2010). Although we did not consider issues of scale in our review, we recommend considering it when selecting umbrella species using BBNs or other methods to identify umbrella taxa. Unique landscape features important at regional scales continue to warrant the investigation of locally appropriate umbrella taxa (e.g., migratory fishes; Agostinho et al., 2005). Furthermore, the existence of species with unique habitat requirements or small ranges that do not overlap with umbrella taxa necessitate that conservation approaches maintain a breadth of strategies including programs surrounding focal taxa representative of unique habitats with specific threats (Lambeck, 1997).

### 5.2. BBN model construction

Bayesian belief network models are unique in their ability to incorporate expert opinion and refine the identification of sources of uncertainty by developing gamma models. If models rely heavily on expert opinion there is a danger that they do not adequately reflect reality due to linguistic uncertainty (when words have imprecise or different meanings to different people), overemphasis of rare cases stemming from specific memorable experiences by experts, or simply the reliance on memories and not empirical data (Meyer and Booker, 1991; Morgan

and Henrion, 1990). A strength of BBNs is that they are also able to incorporate missing values in input data and perform accurate predictions with the model built from them (although not a unique to BBNs; Uusitalo, 2007). The development of gamma models (incorporating data to validate alpha or beta models) provides the opportunity to support or refute our understanding of relationships between species and their environment. Gamma models also enable refinement of identifying sources of uncertainty in resultant SDMs. To this end, we found that over half of the articles we reviewed validated their models with data. Through an iterative process of developing and updating BBN models with monitoring data, BBNs can provide an ideal modeling approach to facilitate adaptive management (Henriksen and Barlebo, 2008; Nyberg et al., 2006). Thus, a BBN approach to understanding species distributions can be powerful due to improved accuracy in modeling species habitat relationships.

As all models we reviewed were process models (with the exception of one dynamic model), seasonal processes are currently inadequately represented for the comparison of BBN models either within or among wetland types. Wetlands are, by definition, a hydrologically dynamic ecosystem defined by seasonal hydroperiod (Cowardin et al., 1979). The use of dynamic models that track habitat requirements across seasons may thus be more appropriate than the commonly used process models. However, there is an innate problem in finding convergence using Markov chains employed in dynamic BBN models which requires limiting the number of times the model can be updated (Wu et al., 2018). Further research developing BBNs as seasonal dynamic models could improve their utility in biological conservation.

Our review identified an overall lack of spatial statistical frameworks. In the absence of using spatial statistics, it may be difficult to identify when and where habitat is most likely needed to fulfill the life history needs of species within an ecosystem. Most wetland management initiatives focus on individual wetland creation, although strategic restoration planning may yield the greatest benefit using state-wide or watershed-wide perspectives (Horvath et al., 2017). Many challenges to wetland conservation planning could benefit from a spatially explicit, BBN approach. For example, wetland management remains challenging due to limited resources for acquiring new data (Margules et al., 2002), large areas of managed wetlands (Semlitsch and Bodie, 1998), limited ecological data on wetland characteristics and seasonal conditions (Zedler, 2000), and responses to changes in flow regimes in channelized river systems (Bunn and Arthington, 2002). Each of these issues could benefit from a spatially explicit risk assessment, to ease economic strain and use limited funds in the locations with the best cost-benefit ratio. However, many small-scale species requirements remain unavailable in spatial format (e.g., topographic, geomorphic, edaphic) and so are omitted from typical SDMs (Sinclair et al., 2010). Exclusions of these species can lead to error in SDMs, and few studies quantify the uncertainty generated by these incomplete data (Beale and Lennon, 2012; Elith and Leathwick, 2009).

Approaches to identifying umbrella taxa that employ a spatial statistical framework (e.g., clustering analyses such as calculating Ripley's K statistic, or other statistics for point processes) could improve the development of finer-scale range maps that can be used to aid in identifying areas of conservation priority. The use of a spatial statistical framework in a BBN approach would include node-specific estimates of uncertainty in probabilities of species occurrence with respect to environmental data gathered from a variety of sources (e.g., expert opinion from systems experts and curated GIS layers). Some new computational tools for calculating risk assessments of alternative conservation actions; including spatial statistical approaches for identifying important areas for conservation; are currently in beta testing through the GeoNetica (GeoNetica™, Norsys Software Corporation) plug-in of the popular BBN computational tool, Netica (Netica 6.0, Norsys Software Corporation).

