Improving the predictive power of spatial statistical models of stream macroinvertebrates using weighted autocovariance functions

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ARTICLE INFO

ABSTRACT

Spatial statistical stream-network models are useful for modelling physicochemical data, but to-date have not been fit to macroinvertebrate data. Spatial stream-network models were fit to three macro-invertebrate indices: percent pollution-tolerant taxa, taxa richness and the number of taxalacking out-of-network movement (in-stream dispersers). We explored patterns of spatial autocorrelation in the indices and found that the 1) relative strength of in-stream and Euclidean spatial autocorrelation varied between indices; 2) spatial models outperformed non-spatial models; and 3) the spatial-weighting scheme used to weight tributaries had a substantial impact on model performance for the in-stream dispersers; with weights based on percent stream slope, used as a surrogate for velocity because of its potential effect on dispersal and habitat heterogeneity, producing more accurate predictions than other spatial-weighting schemes. These results demonstrate the flexibility of the modelling approach and its ability to account for multi-scale patterns and processes within the aquatic and terrestrial landscape.

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Software availability

Name of software: SSN
Developer: Jay Ver Hoef and Erin PetersonDr Erin Peterson, CSIRO Division of Computational Informatics, EcoSciences Precinct, PO Box 2583, Brisbane, Qld, Australia, 4001.
Ph: +61 7 3833 5536, Email: support@spatialstreamnetworks.com
First year available: 2013
Hardware required: Standard laptop or desktop, with Windows or Linux OS
Software Required: R statistical software
Availability and Cost: Available for free online at http://cran.r-project.org/web/packages/SSN/index.html
Program language: R
Size: 5.72 MB
Name of software: STARS (Spatial Tools for the Analysis of River Systems)
Developer: Erin PetersonDr Erin Peterson, CSIRO Division of Computational Informatics, EcoSciences Precinct, PO Box 2583, Brisbane, Qld, Australia, 4001.

Ph: +61 7 3833 5536, Email: support@spatialstreamnetworks.com
First year available: 2013
Hardware required: Standard laptop or desktop, with Windows OS
Software Required: ESRI ArcGIS version 9.3.1, with ArcInfo License
Availability and Cost: Available for free online at http://www.fs.fed.us/rm/boise/AWAE/projects/SpatialStreamNetworks.shtml
Program language: Python version 2.5
Size: 135 KB
Name of software: FLoWS (Functional Linkage of Waterbasins and Streams)
Developer: David M. TheobaldConservation Science Partners, 11 Old Town Square, Suite 270, Fort Collins, CO, USA, 80524
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Ph: +61 7 3833 5536, Email: Erin.Peterson@csiro.au
First year available: 2006
Hardware required: Standard laptop or desktop, with Windows OS
Software Required: ESRI ArcGIS version 9.3.1, with ArcInfo License
Availability and Cost: Available for free online at http://www.fs.fed.us/rm/boise/AWAE/projects/SpatialStreamNetworks.shtml
Program language: Python version 2.5
Size: 556 kB

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1. Introduction

Spatial autocorrelation represents the degree of spatial dependency in measurements collected in geographic space. It is an inherent characteristic of data collected in stream and river environments, where longitudinal and lateral connectivity, nested catchments, and broad-scale topographic and climatic gradients produce multiple, multi-scale patterns of spatial autocorrelation (Peterson et al., 2013). Spatial autocorrelation is often viewed as problematic; when traditional, non-spatial models are used to analyse spatially correlated data, it can lead to biased parameter estimates and invalid statistical inferences (Legendre, 1993). Alternatively, spatial statistical methods, such as geostatistical modelling (i.e. universal kriging) can be used to model spatially correlated data, account for influential covariates, and generate predictions with valid estimates of uncertainty at non-sampled locations (Cressie, 1993). These methods have recently been extended to represent the unique spatial relationships in stream networks (Ver Hoef et al., 2006; Ver Hoef and Peterson, 2010), which include the branching structure of the dendritic network, flow connectivity, the directionality of flow, and the 2-D terrestrial environment within which the network is embedded (Peterson et al., 2013). This provides a flexible modelling framework that can be used to account for *both* in-stream and Euclidean patterns of spatial autocorrelation in a single model (Peterson and Ver Hoef, 2010). Previous studies have been somewhat limited because proximity is based solely on Euclidean distance (e.g. Bonada et al., 2012; Shurin et al., 2009) or in-stream distance is used to study spatial relationships along a single, non-branching channel (e.g. Grenouillet et al., 2008).

Spatial stream-network models have been successfully applied to a number of physicochemical indicators, including temperature (Isaak et al., 2010; Jones et al., 2013; Ruesch et al., 2012), nitrate (Gardner and McGlynn, 2009) and dissolved oxygen (Cressie et al., 2006), as well as *E. coli* measurements (Money et al., 2009) and a modelled fish index (Peterson and Ver Hoef, 2010). There is thus a growing body of evidence suggesting that these methods are useful for up-scaling site-based measurements collected on stream networks to provide a more continuous perspective of stream characteristics (Cressie et al., 2006; Isaak et al., 2010; Money et al., 2009; Peterson and Ver Hoef, 2010; Ruesch et al., 2012), which is crucial for the spatial prioritization of management actions (Fausch et al., 2002). In contrast to many physicochemical variables, macroinvertebrate community indices are often strongly related to a combination of local-scale physicochemical and biological conditions (Downes et al., 1993; Minshall, 1984; Sawyer et al., 2004), which suggests that spatial autocorrelation may not be as prevalent in these data. Yet, many of these local-scale characteristics are thought to be influenced by the interaction of broader-scale network structure, geomorphology, and disturbance regimes (Benda et al., 2004), as well as, water chemistry and land use (Kratzer et al., 2006). Thus, it remains unclear whether this relatively new family of spatial statistical models will be equally suitable for predicting biological variables, such as macroinvertebrate indices, commonly used in broad-scale monitoring programs (e.g. Munné and Prat, 2009; Smith et al., 2011).

Another important aspect of modelling spatial relationships in stream networks is allowing for potential disjunctions at stream confluences (Peterson et al., 2013). Confluence zones (i.e. stream junctions) are biologically important elements of streams (Illies, 1961; Rice et al., 2006; Statzler and Higler, 1986), and have been linked to changes in macroinvertebrate densities (Katano et al., 2009; Rice et al., 2001). For example, Kiffney et al. (2006) found that small streams funnel materials such as nutrients and woody debris into wider main stem channels, and that this produced peaks in macroinvertebrate densities downstream of confluences; likely due to increased productivity and habitat complexity. Small, steep headwater streams may also be important drivers of downstream food webs, through the entrainment of leaf litter, in northern hemisphere streams with deciduous riparian vegetation (Cummins, 1974; Vannote et al., 1980). However, Bunn et al. (1999) showed that algae, rather than inputs of leaf litter, were the main driver of macroinvertebrate food webs in northern Queensland, Australia, where riparian vegetation tends to be evergreen. Furthermore, while macroinvertebrates in the northern hemisphere are often productive in small, steep headwater streams and drift downstream (Meyer et al., 2007), Australian studies have found that drift is usually related to death or catastrophic events (e.g. flooding) and may not be important for dispersal (Kerby et al., 1995). Although there may be uncertainty about what is causing disjunctive biological conditions at confluences, it is clear is that those drivers may be substantially different than those influencing physicochemical discontinuities at confluences.

