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WIREs Wiley Interdisciplinary Reviews

Article Title: Climate change and freshwater ecology: hydrological and ecological methods of comparable complexity are needed to predict risk

Article Type:

○ OPINION	○ PRIMER	○ OVERVIEW
○ ADVANCED REVIEW	● FOCUS ARTICLE	○ SOFTWARE FOCUS

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This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1002/wcc.692

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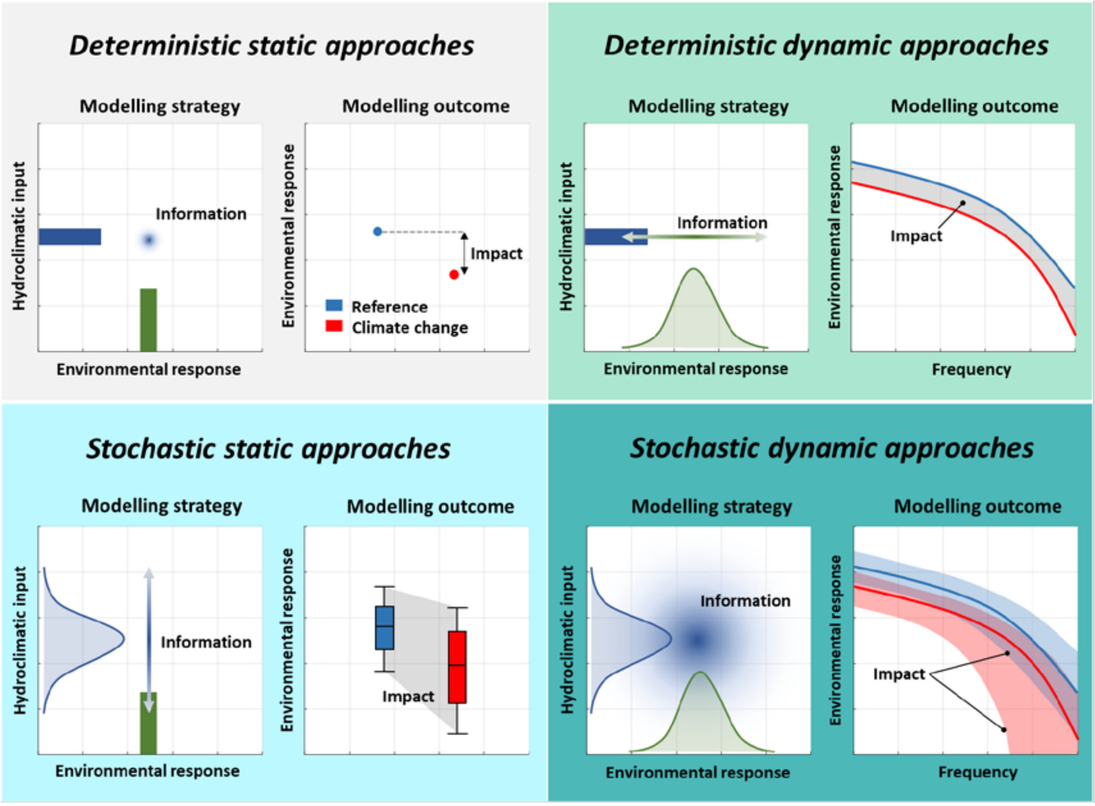
Abstract

Many freshwater ecosystems are in decline because of anthropogenic disturbance including climate change, yet our understanding of ecological vulnerability to future conditions including climatic variation is limited. Understanding climate risks to freshwater ecosystems requires combining hydrological and ecological knowledge. While there have been significant advances in ecohydrological approaches when applied within the large array of methods available for undertaking impact assessments, the ecological and hydrological elements are often not well-integrated. This results in a mismatch in their ability to accommodate the inherent uncertainty in both impacts and responses. We examine published literature that assesses climate change impacts on freshwater ecosystems using both hydrological and ecological models to better understand method choices. We identify four fundamentally distinct modelling approaches used to assess climate change risk. We discuss which approaches are less useful for predicting ecological impacts under climate change, and highlight approaches of comparable complexity that can maximize the utility of dynamic, process-based modelling while capturing the effects of climate uncertainty and variability. Using an illustrative case study of riparian vegetation health under climate change, we show how the four alternate modelling approaches feature different degrees of information in their outcomes and inferences about future risk. Most current studies that examine climate change risks to freshwater ecosystems use simplified methods or inadequately combine key elements. However, unless the interactions between changing hydrologic variability and ecological responses are explicitly captured in scale-sensitive modelling methods, the risks of climate change to freshwater ecosystems will likely be substantially misrepresented, with negative consequences for effective management responses. Capturing these interactions requires combining ecological and hydrological methods of comparable complexity.

Graphical/Visual Abstract and Caption



Combinations of alternate modelling methods leads to different kinds of outcomes when assessing climate change risk. Stochastic dynamic approaches which can project sequential ecological outcomes and accommodate climate variability are underrepresented in the literature.

1. INTRODUCTION

Freshwater ecosystems face degradation from threats such as over-exploitation, water pollution, flow modification, habitat degradation and species invasions (Dudgeon et al., 2006; Reid et al., 2019; Vörösmarty et al., 2010). Climate change will compound these threats with direct effects on habitat (Thomas et al., 2004) and diverse secondary effects through ecosystem interactions and responses to mitigation or adaptation measures (IPCC, 2014). Assessing and managing risks from climate change is a pressing global challenge to ensure the sustainability of river health and the communities and livelihoods that depend on these systems (Arthington et al., 2018). Meeting this challenge requires an integrated approach that draws upon knowledge of climatology, hydrology and ecology. While each of these disciplines have seen significant advances in recent years, we question how well they are being combined under an integrated ecohydrological modelling framework to inform our understanding of climate change risks to freshwater ecosystems.

Conservation efforts are supported by *climate change impact assessments* that seek to understand how ecological systems respond to climate change (Dawson et al., 2011). However, adoption of different methods of simulating future impacts and inferring ecological responses can lead to substantially different assessments of risk and hence management recommendations for the same case study (Wheatley et al., 2017). A mismatch of modelling assumptions behind the ecological responses and hydrological impacts may undermine the validity of the assessed risks to freshwater ecosystems.

The assumption of stationarity in hydroclimatic conditions and ecological relationships has challenged existing approaches to freshwater ecosystem modelling under change (Poff, 2018). For decades, this assumption has implied that climatological inputs and hydrological relationships are either fixed or conform to defined probability distributions, a premise that is inconsistent with ongoing climate change and recently observed hydrologic behavior (Milly et al., 2008; Saft et al., 2015). Non-stationarity also applies to the behavior of ecological systems and processes. Anthropogenic disturbance and climate change are creating novel environments (Hobbs et al., 2009), changing the way species interact (Rahel & Olden, 2008), and even leading to evolutionary changes in the near-term (Hoffmann & Sgró, 2011). Also, non-linearities in hydrological and ecological responses make extrapolation under these changing conditions difficult (Suding et al., 2004; Tonkin et al., 2019). If climate change impact assessments do not account for changes in the relationship between climate and hydrological and ecological variables, projected outcomes will be undermined. These effects of non-stationarity may also limit the use of established techniques that are based on historical reference conditions for riverine conservation or restoration (Poff, 2018).

The challenge in accounting for non-stationary hydrology is confounded by the fact that natural hydrologic variation is central to ecological performance. Much research has shown the importance of regimes of variability in shaping ecosystems (Bunn & Arthington, 2002; Poff et al., 1997), and growing recognition that individual hydrologic extreme events can have large ecological effects (Bogan & Lytle, 2011; Ruhí et al., 2016). This highlights the required link between ecology and hydrology, as we must consider how sequences of extremes might fundamentally alter ecological trajectories in addition to how hydrologic regimes are shifting (Anderson et al., 2006; Horne et al., 2019; Poff, 2018; Wang et al., 2018). However, freshwater ecosystem management usually relies on regime-averaged metrics or model predictions over long time scales (Shenton et al., 2012). These measures of response can include representation of flow extremes, such as the annual flow maxima and minima (Richter et al., 1996) and are commonly employed in climate change impact assessments. While they are useful for representing long-term changes in average environmental behavior, they cannot be used to assess sensitivity to particular sequences of extremes. This is because of their inability to project ecological outcomes through time (Urban, 2019).

