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APPLIED ISSUES

A comparison of spatially explicit landscape representation methods and their relationship to stream condition

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SUMMARY

1. Biodiversity, water quality and ecosystem processes in streams are known to be influenced by the terrestrial landscape over a range of spatial and temporal scales. Lumped attributes (i.e. per cent land use) are often used to characterise the condition of the catchment; however, they are not spatially explicit and do not account for the disproportionate influence of land located near the stream or connected by overland flow.
2. We compared seven landscape representation metrics to determine whether accounting for the spatial proximity and hydrological effects of land use can be used to account for additional variability in indicators of stream ecosystem health. The landscape metrics included the following: a lumped metric, four inverse-distance-weighted (IDW) metrics based on distance to the stream or survey site and two modified IDW metrics that also accounted for the level of hydrologic activity (HA-IDW). Ecosystem health data were obtained from the Ecological Health Monitoring Programme in Southeast Queensland, Australia and included measures of fish, invertebrates, physicochemistry and nutrients collected during two seasons over 4 years. Linear models were fitted to the stream indicators and landscape metrics, by season, and compared using an information-theoretic approach.
3. Although no single metric was most suitable for modelling all stream indicators, lumped metrics rarely performed as well as other metric types. Metrics based on proximity to the stream (IDW and HA-IDW) were more suitable for modelling fish indicators, while the HA-IDW metric based on proximity to the survey site generally outperformed others for invertebrates, irrespective of season. There was consistent support for metrics based on proximity to the survey site (IDW or HA-IDW) for all physicochemical indicators during the dry season, while a HA-IDW metric based on proximity to the stream was suitable for five of the six physicochemical indicators in the post-wet season. Only one nutrient indicator was tested and results showed that catchment area had a significant effect on the relationship between land use metrics and algal stable isotope ratios in both seasons.
4. Spatially explicit methods of landscape representation can clearly improve the predictive ability of many empirical models currently used to study the relationship between landscape, habitat and stream condition. A comparison of different metrics may provide clues about causal pathways and mechanistic processes behind correlative relationships and could be used to target restoration efforts strategically.

Keywords: ecosystem health, GIS, hydrologic activity, inverse-distance weighting, land use

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Introduction

A central tenet of freshwater ecology links stream processes and condition to the characteristics of the surrounding landscape (Hynes, 1975), with aspects of landscape condition known to influence in-stream physical, chemical and biological patterns and processes (Townsend, 1996; Allan, 2004). These relationships were initially observed at the site or small catchment scale. More recently, the advent of the geographic information system (GIS) and the increase in the amount of readily available remotely sensed and GIS land use, land cover and altitude data have allowed researchers to consider this relationship at broader spatial scales (Turner, Gardner & O'Neill, 2001).

The 'lumped' approach is a popular method of landscape representation and is based on summary statistics such as the percentage, proportion or mean of a landscape characteristic within a pre-designated area. Frequently, this area represents the entire catchment (Johnson *et al.*, 1997) or land within a specific distance of a feature (i.e. a buffer) such as a shoreline (King *et al.*, 2007), a stream (Strayer *et al.*, 2003) or a site (Comelo *et al.*, 1996). The popularity of the lumped method is probably due to the general applicability of the approach: (i) the GIS data requirements are relatively small, (ii) the method can be applied in the same way throughout different physiographic, ecological or climatic regions, (iii) no *a priori* decisions must be made about the importance of a particular land use or parameter value and (iv) it is not necessary to calibrate a model to generate the metric.

Despite the operational advantages, the lumped method is clearly an extreme oversimplification of Hynes (1975) description of the linkages between a stream and its valley. It is a non-spatial representation of characteristics in the catchment and, as such, the underlying assumption is that each portion of the catchment has equal influence on in-stream conditions (King *et al.*, 2005). However, we know that the spatial location of specific land use activities matters. For example, Wang *et al.* (2001) studied catchments with varying degrees of urbanisation and found that impervious surfaces within 3.2 km of a survey site had a stronger influence on fish assemblages than impervious surfaces further away. We also know that riparian stream buffers are commonly used to reduce the negative impacts of timber harvests on in-stream conditions (Wilkerson *et al.*, 2006). Nevertheless, the width of the buffer represents a subjective decision about which portions of the catchment affect in-stream condition. Given these issues, our goal is to compare a suite of methods to determine whether the effects of spatial proximity can be represented using simple and generally applicable landscape representation methods.