Building spatially scalable wetland models that can accommodate the seasonal ranges in hydrological nodes, as well as differences in mobility of wetland taxa (e.g., pollinator vs. amphibian vs. riverine fish vs. migratory bird) may also aid in efforts to identify umbrella taxa in seasonal ecosystems. The complexity of seasonally fluctuating ecosystems, such as wetlands, therefore requires either the logical integration of multiple process models, or small dynamic BBN models (e.g., four seasons) equipped with scalability options to inform conservation plans appropriate for each season and location.

Although alpha models in our review were appropriately developed using empirical literature and combined with information provided by taxonomic experts to create beta models, ecological BBNs may benefit from also interviewing ecosystem experts. Particularly in wetlands, experts knowledgeable of hydrology and geomorphology could provide information regarding systems processes that likely influence physical habitat characteristics. For example, the frequency and timing of flooding in wetlands was important in many of the BBN models that we reviewed but there was little reference to the source of floodwaters. It was unclear whether floodwater resulted from rainfall (as in playa wetlands, ombrotrophic bogs or pocosins), river connection (as in alluvial swamps, montane or streamside wetlands), groundwater discharge (as in discharge wetlands such as prairie potholes, or fens) or whether water pumped into wetlands from a municipal source was sufficient (wetland hydrological characteristics from Brinson, 1993). Similarly, pedologists or edaphologists would know the types of plants best suited to soil characteristics and identify potential wetland areas for restoration given regional soil characteristics. The current lack of distinction among similar nodes across taxon-centered BBN models of freshwater wetlands is a major caveat because we lack relevant take-away actions for wider conservation planning. Including systems experts in the design of ecological BBN models may improve the use of BBNs as decision-support tools for conservation planning as they would enable higher accuracy in distinguishing relevant landscape variables at the ecosystem scale.

### 5.3. BBNs as tools for biological conservation of freshwater wetlands

Our review produced mixed results with respect to the integration of BBNs into biological conservation. On the one hand, the majority of peer-reviewed articles were funded by government agencies with a primary mission to support applied research. On the other hand, the majority of literature sources appeared in journals contributing to conservations among modelers, not in journals likely to inform wetland management and conservation communities. In general, even when the primary purpose of developing taxon-centered BBN models is for use as a decision-support tool for conservation planning, few studies fully transition from pilot to implementation. The majority of management decisions are not developed using decision-support tools, even when the primary purpose of developing taxon-centered BBNs is for future use as a decision-support tool for conservation planning. Although there have been consistent calls in the conservation literature for mechanistic models in defining species-habitat associations (i.e., those that test a specific mechanism driving species outcomes; Landuyt et al., 2013; McCann et al., 2006; Nyberg et al., 2006), this failure is not unique to BBNs. In a survey of over 1000 protected areas in Australia, Cook et al. (2010) found that approximately 60% of management decisions relied primarily on experience-based information. Sutherland et al. (2004) found that only 2% of conservation actions undertaken in an English wetland were based on verifiable evidence, while 77% of actions were based entirely on experience. A major hurdle supported by statements in almost all articles in our review was that taxon-centered BBNs were

not adopted as support tools by land managers responsible for conservation.