In this paper we explore and document the state-of-the-art in climate change impact assessments for freshwater ecosystems. We highlight how current approaches to impact assessments require the integration of the three disciplines of climatology, hydrology and ecology and how the integrated discipline of ecohydrology has emerged in recent decades. We examine the links between ecohydrological modelling methods used in impact assessments and then discuss the shortcomings and future directions of each. Using a systematic search of published studies that combine hydrological and ecological models to undertake impact assessments, we show how choice of methods used in assessing hydrological impacts and resulting ecological responses (which can be thought of as exposure and sensitivity, respectively as defined by Dawson et al. (2011)) influences the information available from assessment outcomes. We illustrate this using a case study of riparian vegetation health under projected climate change. To advance our understanding of ecological response and vulnerability under climate change we discuss the need to use approaches of comparable complexity.

2. METHODS AND TOOLS FOR ASSESSING CLIMATE CHANGE IMPACTS ON FRESHWATER ECOSYSTEMS

Approaches to assessing climate change impacts on freshwater ecosystems include three key components (Foden et al., 2018): (1) a selection of environmental stressors that act on freshwater ecosystems and are dependent on climate; (2) perturbation from some reference condition attributed to anthropogenic causes; and (3) representation of the ecological response to these perturbations. These components can be different when assessing ecosystem responses versus the responses of individuals or specific species. There are key differences in modelling habitat or distribution (Kearney, 2006) versus direct modelling of organisms and their interactions (Ockendon et al., 2014).

Within freshwater ecosystem assessments, these three components are informed through a combination of the disciplines of climatology, hydrology and ecology. Each of these fields have independently developed many tools and methods that can be linked to inform assessment outcomes. A legacy of threats to freshwater ecosystems is the emergence of the field of ecohydrology, where the objective is to integrate hydrological and ecological knowledge (Bunn & Arthington, 2002), recognizing that hydrology and ecology are strongly linked and their interactions determine freshwater ecosystem outcomes. Ecohydrology can serve as a foundation to project future climate impacts on hydrologically-dependent freshwater ecosystems. Below we provide a brief overview of modelling approaches that have arisen out of the disciplines of climatology, hydrology and ecology. We use this discussion as context for the review of climate change impact assessments on freshwater ecosystems. Although we separately describe the disciplines below, the combination of different types of modelling captures the approaches adopted in many ecohydrological investigations.

2.1 Global climate modelling

Much of the current analysis of climate change impacts on water resources and ecological systems relies on predictions from general circulation models (GCMs), which are the best means available to understand global climatic response to greenhouse gas emissions. Contemporary GCMs include advanced representation of land surface processes, including the terrestrial carbon cycle and nested hydrological components within land surface models (IPCC, 2013). However, GCMs have distinct shortcomings when used for eco-hydrological analyses. The nature of global scale climate modelling means that important hydrological processes cannot be explicitly resolved at the catchment scale. GCMs typically predict rainfall too regularly, and in too small quantities (Stephens et al., 2010) and many do not robustly represent major climatic drivers of natural variability such as the El Nino Southern Oscillation (Bellenger et al., 2014). This means that the available spatial and temporal scales of GCM process descriptions are not well suited to the assessment of ecohydrological responses and many management decisions.

2.2 Hydroclimate impact modelling

Although GCMs are currently limited in their ability to accurately and precisely predict regional rainfall changes, downscaling techniques can be used to transform information from GCMs to a more local scale. Downscaling techniques can be divided into two broad approaches: statistical downscaling involves the development of functional relationships between large scale climate variables to those at local scales (Ekström et al., 2015; Fowler et al., 2007), and dynamical downscaling involves the nesting of a fine-resolution regional climate model within a GCM (Di Luca et al., 2015; Prein et al., 2015). Within the hydrological sciences, the most common statistical downscaling approach is the delta change method, which superimposes a change signal on an observed record (conditioned by annual, seasonal, or quantile factors). However, this assumes that climatic stationarity prevails over the period of record and that the derived time series is extensive enough to characterize natural climatic variability over time scales of relevance to environmental performance. The use of historical observations also assumes that the past sequence of wet and dry periods will be repeated in the future, even though future droughts and floods will not necessarily unfold in an identical pattern to those previously observed. The unjustified assumption that the sequence of future events will be the same as in the past can lead to substantially different impacts on riverine ecology (Lake, 2003; Wang et al., 2018). This limitation can be overcome by using weather generators to simulate stochastic climatic sequences, where a climate change signal is imposed by perturbing model parameters (Poff et al., 2016; Wang et al., 2018). However, there are difficulties in applying these approaches to large catchments and in preserving temporal characteristics over finer timescales and interannual or interdecadal variability (Wilks, 2012).

Once future projections of climate (precipitation and evaporation) are available, hydrological models are used to transform the projected inputs into streamflow. Streamflow is recognized as the “master variable” governing riverine ecosystem condition (Power et al., 1995) and thus the step of transforming precipitation into streamflow is an important aspect of climate change impact assessments. However, many existing climate impact studies use precipitation statistics as inputs (Cianfrani et al., 2018; Pandit et al., 2017; Sleith et al., 2018) and hence are unable to consider the non-linearity (Peel et al., 2015) and possible non-stationaries (Saft et al., 2015) involved in the transformation of precipitation into streamflow. A range of conceptual and physically based models are available to convert climate inputs into a timeseries of streamflow (Singh & Woolhiser, 2002) and to simulate the behavior and management of water resource systems (Welsh et al., 2013).

2.3 Scale and resolution issues of hydrological and ecological timeseries

Predicting ecological responses from hydrologic information is complicated by issues of scale dependency between observed ecological patterns and the mechanisms that underpin them (Levin, 1992; Wheatley et al., 2017). Further, the spatial and temporal grain of hydrologic and ecological data and the ecological inferences possible through interdisciplinary modelling are strongly linked (Poff, 2018). For example, the temporal resolution of hydrological series is typically much finer than the resolution of ecological changes, but long-term ecological responses can be caused by hydrological processes that occur over short timescales (such as flooding). There are also challenges arising from the differing spatial scales of information. Hydrologic records are site-based whereas ecological monitoring represents influences over varying scales from local to landscape level. Nonetheless, data products and frameworks exist that attempt to bridge the issues of required scale and resolution for ecological responses with those which are typically provided by climate models. One example is the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP) (Schellnhuber et al., 2014; Warszawski et al., 2014). The cross-sectoral nature of ISIMIP facilitates a more holistic modelling framework consistent with a broader ecohydrological science. One residual issue is that while modelling at finer temporal and spatial scales may better represent ecological responses, this is only worthwhile if we have confidence in the projected climate change impacts at these scales.

We also cannot assume that the observed timeseries of hydrological and ecological records are stationary (Saft et al., 2015). It is common to be calibrating models across non-stationary data records due to ongoing land-use change, realized climate change, infrastructure and policy development affecting water and ecosystem management. However, many derived flow-ecology relationships still assume stationarity (Poff, 2018).

2.4 Ecological response modelling

There are several recent reviews that describe the broad issues involved in the assessment of ecological vulnerability to climate change (Foden et al., 2018; Pacifici et al., 2015). Here we focus on the elements related to freshwater ecosystems, including species performance and ecosystem functions and the links between hydrological inputs and ecological response. Representing ecological responses under changing climate can be classified into three main approaches: correlative, trait-based and mechanistic (Pacifici et al., 2015). Correlative approaches statistically relate the responses of target species to prevailing climate or hydrological variables. These methods can be simple to apply for spatially-explicit responses over a range of taxonomic groups (Pyne & Poff, 2017), and application is aided by large-scale environmental data sets and climate projections (Fick & Hijmans, 2017). However, they assume stationarity in their lumped parameterization of complex environmental relationships and are usually used to assess change over long time periods. Trait-based approaches assess vulnerability using species traits. These consider environmentally-sensitive species attributes that can be generalized across broad geographic extents making them rapid to apply (Pacifici et al., 2015). Mechanistic approaches use physiological relationships such as tolerances, species interactions or life-history components to model ecological response, and hence they are expected to be more suitable for extrapolation under novel or non-stationary conditions (Kearney & Porter, 2009; Poff, 2018; Tonkin et al., 2019). They may also be better for simulating compound threats such as land-use and climate change (Mantyka-Pringle et al., 2014).