Spatial stream-network models account for potential disjunctions at confluences using a spatial-weighting scheme that determines the degree of influence that each converging stream segment has on downstream locations (Peterson and Ver Hoef, 2010). To date, a spatial-weighting scheme based on Shreve's stream order (Shreve, 1966) has been used to generate spatial stream-network models (Cressie et al., 2006; Garreta et al., 2010), as well as spatial weights based on catchment area (Gardner and McGlynn, 2009; Isaak et al., 2010; Peterson et al., 2006; Peterson and Ver Hoef, 2010; Ruesch et al., 2012). Note that, Shreve's stream order has been used because it is additive, but Strahler's stream order (Strahler, 1957) could also be used. Catchment area and stream order have been used as surrogates for flow volume, a conceptually intuitive approach for water quality, temperature and fish because of the strong effects of longitudinal connectivity on these variables. However, catchment area and Shreve's stream order may not be as relevant for macroinvertebrates, which are strongly affected by local characteristics (e.g., Downes et al., 2000). In addition, there a variety of macroinvertebrate metrics including trophic and dominance indices, diversity, richness, and composition metrics, as well as, indices designed to represent feeding strategies, pollution tolerances, and habitat measures (Barbour et al., 1999). There are also numerous ways to construct indices within these categories and each index will have a metric-specific response to environmental perturbation. It is therefore unlikely that a single spatial-weighting scheme will be suitable in all cases given the broad range of physicochemical and biological processes affecting macroinvertebrate distribution and the diversity of indices available.

In this analysis, we used spatial stream-network models to explore patterns of spatial autocorrelation in a suite of macroinvertebrate indices collected in the wet tropics of Queensland, Australia. In particular, we wanted to test whether 1) accounting for spatial autocorrelation improved the predictive power of the models fit to biological indices; 2) patterns of spatial autocorrelation differed depending on the macroinvertebrate index used; and 3) the choice of spatial-weighting scheme affected the predictive power of the spatial model.

2. Materials and methods

2.1. Data and study area

Macroinvertebrate data were collected at 60 sites in July and September 2009 (austral winter) in a sub-catchment of the Tully River Basin in the Wet Tropics bioregion of Queensland, Australia (Fig. 1). We collected data within a single season because there is little evidence of seasonal variability in Australian macroinvertebrate indices (Chessman et al., 1997; Marshall et al., 2001), which do not receive seasonal pulses of litterfall and subsequent increases in nutrients and productivity (Abelho and Graca, 1996; Boulton and Brock, 1999). The climate in the Tully

River Basin is characterized by humid, wet summers and mild, relatively dry winters (Kroon, 2008). Elevation in the sub-catchment ranges from approximately 15 m–1100 m, with upper elevations dominated by tropical rainforest, primarily in conservation zones such as national parks and state forests. Land use at lower elevations is mainly sugarcane agriculture, accounting for approximately one quarter of the total sub-catchment area. To our knowledge, there are no significant point sources of pollution in the sub-catchment and the topology of the stream network is relatively unmodified by stormwater drainage systems.

Sampling was primarily focussed around stream confluences, with two samples located approximately 50 m upstream of each confluence and one sample approximately 50 m downstream. A modified version of the Generalised Random-Tessellation Stratified (GRTS; Stevens and Olsen, 2004) survey design was used to select confluences for sampling. Two attractive properties of GRTS are that it 1) is probability-based and 2) provides spatial balance in the survey sites across the study area (Fig. 1). We also modified the GRTS design to ensure that sites provided uniform coverage of fine-scale (<500 m) and medium-scale (1–10 km) hydrologic and Euclidean distances (Appendix A).

Macroinvertebrates were sampled with a dip net from 10 m of edge habitat (within 0.5 m of the stream bank) using short sweeps perpendicular to the bank. The samples were live-picked in the field (maximum picking time of 60 min), and subsequently identified in the laboratory. Please see DNRM (2001) for additional details about the field protocol. Macroinvertebrates were identified to family level, with the exception of Chironomidae, which were identified to sub-family level. In addition, Porifera, Nematoda, Nemertea, Oligochaeta, Acarina, and Ostracoda, Copepoda, and Cladocera were not identified further. Additional details about the taxonomy used to calculate all three indices can be found in Chessman (2003).

We calculated three indices from the macroinvertebrate counts. Observed versus expected metrics based on percent pollution-tolerant taxa (% tolerant) and total macroinvertebrate taxa richness (total richness) are both used by the Queensland Stream and Estuary Assessment Program (SEAP) to monitor and assess condition and trend in aquatic ecosystems (Negus et al., 2009). However in this study, we focused on the metrics themselves, rather than standardising them using reference condition. Percent tolerant is based on the Stream Invertebrate Grade Number Average Level version 2 (SIGNAL2.IV) index of pollution tolerance (grades 1–10; Chessman, 2003), and represents the proportion of taxa with a SIGNAL2.IV grade $\leq$ 3 (highly pollution-tolerant families). SIGNAL scores are used to assess the cumulative anthropogenic impacts on macroinvertebrates, including those related to catchment land use, riparian composition and condition, channel condition and form, and in-stream habitat (Chessman et al., 1997). Note that, % tolerant scores are expected to be higher at sites experiencing negative anthropogenic impacts. Total richness is a commonly used macroinvertebrate metric (e.g. Borja et al., 2009; Mac Nally et al., 2011; Smith et al., 2011), but decreases in richness are not guaranteed to occur at anthropogenically impacted sites (Koperski, 2011). As a result, the SEAP program assesses site condition based on the expected range of richness (Dobbie and Negus, 2013). Lastly, we calculated the number of families found at each site that lack the capacity for active, aerial out-of-network movement at all life stages (in-stream dispersers) because dispersal traits have been found to play an important role in metacommunity dynamics of stream macroinvertebrates (Brown and Swan, 2010).

2.2. Covariates

The majority of potential covariates were calculated in ArcGIS version 9.3.1 (ESRI, 2009) based on remotely derived datasets (see Appendix A, Table A.2). Areal percentages of land use and forest were calculated at three spatial scales (Fig. 2): the catchment, riparian buffer, and site buffer scales. The 'catchment' scale includes the entire area that drains to the survey site (Fig. 2a), while the 'riparian buffer' represents the area within 50 m of the stream and 1 km upstream from each site (Fig. 2b). 'Site buffers' with a 200 m circular radius centred on the sample sites were also created (Fig. 2c). In addition, potential covariates were calculated for entire stream segments (i.e. line segments) in the geographic information system (GIS; Fig. 2d), summarised over a 100 m reach (Fig. 2e), or extracted for each site (Fig. 2f); hereafter referred to as the 'segment', 'reach', and 'point' scales, respectively. We calculated point-scale variables for air temperature and rainfall because we were interested in capturing the potential climatic influence of different sample dates. We also considered a categorical variable indicating whether the stream orientation is East/West (45° to 135° and 225° to 315°) or North/South (135° to 225° and 315° to 45°) because stream orientation has been linked to seasonal differences in light intensities (Davies et al., 2006). Finally, a number of physicochemical variables collected within and adjacent to the stream were also considered, as well as the experience level of the field worker who picked the sample. Please see Appendix A for a full description of all the potential covariates and the GIS processing steps used to derive them.