The distance-weighted approach is a generally applicable method of representing the landscape that provides a spatially explicit alternative to lumped metrics. Influence declines as a function of distance, which is typically represented using Euclidean or flow length distance from the source (each raster cell in a catchment) to the destination (either the stream or the catchment outlet). Note that when a catchment is delineated for a survey site, the spatial location of the survey site and the catchment outlet are equivalent. The flow length represents the overland flow path, which is based on the topography of the hillslope. The decline in influence has been represented using an inverse-distance function (Comelo *et al.*, 1996; King *et al.*, 2004, 2005, 2007; DeLuca *et al.*, 2008; Van Sickle & Johnson, 2008) and an exponential function (Johnson *et al.*, 2007; Van Sickle & Johnson, 2008), but any function could be used. Distance-weighted metrics are usually based on a single distance-decay function, but two-component metrics have also been generated (Johnson *et al.*, 2007; Poor, McDonnell & Bolte, 2008; Van Sickle & Johnson, 2008). In this case, the flow length from each raster cell to the survey site is split and a unique decay function is used for each part: one for the distance travelled across the terrestrial landscape to the stream and another for the distance travelled within the stream to the survey site. Although the choice of distance-decay function can also be viewed as an *a priori* decision, an optimisation procedure can be used to estimate the parameters (Van Sickle & Johnson, 2008) if there are concerns about the weighting scheme.

Distance-weighted metrics have been shown to improve stream and estuary data predictions for a variety of data types including those on fish (King *et al.*, 2004; Van Sickle & Johnson, 2008), nutrients (King *et al.*, 2005; Poor *et al.*, 2008), invertebrates (King *et al.*, 2005; Johnson *et al.*, 2007), metals (Comelo *et al.*, 1996), invasive plants (Johnson *et al.*, 2007; King *et al.*, 2007) and water birds (DeLuca *et al.*, 2008). The type of distance-weighted metric that explains the most variability in the data will probably vary depending on which conditions and processes that the biological, physical or chemical data are most strongly related to (Strayer *et al.*, 2003). For example, some evidence suggests that inverse-distance-weighted (IDW) metrics based on distance to the stream explain more variability in fish data compared to lumped metrics (King *et al.*, 2004; Van Sickle & Johnson, 2008); this makes sense from an ecological perspective since fish distribution generally reflects multi-scale environmental conditions from the landscape, the riparian zone and in-stream habitat (Gregory *et al.*, 1991; Pusey & Arthington, 2003; Allan, 2004). In contrast, an IDW metric based on distance to the catchment outlet (also known as the survey site or the 'outlet') may explain more variability in invertebrate data (King *et al.*, 2005), since invertebrates generally have a shorter lifespan and a more limited mobility than fish (Rosenberg & Resh, 1993).

Land use near the stream or survey site clearly has the potential to influence in-stream conditions strongly. However, the relationship between the broader-scale landscape and in-stream condition is complex, with observable in-stream patterns resulting from multiple spatially and temporally dependent processes (Wiens, 2002). As such, the potential influence of land use will probably be affected by other processes. For example, Stauffer, Goldstein & Newman (2000) found that areas of low riparian cover were not associated with poor scores for the fish Index of Biotic Integrity (IBI) unless those areas also had a high runoff potential. A number of methods, such as flow accumulation thresholds (Hunsaker & Levine, 1995) and simple hydrologic models (Burcher, 2009), have been proposed to identify hydrologically active areas, but the methods were not designed to be generally applicable. For example, it may be difficult to choose the appropriate threshold or to estimate a model parameter in hydrologically dissimilar regions. Despite these issues, we believe that a generally applicable metric that accounts for *both* hydrological effects and proximity of land use to the stream has the potential to explain additional variability in water quality and biotic data.