Within these three broad approaches, different types of methods are used to predict ecological response. These types are diverse but can be broadly divided into three groups: key metrics, distribution (or niche) models, and demographic models (Ekström et al., 2018; Pacifici et al., 2015). Key metrics are used to relate responses to changes in environmental variables. These indicate the relative impact of changed conditions, but without estimating the direct impact on species or probability of extinction (for the example, the Indicators of Hydrological Alteration (Richter et al., 1996)). Distribution models provide spatially explicit representations of a realized niche for a taxonomic group. Model outputs include the area of suitable habitat or probability of occurrence, usually evaluated as an equilibrium response over multiple decades (Chapman et al., 2014). Distribution models commonly use correlative approaches derived from previously available environmental data, although combined correlative-mechanistic examples are emerging (Keith et al., 2008). Demographic models calculate changes in abundance at species or ecosystem levels. These can be process-based simulations that attempt to evaluate life-history events and interactions through ecological dynamics. As such, the models provide time-varying outputs at a resolution that includes all processes of interest, and thus they can evaluate ecological response over short timescales or against environmental events. Demographic model outputs are sensitive to the range of processes and interactions included in the modelling framework and are restricted to species with extensive data and understanding (Urban et al., 2016).

3. HOW ARE CLIMATE CHANGE IMPACT ASSESSMENTS FOR FRESHWATER ECOSYSTEMS BEING CONDUCTED?

Decisions made on methods and data for simulating hydroclimate impacts will influence the analyses of ecological responses in the assessment (Foden et al., 2018). Lack of suitable data, resources, institutional capability and access to technical expertise will continue to affect how assessments are undertaken around the world. Unique target species or taxonomic groups may support the adoption of specific response models, with implications for the data needed for their application. We used a systematic search of published literature to understand which combinations of hydrological and ecological methods are being used in modelling climate change impact assessments for freshwater ecosystems.

3.1 Review of published assessments

We extracted categorical information on methodological choices encompassing scale, resolution, treatment of uncertainty and various other characteristics (see supplementary materials S1 for a full list and methods, including details of keywords, parameters and dates). We chose a large range of categorical variables to reflect the breadth of complexity of assessments and to provide enough information to capture key variations in methodologies.

Our set of keyword phrases in Clarivate Analytics Web of Science database yielded 214 studies. This was refined to a final sample of 61 after removing studies that did not satisfy inclusion criteria relevant to the study objectives. We excluded studies that were not related to freshwater ecosystems, those that did not include a modelling approach that could be categorized (e.g. reviews or syntheses), or studies that failed to define their methodology sufficiently to allow full set of relevant categorical data to be confidently extracted. Studies that were retained included those that reported on ecosystem services, and those that considered broad ecological indicators or specific taxa. Studies with multiple impact assessments in one article were treated as independent samples.

Geographically, studies spanned all populated continents, although site-specific examples and smaller regional assessments were confined to the North American, European, Asian and Australian continents (Figure 1). Other reviews have made similar observations regarding climate change impact assessments on freshwater taxa (Pacifici et al., 2015). Most assessments were conducted at regional scales (typically between 100 and 10,000 km^2 – 59% of studies), with fewer at continental or global scales (20%).

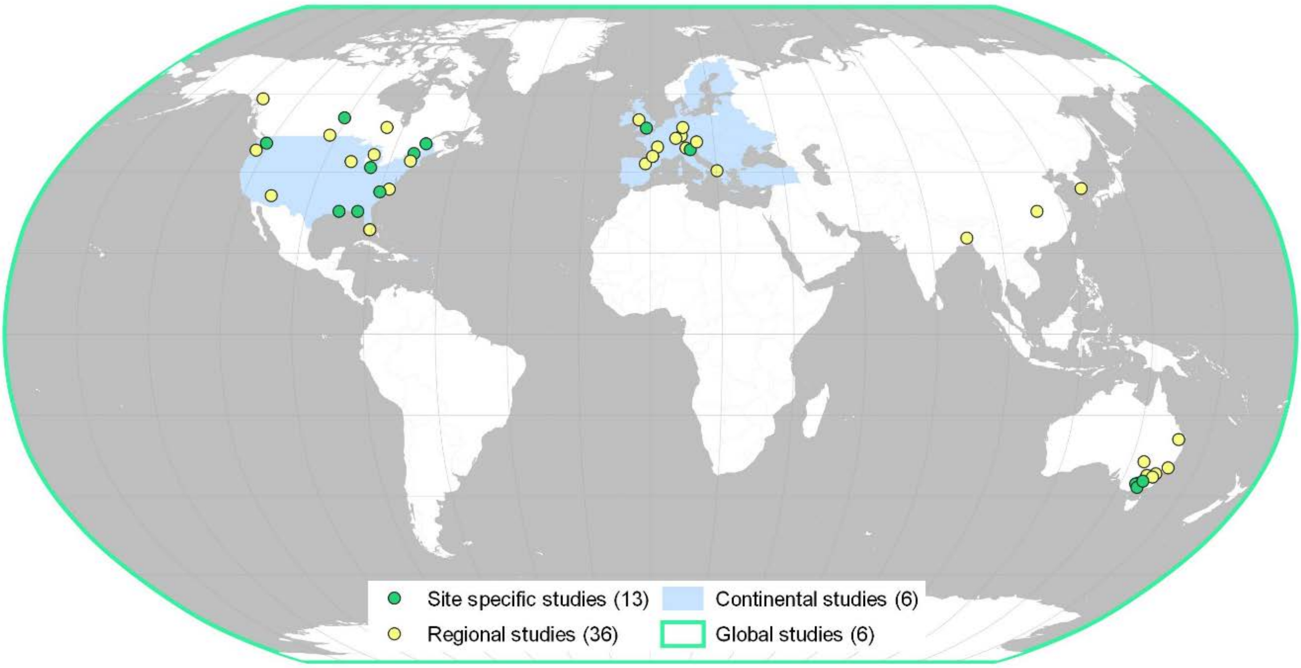


Figure 1. Global range and spatial scale of climate change impact assessments on freshwater ecosystems. Some regional and site-specific studies overlap. Of the six continental scale studies, three each were focused on the contiguous United States and greater Europe (these areas highlighted indicatively).

We classified the studies to understand which characteristics best described the array of different methodologies used. To this end, we used multiple correspondence analysis (MCA) to highlight principal components (i.e. common key features) amongst the different approaches, and hierarchical clustering to explore the degree of similarity across the groupings of data extracted (see supplementary materials for detailed methods). Information relating to model resolution (spatial and temporal) was not used in the construction of principal components in the MCA; while these factors influence uncertainty, we do not consider them to fundamentally represent alternate modelling approaches (Table 1). Certain hydrological and ecological processes exhibit scale dependence and may be limited by modelling resolution (e.g. rainfall infiltration, chemical processes or the dynamics of individual organisms). However, incorporating these scaled processes lies beyond the scope of this study. This does not preclude additional insights being gleaned from analyzing spatial and temporal resolution in more detail. To this end we supply the full range of data extracted from the review in the supplementary materials.

The first two principal components generally align with ecological and hydrological categorical variables, respectively (Table 2). Clustering supports four main groups, mostly described by combinations of hydrological and ecological methods (Figure 2 and Table 3). Confidence intervals (95%) for clusters shown in Figure 2 are quite distinct, with only small sections overlapping although some studies lie close to interval boundaries. Due to the relatively low dimensionality inherent in categorical data, several studies occupy the same space in Figure 3, meaning they share precisely the same characteristics defined by Table 1. Many, but not all, used the same datasets such as WorldClim (Hijmans et al., 2005).

Table 1. Key categorical variable inputs to the MCA used to characterize principal components and cluster analysis.

Cluster analysis input categories	Description	Categorical variables
Flow as variable	Was flow (or runoff etc.) the primary hydrological variable in the study?	Yes, no
Natural variability	How is natural variability explored in the input data?	Single sequence, ensemble/stochastic
Climate uncertainty	How is uncertainty explored in the climate impact?	None, scenario, exploratory
Response interactions	Does the response model include interactions/feedbacks with other components or state variables that are affected by the input data?	Yes, no
Response resolution	Is the response model time-varying or a time-	Time-averaged, time-

averaged metric?	varying

Table 2. Category contribution to construction of the first two principal components in the MCA. Variables within each category are summed for the total weight. In general, ecological features are represented in dimension 1, and hydrological in dimension 2.