2.3. Covariance models and spatial-weighting schemes

Two classes of autocovariance models have been designed for use in stream networks: the 'tail-down' (TD) and 'tail-up' (TU) models (Ver Hoef and Peterson, 2010). The models are based on a moving-average construction and use hydrologic (i.e. in-stream), rather than Euclidean distance (Fig. 3). Spatial correlation between sites occurs when their moving-average functions overlap; as such, the TU and TD models differ in the way they represent flow-connected and flow-unconnected spatial relationships in the spatial stream-network model. Two locations have a flow-connected relationship if water flows from an upstream location to a downstream location. In contrast, a flow-unconnected relationship exists when two locations share a common junction downstream, but are not flow-connected. The moving-average function for the TD models points in the downstream direction and so spatial correlation is permitted between both flow-connected and flow-unconnected locations (Fig. 3a). In contrast, the moving-average function for the TU model points upstream and as a result, spatial correlation is restricted to flow-connected locations (Fig. 3b). Spatial weights (described in more detail below) are also used in the TU model at stream confluences, which allows more weight to be allocated to data on tributaries thought to have a stronger influence downstream. In addition, a spatial stream-network model may be fit using a mixed-covariance structure, which is based on a combination of two or more autocovariance models (Peterson and Ver Hoef, 2010).

A covariance mixture may be composed of any combination of models, including a traditional covariance structure based on Euclidean distance, as well as the TU and TD autocovariance models. When a single autocovariance function is fit to the data, three parameters are estimated: the nugget effect, the partial sill, and the range parameter. The nugget effect captures variability that occurs at a scale finer than the
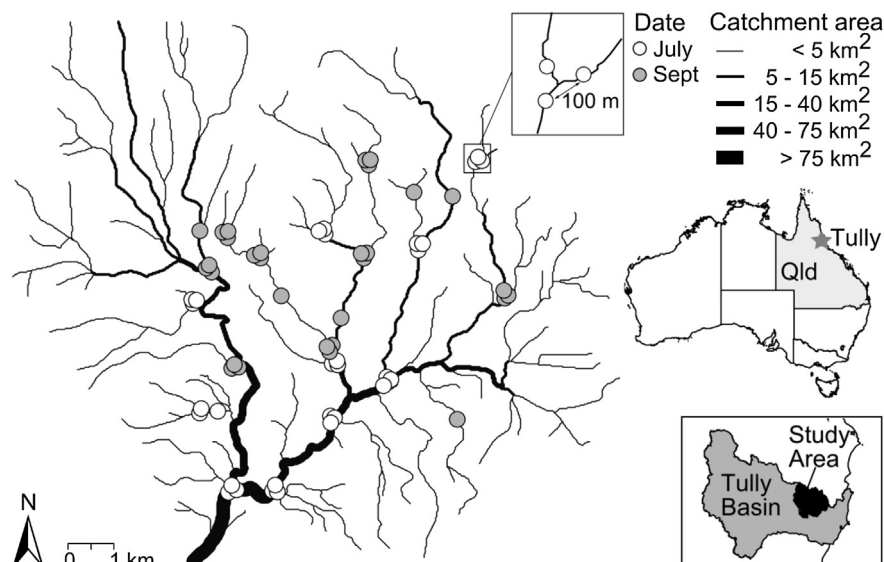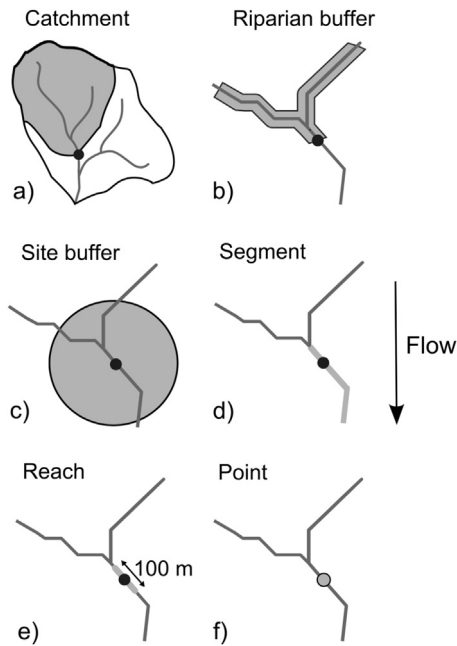

Fig. 1. Macroinvertebrate sample site locations in a sub-catchment of the Tully River Basin, Queensland (Qld), Australia.

Fig. 2. Scales at which covariates were calculated: a) the catchment represents the entire area that drains to a site, while the b) riparian buffer includes areas within 25 m either side of the stream, extending 1 km upstream and the c) site buffer represents an area of 200 m radius centred on the site. The d) segment scale represents the geographic information system (GIS) line segment on which the site lies, while the e) reach scale extends along the GIS line segments for 50 m up and downstream of the sampling location. Variables at the f) point scale were extracted at the site location.

closest measurements, as well as measurement error (Cressie, 1993). The partial sill represents the variance of the autocorrelated process without the nugget effect, while the range describes how quickly autocorrelation decreases with distance (Cressie, 1993). In a covariance mixture, a partial sill and range parameter are estimated for each model, as well as, an overall nugget effect, and these parameters determine the relative influence that each component will have on the mixture (Ver Hoef and Peterson, 2010); so, there is no need to determine *a priori* which covariance models to include. The potential disadvantage to using a covariance mixture is that it increases the number of parameters that must be estimated. However, the influence of individual models can be assessed and components subsequently removed if they do not improve the predictive power of the model. Thus, the covariance mixture provides a flexible approach that can be used to capture complex and multi-scale spatial patterns often found in stream datasets (Peterson and Ver Hoef, 2010).

Spatial-weighting schemes for TU stream-network models are often based on catchment area, but can be calculated based on any ecologically relevant variable that is available for every line segment in a streams dataset. Here we define the line segment in terms of a GIS polyline feature, which is bounded by an upstream and a downstream node. The first step in calculating spatial weights at nodes is to
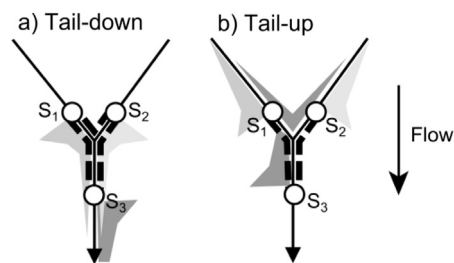
Fig. 3. The tail-up and tail-down autocovariance models are based on moving-average (MA) functions (shown in grey) and use hydrologic distance (dotted lines). Spatial autocorrelation occurs between locations when the MA functions overlap. (a) The tail-down model permits correlation between flow-connected (S_3 and S_1, S_3 and S_2) and flow-unconnected (S_1 and S_2) relationships, while the (b) tail-up model restricts correlation to flow-connected locations. The tail-up MA functions must be split at stream confluences using spatial weights to ensure that more influential segments receive a stronger weighting in the models.

calculate a measure of influence for each line segment on the segment directly downstream. We refer to this as the segment proportional influence (PI) because the segment PIs upstream from a node always sum to 1. The segment PIs ($0 \le w_k \le 1$) are calculated by dividing each segment's attribute (i.e. catchment area) by the cumulative sum of the attribute at its downstream node (Fig. 4a). The spatial weights between locations are then equal to the square root of the product of segment PIs for the set of all segments located in the path between them, $\prod_{k \in B_{s_i, s_j}} \sqrt{w_k}$ (Fig. 4b).