Conservation planning may understandably dismiss species-specific BBNs due to a misguided assumption (from a modeling perspective) that BBNs are built considering the inappropriate landscape settings and may fail to include relevant dynamic physical features of the ecosystem if they are built exclusively through a taxonomic lens. Disconnection between the scientific research community and area managers occurs when scientific information is acquired and assembled without consideration of management implications, the results are not easily accessible or applicable to area managers (Bouska et al., 2016; Cook et al., 2012; Pullin and Knight, 2005), or there are perceived conflicts between single taxa model recommendations and the needs of multiple species in a complex system. Some attribute the limited adoption of decision-support tools by conservation planners to a lack of engagement between researchers and managers across multiple studies (Gawne et al., 2012; Goosen et al., 2007; Kroon et al., 2009), although adaptive resource management through collaborative efforts has been adopted in some areas (King et al., 2010; Richter and Thomas, 2007). Wetland restoration is thought to be effective at restoring both biodiversity and ecosystem services (Meli et al., 2014). Thus, the development of decision-support tools, such as BBNs, that synergize empirical data with expert knowledge from within a hypothesis-testing framework have the potential to drive critical gains in selecting effective criteria for conservation action if they were framed for more widespread utility.

### 5.4. Conclusion

The adoption of a systems-oriented BBN approach to conservation planning could aid the identification of effective umbrella taxa. The identification of umbrella taxa is often hindered by inconsistent methods for determining habitat requirements in species distribution models as well as inadequate prior knowledge of biotic and abiotic landscapes. As BBNs can include expert knowledge, they may provide a more robust assessment of ecosystems and improve conservation planning. As a decision-support tool for conservation planning, BBNs can be updated via monitoring to minimize uncertainties over time to achieve more rapid restoration success.

Although an umbrella approach to conservation may not protect habitat requirements for all species, comparing habitat requirements using a BBN approach to building species distribution models, as discussed here, allows for the identification of umbrella species. A BBN approach to identifying umbrella taxa can also quantitatively estimate which taxa may not benefit from conservation action targeted at umbrella taxa by identifying those with unique habitat requirements not shared with umbrellas. Thus, using a BBN approach to building SDMs has the potential to improve our capacity for effective biological conservation.

As BBNs are relatively easy to construct and understand due to their visual nature (Douglas and Newton, 2014), they have the potential to substantially improve coordinated efforts translating empirical research on species distributions into useable outputs in the hands of conservation planners. BBNs are flexible in their applicability and are particularly useful to build SDMs of data-poor species through the incorporation of expert knowledge (e.g., Drew and Collazo, 2014). Comparing important nodes and measures of uncertainty from multiple network models is a new methodology to identify critical habitat criteria shared across taxa. Using BBNs to identify taxa that have the highest degree of overlap in habitat requirements within an ecological community also enables a quantitative assessment of potential umbrella taxa which can then be the focus of conservation in an adaptive resource management framework.

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We identified a total of 53 articles with ecological BBNs for freshwater wetland-dependent taxa; consisting of 33 peer-reviewed articles, 9 reports or conference proceedings, 10 master of science theses or doctoral dissertations, and 1 book chapter (Appendix 1). The sources of peer-review articles were primarily ecological journals (e.g., Ecological Indicators), the modeling journal, Environmental Modeling & Software (n = 6), and conservation journals such as Biological Conservation (n = 2) and Conservation Biology (n = 1). Lead authorship on peer-reviewed articles and reports was rarely by graduate students or early-career scientists such as postdoctoral researchers (26%), and more commonly by research fellows or senior researchers at the time of publication (Appendix 2).

The earliest evidence we found of BBNs being used to model habitat requirements of freshwater wetland species was from 2003, with an accelerated rate of increase in peer-reviewed literature using BBNs to explore habitat relationships of wetland taxa as years have gone on (Fig.

2). The majority of articles focused on Australasian wetlands (including Australia, Tasmania, Papua New Guinea, and New Zealand; 42%), but wetlands from all continental regions (excepting Antarctica) have been represented by BBNs in the peer-reviewed literature (Appendix 1).

Based on information in the acknowledgements sections, the majority of peer-reviewed articles were funded through government agencies with a primary mission to support applied research to improve natural resource management, such the National Climate Change Adaptation Research Facility (Australia), the United States Fish and Wildlife Service (USA), and the United States Geological Survey (USA) (Appendix 2). There were fewer instances of funding from government agencies with a primary mission to advance science theory, such as the National Science Foundation (USA), the National Science Council (China) or the Natural Sciences and Engineering Research Council (Canada). Very few articles cited funding from nongovernmental organizations concerned with ecological restoration or biological conservation.

Supplementary Figures

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