	MCA sum of variable weights (%)	
Categories	Dimension 1	Dimension 2
Flow as variable	25.3	2.5
Natural variability	9.6	35.0
Climate uncertainty	7.8	48.5
Response interactions	26.6	4.5
Response resolution	30.7	9.5

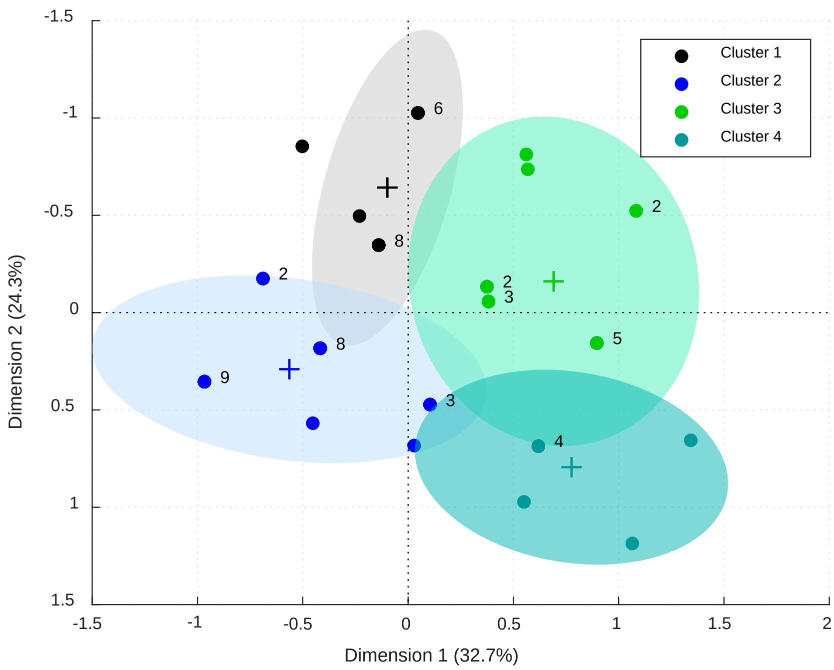


Figure 2. Cluster analysis and MCA results for methodologies in climate change impact assessments on freshwater ecosystems. Numbers represent multiple studies that occupy the same space. Ellipses represent the 95% confidence interval for membership, and plus symbols indicate the centroid of each cluster. Note the y-axis is inverted to keep cluster positions consistent with following figures.

Table 3. Most prominent categorical variables associated with each cluster. Variables are arranged in descending order of significance (by v-test).

Cluster	Dominant variables (p<0.05)
1	Natural variability = Single sequence Response resolution = Time-averaged Climate uncertainty = None Response interactions = No
2	Natural variability = Ensemble/stochastic Flow as variable = No Response interactions = No Climate uncertainty = Scenario Response resolution = Time-averaged
3	Natural variability = Single sequence Response interactions = Yes Response resolution = Time-varying Flow as variable = Yes
4	Response resolution = Time-varying Response interactions = Yes Climate uncertainty = Exploratory Natural variability = Ensemble/stochastic

3.2 Synthesis of modelling strategies

To allow for generalization of these results, we developed four distinct groups based on hydrological and ecological methods (degree of separation of hydrological and ecological modelling methods in Figure 2 and the dominant variables in Table 3). This changed the membership of a small number of studies (see supplementary materials S2), primarily those close to confidence interval bounds, but did not change the overall distribution of groups of studies. The benefit of this re-imagining of the groupings is that it helps ensure that studies within a group all share the same characteristics, while preserving the overall structure suggested by the MCA. The numbering scheme for groups below is consistent with number labels of clusters in Figure 2. The four groups that describe the range of approaches are defined by:

1. *Deterministic – static*: time-averaged response metrics, single sequence of hydrological inputs, precipitation change as proxy for hydrological impact without modelling flow

2. *Stochastic – static*: large ensemble hydrologic modelling, paired with time-averaged or purely correlative ecological responses

3. *Deterministic – dynamic*: demographic models, time-varying responses, mechanistic interactions between species or environment, paired with a single sequence of hydrologic inputs and limited expression of climate uncertainty

4. *Stochastic – dynamic*: stochastic or large ensemble hydrologic simulation of variability and change across several dimensions, paired with mechanistic, time-varying ecological responses.

These four groups represent a fundamental difference in the representation of, and sensitivity to, certain threats. They also represent the different kinds of outputs expected from the analysis, and the handling of input uncertainty and variability (Figure 3 and below). Although we partitioned the approaches here, methodological choices in these domains represent a continuum because of the combination of ways that complexity and modelling processes are incorporated. The groups reflect a distinction in static versus dynamic-based approaches to environment-ecology modelling.

Studies in the first group (Figure 3a – *deterministic – static* approaches) are almost entirely correlative methods based on the use of distribution models. These methods utilize single climatic sequences from the delta-change method or else use a single downscaled GCM to estimate hydrologic impacts. With this group of methods, a single input is paired with a single output representing a very limited expression of natural variability and climate uncertainty. Indeed, the methods assume that the distribution and frequency of future climatic sequences is largely the same as the past. Output metrics are averaged over long timescales, and the methods also assume that future impacts are based on historic dependencies. Outputs from these approaches only give information about the difference between reference and future climate impacts and not the distribution of conditions experienced through time.

Studies in the second group (Figure 3b – *stochastic – static* approaches) use similar ecological methods to the previous group but represent climate uncertainty and natural variability by using ensembles informed by several downscaled GCM projections or stochastic approaches. However, these approaches are still focused on long-term impacts and may overlook ecosystem interactions that could influence assessment outcomes. The information content in these approaches is dominated by variability in model inputs. This account of input uncertainty means the relative impacts of climate change and climate variability can be distinguished, but response models may not be sophisticated enough to represent the impacts. Unlike the first group these approaches provide a distribution or range of possible impacted modelling outcomes, but they only consider uncertainty in climate projections and not the dynamics of environmental response.

In contrast, studies in the third group (Figure 3c – *deterministic – dynamic* approaches) use sequence-dependent approaches to represent ecological condition, but single climatic sequences to represent hydrology. These approaches consider interactions with other environmental variables or feedbacks and can capture the sensitivity to extreme events. This enables impacts to be assessed in terms of changes to the frequency of different conditions in a manner that captures the dynamics of environmental responses. However, these methods are not coupled with exploration of uncertainty in the input data that could substantially change the outcomes, such as those related to the likely changes in the frequency and variability of climatic extremes. This means approaches here are less able to differentiate between climate change and climate variability.

Only the fourth group (Figure 3d – *stochastic – dynamic* approaches) can robustly simulate event-based extreme events and represent the sensitivity of ecosystem interactions to temporal sequences. These studies accommodate ecological dynamics and consider input uncertainty mainly using stochastic approaches. Modelled outcomes provide a distribution of environmental responses that represents the combined impact of climate uncertainty and natural variability. This ability to capture the dynamics of environmental response allows future threats to be compared to the range of behavior experienced under historic conditions. Accordingly, these characteristics mean such studies are good starting points for future assessments that seek to understand the vulnerability of environmental systems to climate change and climate extremes, even though none of them were specifically focused on this in their primary research question.