Spatial weights and the hydrologic distances needed for fitting spatial models to stream-network data were calculated using the Functional Linkage of Water basins and Streams (FLoWS; Theobald et al., 2006) and Spatial Tools for the Analysis of River Systems (STARS; Peterson and Ver Hoef, 2014) toolsets for ArcGIS version 9.3.1. Please see Appendix B for additional details about spatial modelling, the TU and TD autocovariance functions, and the formulation of the covariance mixture.

2.4. Exploratory analysis, model selection, and model evaluation

We used a variety of quantitative measures and graphical tools to learn about the data, as well as, inform model selection and evaluation. There is no one measure or set of measures suitable for evaluating all models; instead, the specific choices depend on the goal of the modelling exercise (Bennett et al., 2013). Our primary goal was to assess the predictive power of the models and the choices we made reflect that. Evaluation strategies for spatial linear models, such as the spatial stream-network models used here, are often (but not always) simple extensions of classical non-spatial linear models. We make a point of highlighting the differences in model selection and evaluation below, which include useful graphical tools, as well as methodological pitfalls associated with parameter estimation and evaluation criteria.

We used R version 2.14.0 (R Development Core Team, 2011) and the SSN package (Ver Hoef et al., 2014) to fit a suite of spatial stream-network models to each of the three response variables. We started by examining maps and histograms of the data, which included a continuous variable (% tolerant) and counts (total richness and in-stream dispersers). We also examined Torgegrams of the raw index data, which allow users to examine the semivariance between flow-connected and flow-unconnected pairs separately (Ver Hoef et al., 2014). We fit preliminary models to the data and examined the residuals using residual plots and QQ plots. These visual examinations of the data and model residuals indicated that it was appropriate to fit Gaussian models to the % tolerant and total richness indices, while a Poisson model was most suitable for the in-stream dispersers index (Appendix A).

We used a two-stage model-selection procedure to evaluate the models so that we could select the most suitable covariance structure, in addition to selecting covariates, which is often the sole focus of a model-selection strategy. The first stage involved selecting covariates using a backwards model-selection technique (see Appendix A for details). During this stage, the full covariance mixture was fixed and included the Mariah tail-up, linear-with-sill tail-down, and exponential Euclidean autocovariance models (Appendix B, Tables B.1 and B.2). Covariate selection was undertaken independently for each of the three macroinvertebrate indices and four spatial-weighting schemes (3 models × 4 spatial-weighting schemes) because 1) we expected different covariates to be significant in each model and 2) it was unclear whether the spatial-weighting scheme would affect the covariate selection.

We used a slightly different procedure for fitting and comparing the Gaussian and Poisson models in the first stage of model selection. Maximum likelihood (ML) was used to estimate parameters in the Gaussian models (% tolerant and total richness) so that we could use Akaike's Information Criterion (AIC; Akaike, 1974) for covariate selection, which helps to prevent over-fitting the model. We could not use AIC to compare in-stream disperser models because the SSN package implements Poisson models as pseudo-models (Ver Hoef et al., 2014) and as a consequence, a real likelihood is not produced. Given that we were unable to use AIC, we chose to estimate parameters in the Poisson model using restricted maximum likelihood (REML) because it is less biased than ML (Cressie, 1993). We used the root-mean-square-prediction error (RMSPE) for the observations and the leave-one-out cross-validation (LOOCV) predictions to compare Poisson models because 1) no assumptions about the distribution of the data or the residuals are required; 2) the RMSPE penalises large errors more heavily; and 3) the error statistic is in the same units as the data (Bennett et al., 2013). Note that, LOOCV was carried out by removing each data point in turn and refitting the model. However, all of the data points were used to estimate the covariance structure.

In the second stage of model selection we focussed on selecting the most suitable covariance structure and spatial-weighting scheme. Models were fit using the final set of covariates identified in the first stage of the model-selection procedure, with covariance mixtures based on every linear combination of TU, TD and Euclidean (EUC) autocovariance functions (7 linear combinations in total). Note that, covariates were fixed and the covariance structure varied in this stage of model selection. Four different autocovariance functions were tested for each model type; namely, the TU and TD spherical, exponential, Mariah, and linear-with-sill functions (Appendix B, Tables B.1 and B.2) and the Euclidean spherical, exponential, Gaussian, and Cauchy functions (Chilés and Delfiner, 1999). We also compared TU models constructed using four spatial-weighting schemes based on catchment area, Shreve's stream order (Shreve, 1966), percent slope for the segment, and equal weights (where
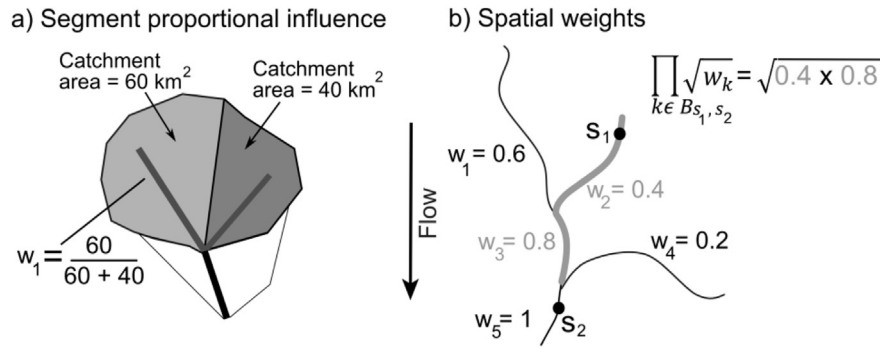
Fig. 4. (a) The segment proportional influence (PI), w_k, is calculated by dividing the segment's attribute (i.e. catchment area) by the cumulative sum of the attribute at its downstream node. (b) The spatial weight between any two flow-connected locations is equal to the square root of the product of the segment PI values found in the path between them, $\prod_{k \in B_{s_i, s_j}} \sqrt{w_k}$, excluding the segment where the downstream location lies, but including the segment where the upstream site resides.

converging stream segments are allocated equal weights). Although catchment area and Shreve's stream order are similar, we tested both measures because Shreve's stream order is computationally more straightforward to calculate (e.g. there is no need to delineate catchment boundaries). We also derived a new spatial-weighting scheme based on percent slope in the stream segment; hypothesizing that it might act as a simple surrogate for flow velocity and hydraulic forces close to the confluence, which have been shown to influence macroinvertebrate taxa richness, abundance, and community composition (Brooks et al., 2005). Equal weights were used to test whether the previous three spatial-weighting schemes have more predictive power than a null model that accounts for the branching structure of the network, but does not include additional information about segment characteristics. Every combination of covariance structure and spatial-weighting scheme resulted in a total of 424 possible autocovariance mixtures per response variable (7 covariance mixtures × 4 covariance models for each component × 4 spatial-weighting schemes for the TU model). Note that, we used REML for parameter estimation in this stage of model selection because ML may produce biased covariance parameter estimates (Cressie, 1993). Once the fitted covariance matrix had been generated using REML, it was used to estimate the fixed effects. This is referred to as "empirical" best linear unbiased prediction (Littell et al., 1996). In addition, a non-spatial model was fit to each of the three macroinvertebrate indices for comparison purposes, using the final set of covariates used in the spatial model.