The strength of the relationship between landscape and stream condition is also likely to change throughout the water year because of seasonal differences in hydrological activity and indicator category. In the wet season, the stream network expands both longitudinally and laterally (Junk, Bayley & Sparks, 1989; Malard, Tockner & Ward, 1999; Wigington, Moser & Lindeman, 2005), resulting in a flushing effect as the flow paths facilitate the movement of physical material, chemicals and nutrients to and within the stream (Robertson *et al.*, 1999; Olivie-Lauquet *et al.*, 2001). During dry periods, the stream network contracts, resulting in reduced connectivity and movement of material (Malard *et al.*, 1999). This seasonal expansion and contraction of the stream network (Junk *et al.*, 1989; Malard *et al.*, 1999; Wigington *et al.*, 2005) may affect the relative influence of catchment land use on in-stream indicators (Bolstad & Swank, 1997; Johnson *et al.*, 1997; Pan *et al.*, 2004; Stedmon *et al.*, 2006). In addition, the affect of season on indicators may not be consistent. For example, strong seasonal differences in the relationship between ambient nutrients and land use were observed by Johnson *et al.* (1997), with total phosphorus and total nitrogen responding quite differently. However, all of the previous studies involving distance-weighted methods were based on a limited number of variables collected during a single season, averaged over multiple seasons or applied to a response that does not vary seasonally. Clearly, this makes it difficult to ascertain whether the performance of spatially explicit landscape representation methods are affected by season or vary by indicator category.

In this study, we compare the performance of generally applicable landscape representation methods, which are commonly used to calculate catchment metrics. We propose a new distance-weighted method for calculating catchment characteristics that accounts for proximity to the stream or outlet and the level of hydrologic activity. More specifically, we use an extensive dataset collected in Southeast Queensland (SEQ), Australia, to compare the ability of lumped catchment metrics, IDW metrics, and these new metrics to account for the variability in 13 indicators of stream ecosystem health (see Bunn *et al.*, 2010). We evaluate model results to determine whether catchment area affects the relationship between in-stream indicators and spatial representation metrics. We also compare ecologically similar indicators to determine whether they behave alike and investigate whether the performance of spatial representation methods varies with season.

Methods

Metric description

Seven land use metrics were evaluated as part of this study, which can be divided into three general metric types (i) lumped, (ii) inverse-distance weighted and (iii) hydrologically active inverse-distance weighted. The formulation for each of these metric types is described below.

Lumped land use metrics. Lumped catchment metrics (Fig. 1) are non-spatial and are generally represented as an areal percentage, proportion or a mean in the catchment:

$$\%\mathrm{LU} = \frac{\sum_{i=1}^{n} I(k) W_i}{\sum_{i=1}^{n} W_i} * 100, \quad (1)$$

where $I(k)$ is an indicator function equal to 1 if a cell, i, contains the targeted land use and 0 for other land uses, n is the number of cells in the catchment, and W_i is equal to 1 for every cell in the catchment.

Inverse-distance-weighted metrics. An IDW metric uses a distance-decay function to give a stronger weight to land use closer to a specific feature of interest, such as the stream or the survey site. Both Euclidean distance and flow length distance have been used to calculate an IDW land use metric. Here, we calculated four IDW metrics by varying the distance measure used: Euclidean distance to the stream (iEucS), Euclidean distance to the outlet (iEucO), flow length to the stream (iFLS) and flow length to the outlet (iFLO) (Fig. 1). The general formula shown in eqn 1 can also be used to calculate the IDW metric. In this case, W_i is the inverse-distance weighting $(d + 1)^{-1}$ from every cell in the catchment to either the survey site or the stream, with $0 < W_i \leq 1$. Distance, d, is represented using either Euclidean distance or flow length to either the outlet or the stream. We chose to use $(d + 1)^{-1}$ because there is some evidence that a model based on a d^{-1} weighting may fit the data better than a $d^{-0.5}$ weighting (King *et al.*, 2004) or a d^{-2} weighting (Comelo *et al.*, 1996). In addition, a d^{-1} weighting creates a smoother weight transition near the stream compared to a d^{-2} weighting. Although the weighting function is not particularly smooth at the source, this seemed reasonable since riparian land is thought to have a stronger influence on stream condition than areas further from the stream (Gregory *et al.*, 1991).