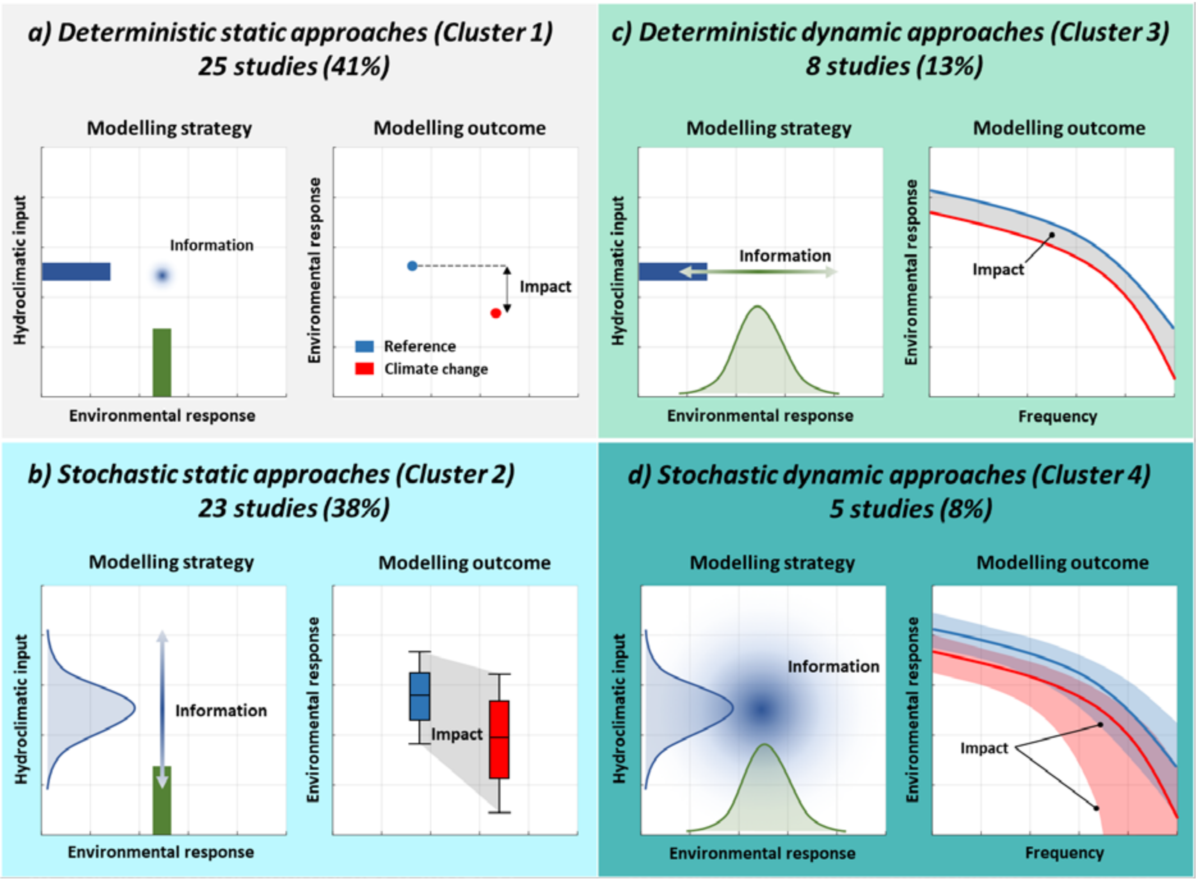


Figure 3. Combinations of hydrological and ecological methods used in climate change impact assessments on freshwater ecosystems based on the clusters shown in Figure 2. Studies are grouped based on their separate methodologies for modelling the hydroclimatic input and environmental response (or exposure and sensitivity, respectively, as defined by Dawson et al., (2011)). Hydroclimatic input and environmental response can be represented by a single value or distribution as illustrated in "modelling strategy." Information content is then the intersection of exposure and sensitivity (which is an analogue of the scope of vulnerability in the absence of adaptive capacity). Impact is the total change attributable to climate change. This impact may be single distance, or a range reflecting uncertainty, and it can be evaluated over one or multiple levels of environmental response using static or dynamic approaches, respectively.

4.1 REVIEW OUTCOMES

Approaches of high complexity with respect to both hydroclimatic inputs and environmental responses are not widely used (*stochastic – dynamic* approaches are used in fewer than 10% of studies). However, this is the only combination of approaches that can accommodate the hydroclimatic and ecological factors of greatest importance, namely: the ability to differentiate between climate change and natural variability (Horne et al., 2019; Nathan et al., 2019), the assessment of vulnerability to event-based threats, and the accounting for ecological feedbacks and non-linearities (Anderson et al., 2006; Tonkin et al., 2019). Using *stochastic – dynamic* approaches is more likely to provide sound predictions under various sources of non-stationarity. These methods are also able to simulate environmental interactions, and hence are more useful for testing mitigation or adaptation scenarios. For example, different management scenarios can be compared based on their ability to rapidly produce desirable ecosystem outcomes or to offer marginal benefit by buffering against the impacts of extreme or cumulative events (Horne et al., 2017). This is especially relevant when active or adaptive management forms part of proposed solutions, since these must respond to specific time-varying conditions. However, when comparing these approaches against simpler ones, it must be recognized that they have large data requirements, high demand for institutional capability and technical skills, and necessitate more computational and financial resources. They also are more suited to local scales due to the modelling complexity and detail required. Thus, care needs to be taken when using them for highly mobile species such as those that migrate or disperse across large ranges.

Current practice is weighted toward assessment of direct climate change impacts over long time periods as evidenced by the 79% of studies that use time averaged response models (*deterministic – static* and *stochastic – static* approaches). This is consistent with previous studies of climate impact assessments (Chapman et al., 2014) and flow-ecology relationships (Wheeler et al., 2018). These simple approaches are useful, as they typically have relatively low data requirements (or use published accessible global datasets) and can be rapid to implement. They may be suitable when data availability and resources are low, river systems are unregulated and there is some confidence in the direction, magnitude and dimensions of future climate changes. Simpler methods may have historically extrapolated better across larger scales, but future uncertainties in precipitation and hydrological response mean that alternative approaches that better incorporate variability, uncertainty and dynamic responses should be used (Brown et al., 2012; Horne et al., 2019).

Half of all studies use approaches that do not adopt a comparable degree of complexity to represent hydrological and ecological responses to climate change (*stochastic – static* and *deterministic – dynamic* approaches), i.e. hydroclimatic input and environmental response differ in terms of the type of data and assumptions used. These approaches are not well suited to assessing the impacts of climate change since they risk:

- Inefficiency – typically *stochastic – static* approaches. Ensemble or stochastic approaches capture projected climate changes; however, they do not fundamentally alter the outcomes of the assessment because simple linear response models are used to derive the ecological predictions or to characterize the adopted historic dependencies; or
- Overconfidence – typically *deterministic – dynamic* approaches. Comprehensive ecological response models consider the important dynamics and interactions with climate; however, they are not exposed to a range of plausible climate futures of possibly differing probabilities and extremes that produce different outcomes.

We note that the categorization of methods presented here is specifically concerned with the ability of approaches to give similar account to the aleatory uncertainty involved in assessing the impacts of natural variability and climate change. We have not considered the relative accuracy or defensibility of the different methods to simulate the hydrological or ecological processes of most interest. Such a comparison would require an assessment of the epistemic uncertainty involved in model parameterization and model structure, an analysis that is heavily dependent on the nature of the available data and performance measures of most relevance to the individual studies. It is expected that the hydrological and ecological models are selected to provide an appropriate match between model complexity and information content – that is, that the models fully exploit the available data without suffering from over-parameterization – and the degree to which the hydrological and ecological models provide comparable treatment of aleatory uncertainty is just one aspect of the broader challenge of model selection.

5.1 HOW DO DIFFERENT MODELLING STRATEGIES AFFECT THE ASSESSMENT OUTCOME?

To illustrate the differences in the four alternate modelling approaches, we provide a case study for the health of a native Australian riparian tree species, river red gum *(Eucalyptus camaldulensis)* under climate change. The case study explores the incremental differences in information content of the outcome of assessments resulting from the application of all four approaches to the river red gum forest in the Ovens River catchment, Victoria, Australia. The case study uses data and methods previously published in Wang et al. (2017), but reframes results to show outcomes from the four approaches. By using four combinations of hydrological and ecological approaches, we mimic the different approaches in Figure 3. These results should be interpreted by contrasting the information in the outcomes rather than specific detail in the underlying models and quantitative outcomes. Additional detail on methods and model diagnostics can be found in Wang et al. (2017), but we have also included an extended methods description in supplementary materials S3. To apply the four different approaches, two broad approaches are required to generate hydrological data, along with two broad methods for modelling ecological responses. These are then combined.

Hydrological impacts are assessed using deterministic and stochastic methods. The former based on factoring the observed precipitation record by a GCM change-signal, while the latter employs 50 replicates of future climate sequences with a consistent change in mean annual precipitation. Ecological responses are modelled using a static and a dynamic model. The static model uses a simple metric based on a seasonal flow threshold that correlates with river red gum forest condition to compare current and projected climate change scenarios. The dynamic response model is constructed using a state-transition model to explicitly predict ecological condition through time based on the sequence of hydrological inputs (Bond et al., 2018; Overton et al., 2014), where condition at a given point in time depends on its initial condition and the sequence of flows over a critical period.