We selected a final model for each response variable and spatial-weighting scheme combination using the RMSPE for the observations and the LOOCV predictions. We chose this evaluation metric because our main goal was to evaluate the predictive power of the models; thus, it made sense to use the data to characterise the model performance (Bennett et al., 2013). Note that, the RMSPE is proportional to the width of the model's prediction interval, and therefore cannot be compared between response variables without considering the measurement units and the order of magnitude of the response values. Therefore, we also calculated the percent difference in the RMSPE between the spatial models and their non-spatial counterparts. This allowed us to evaluate the effect of accounting for spatial autocorrelation on the predictive power of the models, as well as, compare the effect across models fit to different response variables. We also visually examined the relationship between the observed values and the LOOCV predictions using scatter plots and calculated the squared Pearson correlation coefficient (predictive r^2) values because it is a general metric of model performance that most scientists are familiar with (Bennett et al., 2013). Although these plots provide a way to visually examine the overall model fit, they are not inherently spatial. Therefore, we also generated maps showing the LOOCV predictions and prediction standard errors, which allowed us to evaluate spatial patterns in the model fit (e.g. Peterson and Urquhart, 2006).

Once we identified a final model, we examined the influence of each variance component (TU, TD, EUC, and nugget effect). In a spatial stream-network model, the covariance matrix can be partitioned into variance components based on the TU, TD, and EUC models, as well as the nugget effect, and the percent of residual variation described by each component calculated (Ver Hoef and Peterson, 2010). As an example, the percent residual variation accounted for by the TU variance component (VC_{TU}) is given by: $VC_{TU} = [\sigma^2_{TU} / (\sigma^2_{TU} + \sigma^2_{TD} + \sigma^2_{EUC} + \sigma^2_{NUG})]*100$, where σ^2_{NUG} is the nugget effect, and σ^2_{TU}, σ^2_{TD} and σ^2_{EUC} are the partial sills for the TU, TD and Euclidean components, respectively. This allowed us to evaluate the relative contribution of each component to the predictive power of the model and to make comparisons of those relative contributions across models.

3. Results

Overall, the results showed that 1) there was a significant positive relationship between some, but not all of the macroinvertebrate

indices; 2) there were few similarities in the optimal set of covariates for the different macroinvertebrate indices; 3) the optimal covariance structure varied between macroinvertebrate indices; 4) the relative predictive power of models based on different spatial-weighting schemes varied between response variables; and 5) the best spatial stream-network model had more predictive power than the equivalent non-spatial model for each combination of covariance mixture and spatial-weighting scheme. These findings are described in further detail below.

3.1. Macroinvertebrate indices

There was a significant positive relationship between the number of in-stream dispersing taxa and total richness ($r = 0.51$, p-value < 0.001), and a weaker positive relationship between total richness and % tolerant ($r = 0.23$, p-value $= 0.08$). The % tolerant and in-stream dispersers indices were not significantly correlated ($r = 0.12$, p-value > 0.1). Macroinvertebrate reference guidelines have not been developed for the Tully catchment; however, many of the total richness scores were relatively low compared to the reference guidelines for the Barron catchment (Marshall et al., 2001), which is considered similarto the Tully (Table 1). In contrast, the % tolerant index was relatively high at many sites, which suggests that the macroinvertebrate communities in the study area may be negatively influenced by anthropogenic impacts. In addition, 5%–35% of macroinvertebrate families found at each site were classified as in-stream dispersers. Finally, a visual inspection of Torgegrams suggested that each of the indices exhibited flow-connected and/or flow-unconnected patterns of spatial autocorrelation.

3.2. Model selection: covariates

There were few similarities in the optimal set of covariates for the different macroinvertebrate indices (Table 2). When we compared models based on different spatial-weighting schemes for

Table 1
Summary statistics describing the three macroinvertebrate indices, including the minimum (Min.), 20th percentile (20th %), median (Med.), 80th percentile (80th %), and maximum (Max.). Reference guidelines for total richness developed in the Barron catchment are also provided.

Response variable	Min.	20th %	Med.	80th %	Max.
% Tolerant (%)	16.7	25.0	35.7	42.9	62.5
Total richness (No.)	11	17.8	22	25.2	30
Guidelines	–	24	–	30	–
In-stream dispersers (No.)	1	3	4	5	6

each index separately, we found that the same set of covariates was selected for the % tolerant and in-stream dispersers models. However, for the total richness models, slightly different sets of covariates were selected depending on the spatial-weighting scheme that was used. In particular, models based on the slope and Shreve's stream order spatial-weighting schemes contained the same set of covariates, while a simpler model was selected using an area-weighting scheme (substrate heterogeneity was not included) and a more complex model selected based on equal weights (mean water temperature was included). However, in every case the relationships with the covariates were ecologically sensible (Appendix A, Table A.3).

3.3. Model selection: covariance structures

The optimal covariance structure, based on the lowest RMSPE value, varied between macroinvertebrate indices (Fig. 5). For the % tolerant and total richness models, the full TU/TD/EUC covariance mixture had the most predictive power for all spatial-weighting schemes; although the TU/EUC mixture performed nearly as well for the % tolerant model, and the TU/TD models performed almost as well for the total richness model (<1 percentage point difference in RMSPE reduction; Fig. 5a, b). For the in-stream dispersers, the TU/TD, TU/EUC and TU/TD/EUC models had similar predictive power, with the TU/TD covariance mixture based on slope outperforming models based on other spatial-weighting schemes and covariance mixtures (Fig. 5c). Interestingly, for the in-stream dispersers models, covariance mixtures that included a TU component reduced the RMSPE value by between 6.75% and 17.15% compared to the non-spatial model, while covariance mixtures that did not include a TU component reduced the RMSPE value by less than 2% (Fig. 5c). In contrast, the predictive power of the TU model alone was relatively poor for the % tolerant and total richness models (<3% reduction in RMSPE). Nevertheless, the best spatial model had more predictive power than the equivalent non-spatial model for each combination of covariance mixture and spatial-weighting scheme.

Table 2
Final set of covariates for each response variable and spatial weighting scheme. Check marks indicate that the covariate was included in the model, while a star represents covariates that were included in the final model for each macroinvertebrate index.