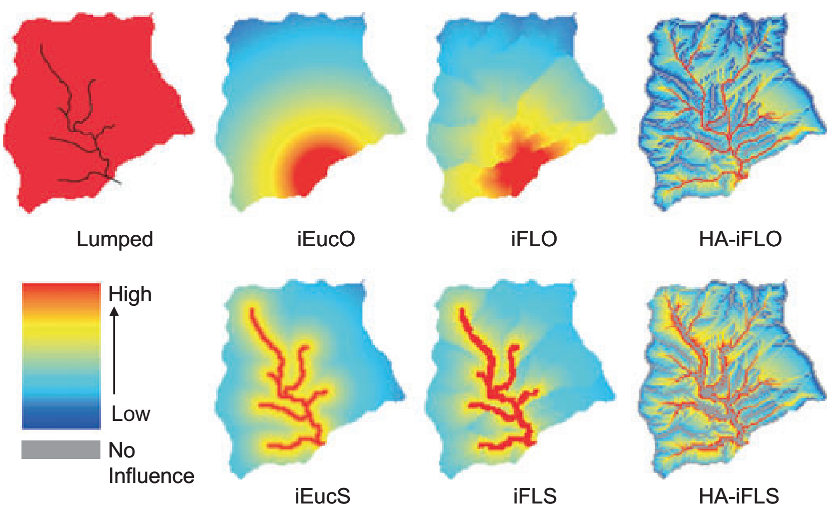

Fig. 1 Landscape representation metrics. Lumped metrics are non-spatial and all cells are considered to have equal influence. In an inverse-distance-weighted (IDW) metric, distance (d) may be based on Euclidean distance (iEucO, iEucS) or the flow length (iFLO, iFLS) either to the stream outlet (iEucO, iFLO) or the stream (iEucS, iFLS). Hydrologically active inverse-distance metrics (HA-IDW) are based on the product of the flow accumulation at each cell and the inverse flow length to the stream outlet (HA-iFLO) or the stream (HA-iFLS). All inverse distances were based on $(d + 1)^{-1}$. For plotting purposes, the HA-IDW metrics were standardised to range from 0 to 1 and weights are shown on the $\log_{10}$ scale with the same minima and maxima. Also, the black lines in the lumped metric represent the stream network.

Hydrologically active inverse-distance-weighted metrics. Inverse-distance weighting gives greater weight to land use areas closest to the stream or the survey site. However, there are also preferential flow pathways within a catchment where greater amounts of overland flow may occur. As such, these land use areas may have a greater influence on the conditions found at the survey site (Stauffer *et al.*, 2000). The general form of the hydrologically active inverse-distance-weighted (HA-IDW) metric (Fig. 1) is:

$$\%\mathrm{LU} = \frac{\sum_{i=1}^{n} I(k)W_i\mathrm{FA}_i}{\sum_{i=1}^{n} W_i\mathrm{FA}_i} * 100 \qquad (2)$$

W_i represents the inverse-distance weighting $(d + 1)^{-1}$, with $0 < W_i \leq 1$, and d is the inverse of the flow length from each cell, i, to either the survey site or the stream. FA_i is the flow accumulation value for each cell, where $\mathrm{FA}_i \geq 0$. Assuming that all precipitation results in overland flow, the FA represents the number of upslope cells that would be expected to contribute flow into each downslope cell based on the topography of the catchment. Areas with high FA values have the potential for concentrated flow, such as perennial or intermittent stream channels and areas with FA values equal to 0 represent hills or catchment boundaries. As with the IDW metrics, the HA-IDW metric may include either the flow length to the outlet (HA-iFLO) or the stream (HA-iFLS).