The type of information in assessment outcomes are markedly different across the four combinations of methods (Figure 4). The first two methods (Figure 4a and b) are static and focused on long-term impacts related to changes in behavior of floodplain inundation; the first method represents this change as a shift in the average frequency of inundation over the simulation period, whereas the second expresses the impact relative to the range of behavior experienced under baseline conditions (or natural climatic variability). The third method (Figure 4c) provides more information on the changes in ecosystem condition by tracking ecological response through time, but like a) there is only a single average prediction for each state in the model. The final approach (Figure 4d) can inform how climate change and climate variability combine to threaten the forest, and model responses in a way that considers sensitivity to extreme events and sequences.

The *deterministic – static* approach, (Figure 4a) shows a reduction in the flow metric from 35% to 28% annual exceedance. In contrast, the *stochastic – static* approach (Figure 4b), predicts a similar median reduction in the flow metric. However, more severe impacts represented by the 5th or 95th percentiles in current and future conditions indicate that under natural variability the change in flow metric could be markedly higher. However, reference to changes in a simple flow metric tells us little about how different sequences of hydrological events across multiple years affect the condition of the forest. The *deterministic – dynamic* approach (Figure 4c) begins to give an appreciation of the severity of impacts by reporting ecological states based on species phenology captured in the state-transition model. However, this is still from a fixed sequence of events derived from historical conditions, to which the employed (dynamic) response model is now sensitive. The *stochastic* –

dynamic approach (Figure 4d) shows that in almost all cases use of the historic sequence led to optimistic predictions of ecological outcomes compared to the range suggested by the stochastic replicates. In fact, the historic record was among the best 5% of replicates in terms of achieving "good" ecological condition under climate change. The median results from this approach suggest much more dire outcomes are possible, with the amount of time that the forest is in "critical" condition rising from 7% to 51% of years.

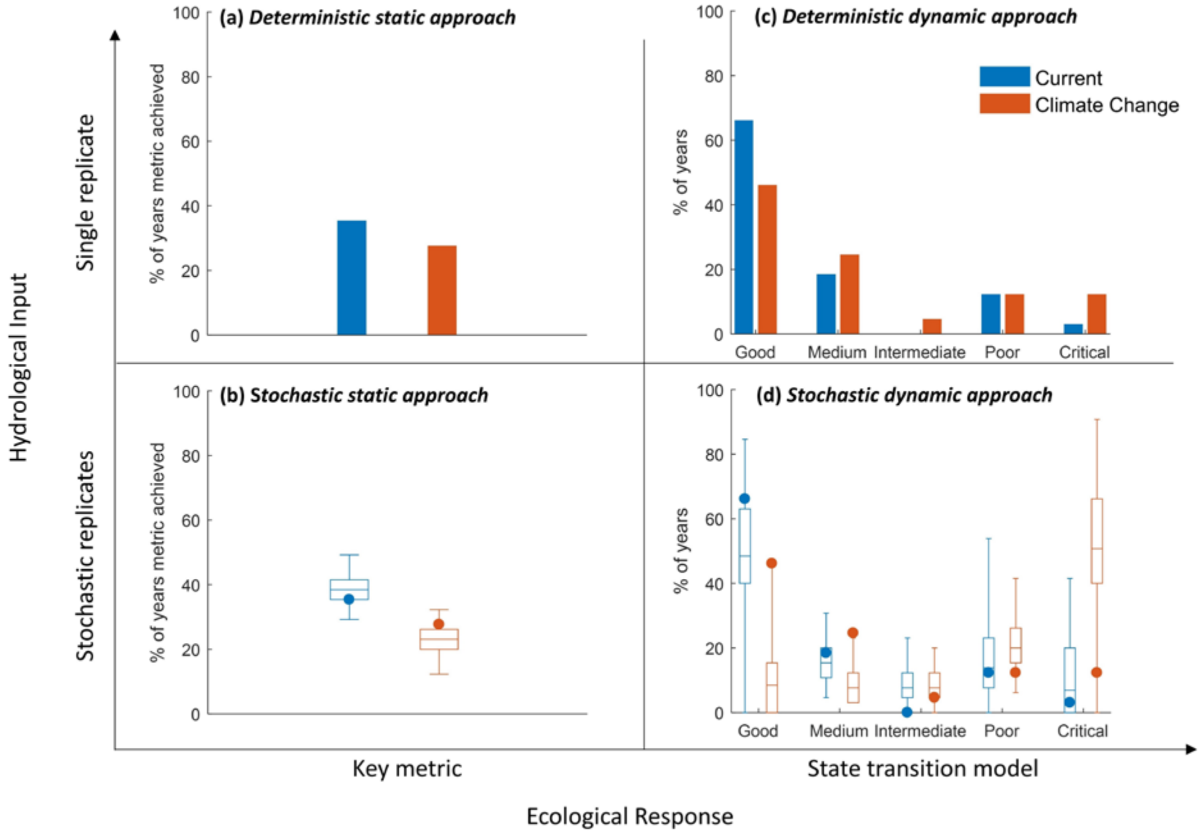


Figure 4. Climate change impact assessment for river red gum forest in the Ovens River catchment, Australia, following four separate modelling strategies. (a): key flow metric as ecological response with single sequence of perturbed hydrology as inputs (*deterministic static approach*), (b): flow metric as response with 50 stochastic replicates of possible future hydrological sequences (*stochastic static approach*), (c): state-transition model that tracks ecological condition through time with single perturbed historical time series (*deterministic dynamic approach*), (d): state-transition model with 50 stochastic replicates of future hydrology (*stochastic dynamic approach*). In (b) and (d), the dots show the equivalent result from methods (a) and (c). Box plots in (b) and (d) show median results, and upper and lower 5th and 25th exceedance percentiles.

Conclusion

Most current ecohydrological studies that examine climate change risks to freshwater ecosystems use methods that inadequately combine key elements of the three disciplines used to model risk. Generally, these studies use simplified methods (*deterministic – static*) or approaches lacking comparable complexity (*deterministic – dynamic* and *stochastic – static*), despite the availability of more integrated ecohydrological methods. The mismatch between the levels of complexity of hydrological and ecological response may be influenced by groups with expertise in a specific discipline. However, a robust understanding of freshwater ecosystem impacts under climate change is maximized by adopting strongly integrative approaches that employ methods of comparable complexity. This avoids modelling effort being dominated by hydrological or ecological detail at the expense of the other and is consistent with an ecohydrological perspective that is interdisciplinary, rather than multidisciplinary. Better utilization of interdisciplinary expertise in future studies can more comprehensively assess and understand climate change impacts and future risks. Due to their underrepresentation in existing literature, we recommend more effort be directed to *stochastic – dynamic approaches* to better understand impacts of the full range of threats to rivers in an uncertain future (Horne et al., 2019). However, research is also needed to improve their scalability.

The large uncertainties in predictions of hydroclimatic change and how freshwater ecosystems will respond is likely to persist into the next decades (Maslin & Austin, 2012). There are also many confounding factors other than flow and temperature, including sediment, nutrients and water quality that will influence freshwater ecosystem response to climate change (Poff, 2018). But acknowledging model limitations and incorporating concepts of uncertainty within management will assist in connecting predictions to useful management responses to climate change (Poff et al., 2016). There is significant potential to improve our current understanding of climate change risks to freshwater ecosystems by better capitalizing on and linking the advances currently being made in isolation in the disciplines of hydrology and ecology.

Funding Information

This study was funded by the Australian Research Council (ARC Linkage Project LP170100598), Australian Commonwealth Government under a Research Training Program Scholarship, and several partner agencies including the Department of Environment, Land, Water and Planning; the Victorian Environmental Water Holder and the Bureau of Meteorology. Avril Horne was funded by Australian Research Council DECRA DE180100550.