Response	Covariate	Spatial weights			
		Area	Shreve	Slope	Equal
% Tolerant	Max air temperature °C	★	✓	✓	✓
	Catchment area	★	✓	✓	✓
	Silt/Clay substrate	★	✓	✓	✓
	Orientation (North-South vs. East-West)	★	✓	✓	✓
Total richness	Irrigated agriculture (catchment scale) %	✓	✓	★	✓
	Urban (site buffer) %	✓	✓	★	✓
	Picked by (3 × most experienced operators vs. 2 × inexperienced)	✓	✓	★	✓
	Orientation (North-South vs. East-West)	✓	✓	★	✓
	Catchment area	✓	✓	★	✓
	Substrate heterogeneity		✓	★	✓
	Mean water temperature				✓
In-stream dispersers	Urban (riparian scale) %	✓	✓	★	✓
	Grazing (riparian scale) %	✓	✓	★	✓
	Cobble substrate %	✓	✓	★	✓
	Picked by (1 × most experienced operators vs. 4 × less experienced)	✓	✓	★	✓

The spatial weights are used to construct the TU covariance matrices and so it is interesting that the relative predictive power of models based on different spatial-weighting schemes also varied between response variables. For the in-stream dispersers, TU models generated using spatial weights based on slope clearly had more predictive power than other models (Fig. 5c), decreasing the RMSPE value by an additional 1.9–6.6%, relative to the non-spatial model. Furthermore, models generated using the equal-weighting scheme outperformed the Shreve- and area-based weights by 0.3–3.7%. Interestingly, there was generally little difference in the predictive power of the different spatial-weighting schemes for the total richness and %tolerant response variables (Fig. 5a,b). Spatial weights based on area marginally outperformed other spatial-weighting schemes for the % tolerant models, but only decreased the RMSPE by between 0.2 and 1.6%. The optimum spatial-weighting scheme for the total richness models varied for different covariance mixtures, but differences in predictive power were relatively small (0.1–3.1%; Fig. 5b).

### 3.4. Final spatial stream-network model

Final models for the three macroinvertebrate indices included the covariates shown in Table 2. The spatial stream-network models were fit using the TU/TD/EUC mixture for the % tolerant and total richness models, and the TU/TD model for the in-stream dispersers model, as these were the models with the lowest RMSPE in each case. The final in-stream dispersers and total richness models were fit using a slope-based spatial-weighting scheme, while area was used to generate the weights for the % tolerant model (Table 3). The final spatial statistical models described 28.81%, 57.25%, and 33.64% of the total variation (i.e. predictive r^2 between observations and the LOOCV predictions) in the % tolerant, total richness, and in-stream dispersers indices, respectively; while the same non-spatial models only accounted for 14.64%, 41.83%, and 5.39%, respectively.

The covariance mixture captured both fine- and broad-scale patterns of spatial autocorrelation in each of the response variables, but the relative contribution of each component differed depending on the macroinvertebrate index (Table 3). For example, the total richness model was dominated by broad-scale (range >36.8 km) Euclidean variation (VC_{EUC} = 85.08%), suggesting that all sites in the sub-catchment were spatially correlated to some degree. The majority of the remaining residual variation in this model was captured by a fine-scale (range = 24.4 m) TD model. Fine-scale Euclidean variation dominated the % tolerant model (range = 28.65 m, VC_{EUC} = 84.55%), with the majority of its remaining variation captured by a mid-range tail-up model (range = 3.1 km, VC_{TU} = 15.4%). In contrast, the in-stream dispersers model was dominated by the TU component (VC_{TU} = 58.6%). The range parameter was larger than the total length of the stream network (range = 82.5 km), indicating that measurements at all flow-connected sites were spatially correlated to some extent. Note that the large range parameters observed in the total richness and in-stream dispersers models make it difficult to precisely delineate the partial sills for these models. As a result, the proportion of residual variation described by each variance component must be interpreted with some caution. Nevertheless, the importance of the TU component in the in-stream dispersers model is also supported by the consistently strong predictive power of the covariance mixtures containing a TU component (Fig. 5c).

4. Discussion

4.1. Patterns of spatial autocorrelation in macroinvertebrate indices

Spatial autocorrelation can arise from endogenous ecological processes such as dispersal or competition, but may also be driven
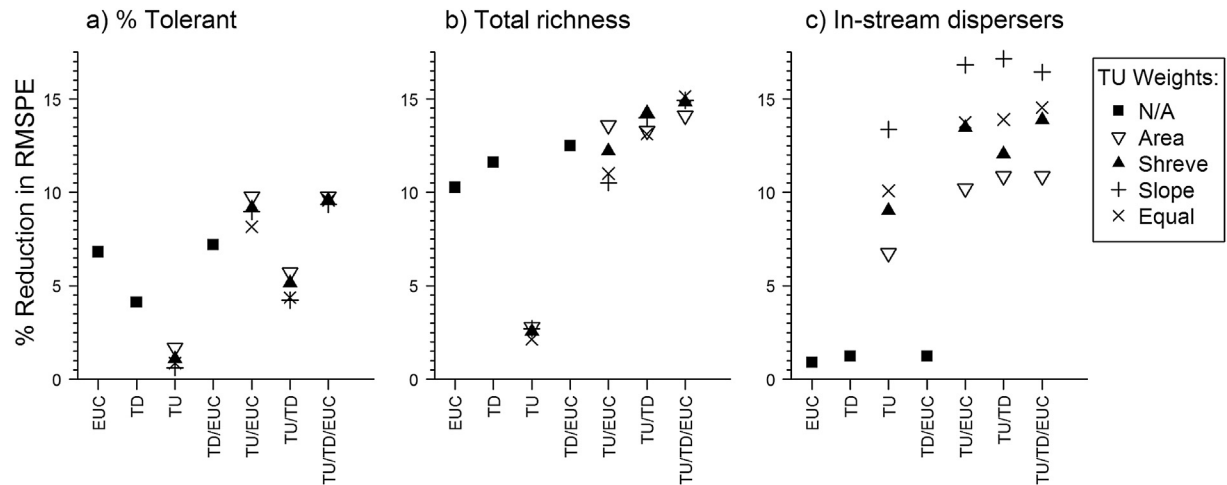
Fig. 5. Percent reduction in leave-one-out cross-validation root-mean-square-prediction error (RMSPE) relative to the equivalent non-spatial model, by covariance mixture (EUC = Euclidean, TD = tail-down, TU = tail-up) and spatial-weighting scheme. The model with the lowest RMSPE is shown for each covariance mixture/spatial-weighting scheme combination. The spatial-weighting scheme is not applicable (N/A) if the mixture did not include the TU model.

exogenously, potentially arising from dependencies between the variable of interest and other spatially structured environmental variables such as broad-scale topography or microclimatic differences (Wagner and Fortin, 2005). Consequently, the spatial structure in the residual error likely represents complex interactions between both endogenous and exogenous processes. While our models allow us to classify the patterns of spatial autocorrelation in the data (i.e. flow-connected, flow-unconnected, Euclidean), it is not possible to obtain a definitive explanation about what is causing the pattern (i.e. correlation does not equal causation). Furthermore, the spatial structure accounts for spatial autocorrelation in the model residuals, *after* the effects of the covariates have been removed. As such, a response variable exhibiting strong instream or Euclidean patterns of spatial autocorrelation may have weak, or no spatial structure in the residuals after the influence of spatially structured covariates are removed. Therefore, the spatial

patterns described by the covariance parameters are data and model specific, and are likely to change if the model covariates change. Nonetheless, the type and scale of the observed spatial patterns may provide clues about important drivers (i.e. missing covariates) that structure macroinvertebrate indices (e.g. McGuire et al., 2014).