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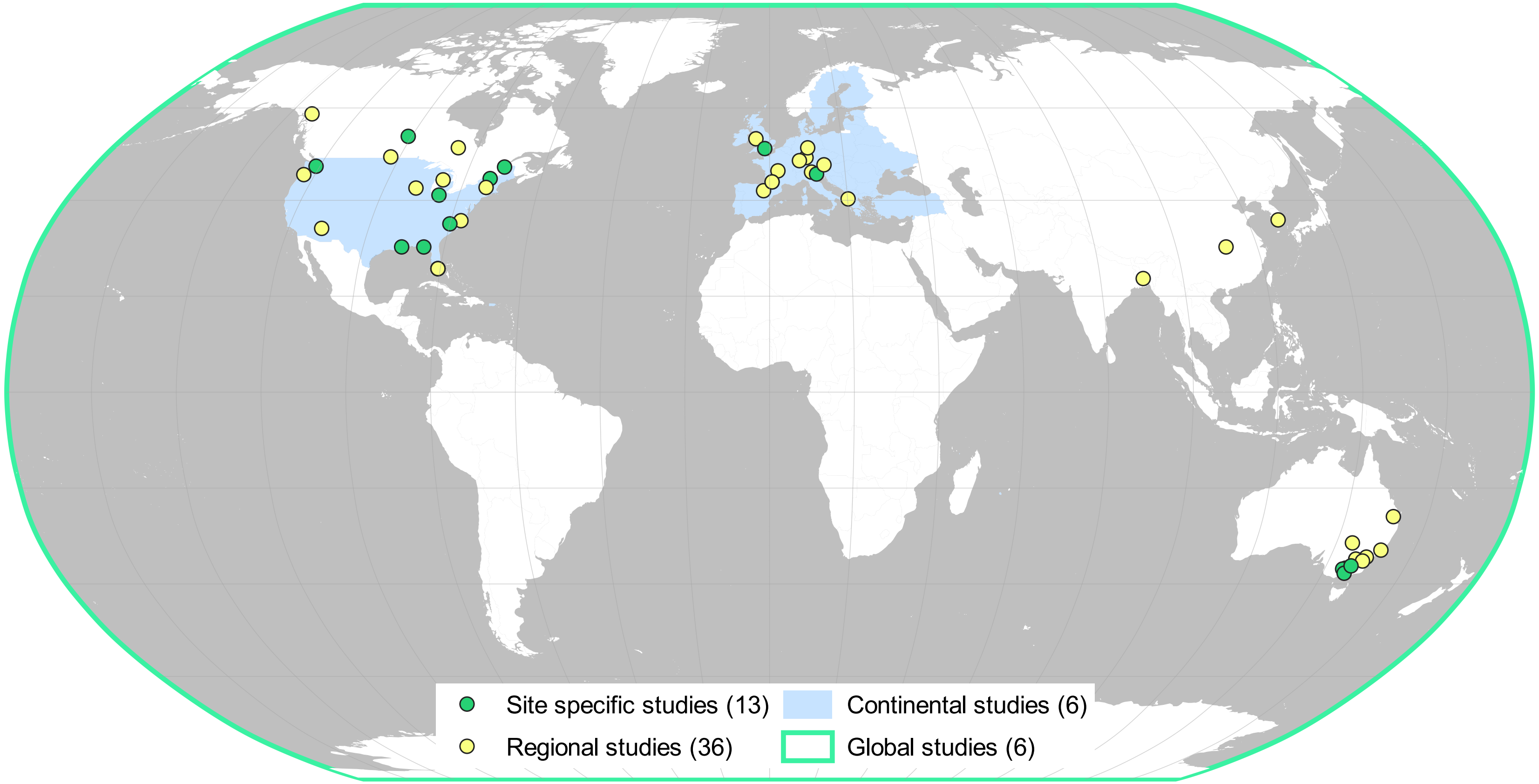
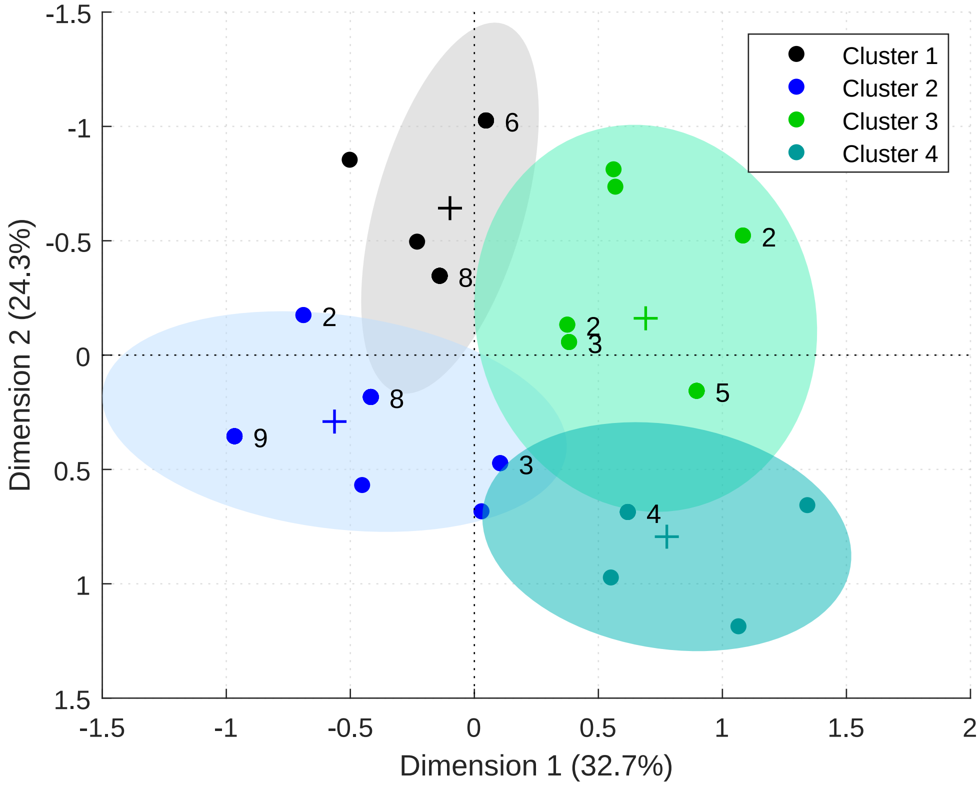
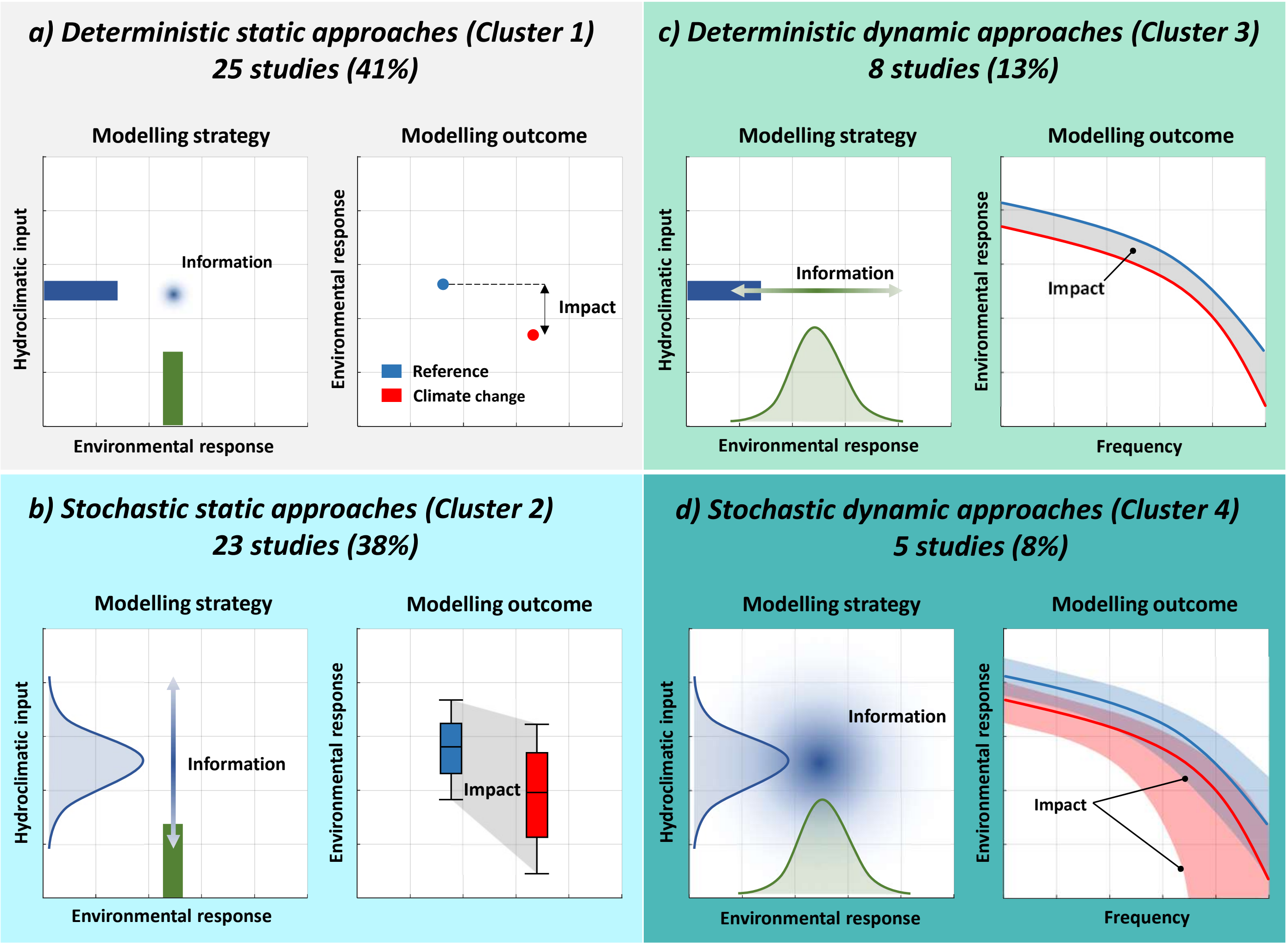
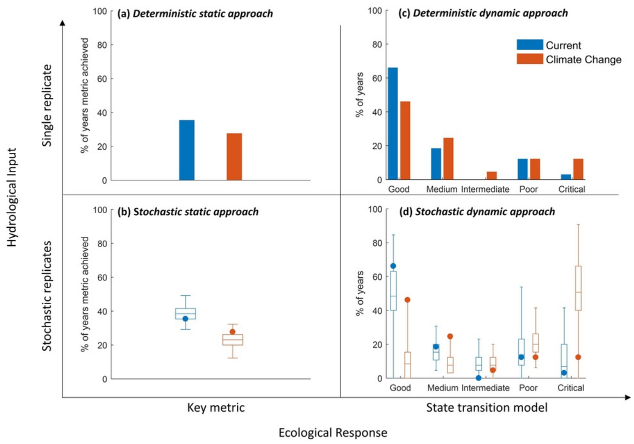
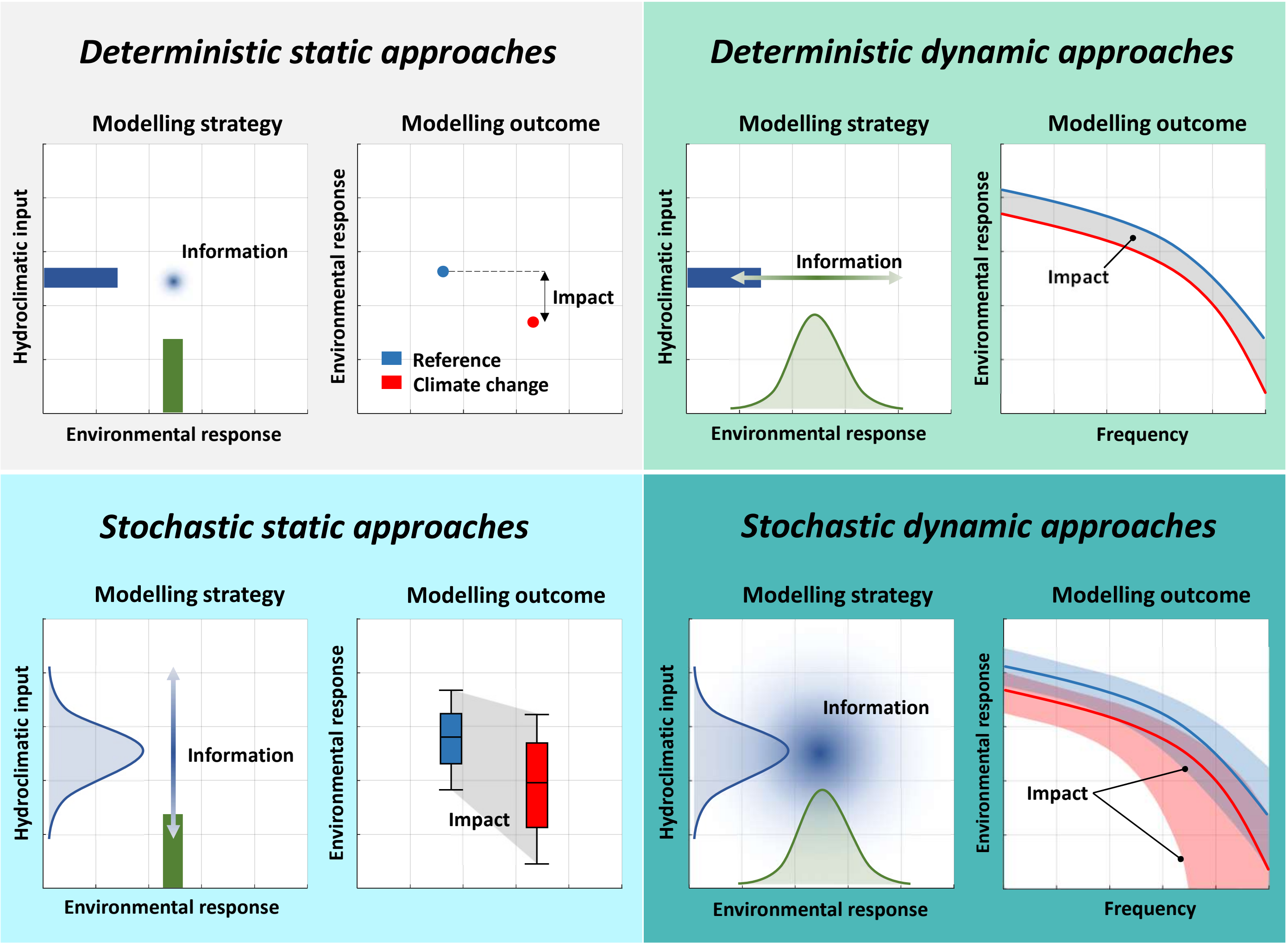