The three macroinvertebrate indices displayed both fine- and broad-scale patterns of spatial autocorrelation, but to different degrees. For example, fine-scale variability was particularly important in the % tolerant model (Table 3), which is not surprising since SIGNAL scores have been shown to be correlated with numerous water-quality variables including nutrients and dissolved oxygen, among others (Chessman, 2003); many of which would be expected to produce fine-scale patterns in the % tolerant index. For example, dissolved oxygen is influenced by local characteristics such as substrate type, stream temperature, local nutrient levels, net primary production, and dissolved organic carbon (Hynes, 1960; Allan, 1995; Angelier, 2003). Other studies have also found significant fine-scale variation in macroinvertebrate data (e.g. Downes et al., 2000; Li et al., 2001) due to variability in rough-textured substrata (Downes et al., 2000), submerged woody debris (Scealy et al., 2007), and trailing riparian vegetation (Milner and Gloyne-Phillips, 2005), which provide important habitat for macroinvertebrates. Egg-laying events can be patchy in both space and time, due to maternal behaviour and an unequal distribution of suitable oviposition sites, and that the effects of this patchiness can persist in juvenile distribution patterns (Lancaster et al., 2011). Furthermore, many of our sites were in rural and semi-rural areas, where variability may be related to localised disturbances such as cattle crossings, which have been found to affect macroinvertebrates in other studies (Kyriakeas and Watzin, 2006).

Broad-scale variation was also important in each of the models, accounting for the majority of residual variation in both the total richness and in-stream dispersers models. Broad-scale patterns of spatial autocorrelation have also been found in previous studies (e.g. Li et al., 2001; Townsend et al., 2003), but the covariance mixture allowed us to identify which spatial relationship best described those broad-scale patterns. Within the in-stream dispersal model, the majority of residual spatial autocorrelation was accounted for using long-range flow-connected relationships (Table 3). In-stream dispersers are essentially confined to the stream channel throughout their entire life-cycle, and may

Table 3
Final spatial stream-network model results for the % tolerant, total richness and in-stream dispersers. Results are reported for each variance component (VC) including the covariance function, optimal spatial-weighting scheme, the covariance parameter estimates (range and partial sill), and the percentage of residual variance accounted for (VC$_{TU}$, VC$_{TD}$, VC$_{EUC}$, VC$_{NUG}$) by each variance component.

Variance component		% Tolerant	Total richness	In-stream dispersers
Tail-up	Covariance function	Spherical	Mariah	Linear-with-sill
	Spatial-weighting scheme	Area	Slope	Slope
	Range (m)	3054	16	82,524
	Partial sill	11.7	0.0	0.3
	VC$_{TU}$ (%)	15.4	0.0	58.6
Tail-down	Covariance function	Exponential	Linear-with-sill	Linear-with-sill
	Range (m)	261.3	24.4	78.3
	Partial sill	0.0	7.6	0.1
	VC$_{TD}$ (%)	0.0	14.9	22.8
Euclidean	Covariance function	Spherical	Gaussian	NA
	Range (m)	28.65	36,772	NA
	Partial sill	64.37	43.49	NA
	VC$_{EUC}$ (%)	84.55	85.08	NA
Nugget	Nugget	0.0	0.0	0.1
	VC$_{NUG}$ (%)	0.0	0.0	18.6

therefore be more strongly influenced by factors within the in-stream environment that vary longitudinally over broader spatial scales, such as substrate characteristics (Rice et al., 2001). In addition, the dendritic structure of the river network is expected to interact with the dynamic disturbance regime (Benda et al., 2004), regardless of whether the source is natural (i.e. flood events or wildfire) or anthropogenic (i.e. bank failure or chemical pollution). For example, large flow events may affect a portion of the branching network and the ability of macroinvertebrates to recolonise sites depends on the availability of nearby terrestrial and aquatic refugia (Sedell et al., 1990). In contrast, the importance of broad-scale Euclidean relationships in the total richness model suggests that all sites in the study area are related, which could indicate that the sites are all connected by dispersal. However, a more likely explanation is that other factors such as cleared and forested land (Genito et al., 2002), riparian tree cover (Petersen et al., 2004) or geology (Neff and Jackson, 2011) produced broad-scale patterns of spatial autocorrelation in the macroinvertebrate indices that our relatively coarse-scale land-use and land-cover data (Appendix A, Table A.2) were unable to capture (Gergel et al., 2007).

The use of macroinvertebrate indices may also have masked some of the spatial patterns in macroinvertebrate community composition, reducing the amount of spatial autocorrelation described by the TU and TD models. Previous research has shown that variability in species abundance differs substantially depending on the species and the spatial scale, suggesting that a variety of processes are driving macroinvertebrate assemblages (Downes et al., 1993). General indices, such as % tolerant and total richness, group macroinvertebrates irrespective of many functional traits, such as feeding mechanisms, habitat preference, or dispersal mechanism. Thus, the relative strength of spatial autocorrelation and increased predictive power of the in-stream dispersers model compared to models of % tolerant and total richness (Fig. 5) suggest that attempts to quantify, and potentially interpret patterns of spatial autocorrelation may be more successful for indices that reflect functional traits with a strong spatial component, such as dispersal.

4.2. Influence of the spatial-weighting scheme

Our results indicate that the choice of spatial-weighting scheme has the potential to affect the predictive power of the model when it contains a relatively strong TU component, as was the case for in-stream dispersers. Surrogates for flow volume (i.e. catchment area and Shreve's stream order) have reflected the relative influence of locations on downstream tributaries for other physicochemical and biological stream characteristics (Gardner and McGlynn, 2009; Isaak et al., 2010; Peterson and Ver Hoef, 2010; Ver Hoef and Peterson, 2010). However, when we restricted consideration to taxa that are limited to in-stream dispersal, weights based on surrogates for flow volume ceased to perform well. In fact, models generated using additive weights (i.e. catchment area and Shreve order) provided less information than an equal-weighting scheme, which accounts for the branching structure of the network without providing any additional information about converging segment characteristics.

The spatial distribution of slope was markedly different than that of catchment area and Shreve's stream order in our study area. Additive measures formed increasing longitudinal gradients of area and stream order from headwaters to larger, lowland streams. In contrast, streams with steeper slopes tended to occur in the upper parts of the sub-catchment in smaller headwater streams, while lower gradient streams occurred throughout the study area. Thus, the relatively strong performance of the model generated using a slope-based spatial-weighting scheme is likely due to its ability to describe local-scale spatial variability and the influence of smaller, steeper tributaries on macroinvertebrate communities. This is not surprising given that headwater streams have been found to have high between-stream diversity due to increased habitat heterogeneity and low physical connectivity (Clarke et al., 2008); with the latter factor expected to be particularly pronounced for in-stream dispersers. Although seasonal inputs of leaf litter from headwater streams in the northern hemisphere increase productivity and influence food webs downstream, this is an unlikely explanation in our study area (Bunn et al., 1999). Instead, it is more probable that flow velocity strongly influences the type and diversity of physical and hydrological habitat, which has a subsequent influence on macroinvertebrate richness, abundance, density, and composition (Brooks et al., 2005; Hoffman et al., 2006; Lancaster, 1999; Pringle et al., 1988; Sheldon and Walker, 1998; Winterbottom et al., 1997).

Our finding that the predictive power of the spatial stream-network model may vary depending on the spatial-weighting scheme is interesting. It provides the first piece of evidence that spatial-weighting schemes based on additive measures are not guaranteed to adequately represent the spatial variability or functional connectivity and influence within a spatial model fit to streams data; in this case, a macroinvertebrate index based on in-stream dispersal. This also demonstrates that the spatial-weighting scheme has the potential to provide ecological insight about the underlying process, in addition to the model covariates, when the primary goal is to explore the explanatory power of the models rather than the predictive ability (MacNally, 2000).

4.3. Predictive power of spatial stream-network models

The predictive power of all three macroinvertebrate index models was relatively weak compared to results found in similar studies focussing on fish (Peterson and Ver Hoef, 2010), water quality (Gardner and McGlynn, 2009) or temperature (Isaak et al., 2010; Ruesch et al., 2012). Spatial modelling approaches tend to perform better than non-spatial models when they can 'borrow strength' from spatially correlated neighbouring sites (Cressie, 1993). In other words, the predictive power of a spatial model depends on both the covariates *and* the covariance structure. In fact, if there is a strong spatial structure in the residual error, a spatial model may produce accurate predictions even without covariates. Given that many of our sampling locations were separated by approximately 100 m (Fig. 1), we were surprised that the spatial models did not substantially outperform the non-spatial models. It is possible that imperfect detection rates could have introduced artificial variability into the data (e.g. Wisniewski et al., 2013). However, macroinvertebrate assemblages are known to exhibit high levels of unexplained fine-scale spatial variation related to physicochemical and biological processes (Downes et al., 2000; Minshall, 1984). There is also evidence that the stochastic effects of recruitment and limited larval dispersal may produce fine-scale variability in species composition and abundance within a reach (Bunn and Hughes 1997; Hughes et al., 1998) and over time (Hughes et al., 2011). Regardless of the source, spatial and/or temporal heterogeneity cannot be described by a spatial statistical model if it occurs at a scale finer than the measurements; thus, it is unreasonable to expect equivalent predictive performance for the macroinvertebrate models compared to the other physicochemical and biological endpoints described above.

There are a number of studies undertaken at the ecoregional scale, which show strong regional similarity (e.g. Townsend et al., 2003). However, these patterns are likely related to broad climate and geologic gradients, which are not the focus of most environmental monitoring programs. Instead, the predictive models must

be able to identify spatial patterns resulting from anthropogenic stressors, which our models were unable to do despite the relatively small extent of the study area and the wide range of anthropogenic stressors. Thus, the combination of weak relationships with the remotely derived covariates and the weak spatial structure in the residuals is problematic for making predictions at independent locations; it reduces the accuracy of predictions and makes extrapolation as part of a broad-scale monitoring program less reliable compared to physicochemical and biological variables predicted in previous studies. This may be a predictable consequence of the variable studied (macroinvertebrate assemblages), rather than the methods used, but these challenges must be considered in future application of these models.

There is an ongoing debate about whether to it is appropriate to use family- versus species-level taxonomic resolution to generate macroinvertebrate indices for biological assessment (e.g. Lenat and Resh, 2001; Jones, 2008); therefore, we questioned whether the use of macroinvertebrate indices based on coarse (mainly family-level) taxonomic identifications may have affected the predictive performance in the spatial models. The utility of using coarse-level taxonomic resolutions generally arises from technical (e.g. difficulty in identifying genus and species due to lack of keys and descriptions) and resourcing (e.g. time and funding) advantages, while disadvantages include a loss of information (Jones, 2008). However, the challenges surrounding taxonomic resolution are more complicated than these few issues (see Chessman et al., 2007; Jones, 2008). In some regions, including several in Australia, evidence suggests that little information is lost by using family over species taxonomic identifications (Marshall et al., 2006; Chessman et al., 2007) and this is especially true when indices based on functional traits like pollution tolerance are used (Chessman et al., 2007; Jones, 2008). Moreover, family-level data are used in many Australian bio-monitoring programs, including those in Queensland (DNRM, 2001). Therefore, it is unlikely that taxonomic resolution had a strong effect on the predictive performance of our non-spatial models. However, it is entirely possible that the use of indices that lump macroinvertebrate families without regard for functional traits may have masked some of the spatial patterns in macroinvertebrate community composition; thus, reducing the ability of the spatial statistical stream-network models to significantly improve on the predictive power of the non-spatial % tolerance and total richness models.

5. Conclusions

The % tolerant, total richness, and in-stream dispersers indices all exhibited multiple, multi-scale patterns of spatial autocorrelation, which is similar to results obtained in other studies (Isaak et al., 2010; Peterson and Ver Hoef, 2010; Ruesch et al., 2012). However, as might be expected of macroinvertebrate data, fine-scale heterogeneity in the indices had a stronger effect than in previous studies focussing on physicochemical (Gardner and McGlynn, 2009; Garreta et al., 2010; Isaak et al., 2010) and biological data (Money et al., 2009; Peterson and Ver Hoef, 2010), and this had a negative impact on the predictive power of the models. Interestingly, the influence of the spatial-weighting scheme also differed amongst the macroinvertebrate indices, depending on the relative importance of the TU component in the covariance mixture. In fact, our results indicate that selecting the wrong spatial weighting scheme for a model with a strong TU component may result in poorer predictive performance than using a spatial-weighting scheme that provides no information about segment characteristics. This finding is especially exciting because it is the first piece of evidence that the choice of spatial-weighting scheme impacts model performance. In addition, it further demonstrates

the flexibility of a spatial stream-network model; users can potentially gain insight into the underlying ecological processes that structure macroinvertebrates through the use of 1) spatially and temporally explicit covariates; 2) in-stream and Euclidean autocovariance functions, and 3) different spatial-weighting schemes derived using a variety of ecologically relevant variables.

Despite the relatively low predictive power of the models, we were able to detect ecologically sensible relationships between the three indices and a range of predominantly GIS-derived covariates. Moreover, spatial autocorrelation was present in all three sets of the model residuals; with relatively strong flow-connected patterns of spatial autocorrelation found in the in-stream dispersers index, which represents a more homogenous set of dispersal traits than the % tolerant and total richness indices. If traditional, non-spatial methods were used to analyse these data, the effects of spatial autocorrelation would effectively be ignored; thus, increasing the chances for biased parameter estimates and rendering statistical inference questionable (Legendre, 1993). These biases may be particularly important when spatially explicit questions pertaining to land-use and climate change impacts, as well as, habitat connectivity, dispersal limitations, isolation and extinction dynamics on macroinvertebrate community structure are explored. Thus, it is important to consider the impact of spatial autocorrelation on model results and subsequent statistical inferences.

Appendix A. Supplementary material

Supplementary material related to this article can be found at http://dx.doi.org/10.1016/j.envsoft.2014.06.019.

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