Site specific studies (13)
Regional studies (36)
Continental studies (6)
Global studies (6)


Cluster 1
Cluster 2
Cluster 3
Cluster 4
Dimension 2 (24.3%)
Dimension 1 (32.7%)
-1.5
-1
-0.5
0
0.5
1
1.5
2
6
8
2
9
3
5
4


a) Deterministic static approaches (Cluster 1)
25 studies (41%)
Modelling strategy
Modelling outcome
Hydroclimatic input
Information
Environmental response
Environmental response
Impact
Reference
Climate change
c) Deterministic dynamic approaches (Cluster 3)
8 studies (13%)
Modelling strategy
Modelling outcome
Hydroclimatic input
Information
Environmental response
Environmental response
Impact
Frequency
b) Stochastic static approaches (Cluster 2)
23 studies (38%)
Modelling strategy
Modelling outcome
Hydroclimatic input
Information
Environmental response
Environmental response
Impact
d) Stochastic dynamic approaches (Cluster 4)
5 studies (8%)
Modelling strategy
Modelling outcome
Hydroclimatic input
Information
Environmental response
Environmental response
Impact
Frequency



WCC_692_Figure 4.jpg


Deterministic static approaches
Modelling strategy
Hydroclimatic input
Information
Environmental response
Modelling outcome
Environmental response
Impact
Reference
Climate change
Deterministic dynamic approaches
Modelling strategy
Hydroclimatic input
Information
Environmental response
Modelling outcome
Environmental response
Impact
Frequency
Stochastic static approaches
Modelling strategy
Hydroclimatic input
Information
Environmental response
Modelling outcome
Environmental response
Impact
Stochastic dynamic approaches
Modelling strategy
Hydroclimatic input
Information
Environmental response
Modelling outcome
Environmental response
Impact
Frequency