Study area and Ecosystem Health Monitoring Programme

The SEQ region is on the eastern coast of Australia and represents 15 major catchments with a combined area of nearly 23 000 km^2 and a peak altitude of 1360 m in the west along the Great Dividing Range (Fig. 2; Abal, Bunn & Dennison, 2005; Bunn *et al.*, 2007). This is a subtropical region with mean annual daily maximum temperatures ranging between 21 and 29 °C. The total annual rainfall ranges between 900 and 1800 mm, with the majority falling during the warm summer season and stream flow in the region is seasonally variable (Pusey, Arthington & Read, 1993; Abal *et al.*, 2005). Approximately two-thirds of the native vegetation in the region has been cleared since the beginning of European settlement in 1840 and the current predominant land uses include natural bushland (37%, native species with variable numbers of invasive and exotic species) and grazing (35%) (Abal *et al.*, 2005). Developed areas, managed forest and plantations, and agricultural land uses are also present in the region (6.5, 9 and 5.9%, respectively).

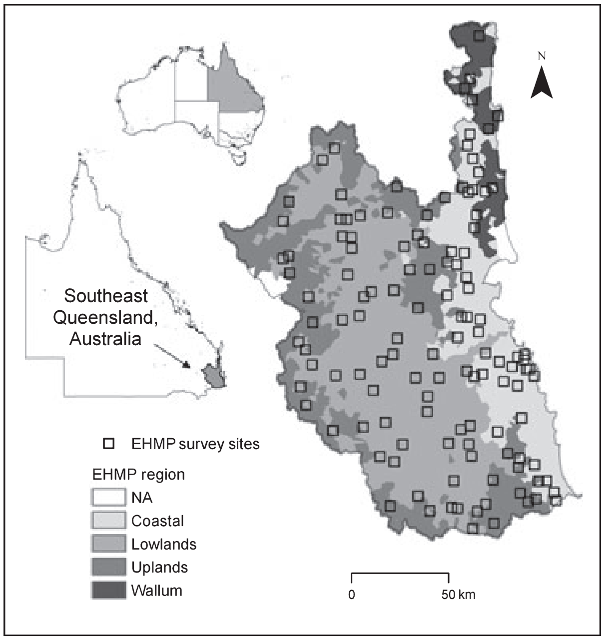

Fig. 2 Ecological Health Monitoring Programme (EHMP) survey sites are located in Southeast Queensland, Australia. Survey sites are distributed throughout the four EHMP regions: Coastal, Lowland, Upland and Wallum.

The SEQ freshwater Ecosystem Health Monitoring Programme (EHMP) has been underway since 2002 (Bunn *et al.*, 2010) and data are used to evaluate the condition and trend in ecological health of streams and rivers. For this study, we used 126 EHMP freshwater survey sites (Fig. 2), where measurements were collected biannually during the dry (austral spring, October to November) and post-wet (austral autumn, April to May) seasons. Survey sites were located on reaches with a Strahler stream order (Strahler, 1957) ≥3 and catchment sizes ranging between 1.39 and 10 320 km^2 (Table 1).

We evaluated 13 indicators of stream ecosystem health that were measured between October 2003 and May 2007, belonging to four general categories: fish, invertebrates, physicochemical and nutrients. A description of the individual indicators, including the abbreviations that will be used hereafter, is included in Table 2 (see also Bunn *et al.*, 2010). We

Table 1 Summary statistics describing Ecosystem Health Monitoring Programme (EHMP) catchment characteristics including area and land use percentages for lumped Grazed and mid-dense forest (MDF). Characteristics describing mean stream width and depth at the survey site are also included

	Min.	First quartile	Median	Mean	Third quartile	Max.
Area (km^2)	1.39	20.41	56.10	217.51	132.11	10 323.17
% Grazed	0	16.96	43.50	44.98	72.40	99.99
% MDF	15.28	39.13	51.26	50.22	61.80	88.61
Mean width (m)*	1.15	4.17	5.65	6.75	8.25	20.16
Mean depth (m)*	0.14	0.28	0.36	0.40	0.52	0.95

*Estimates are based on data collected at 101 EHMP sites in the dry season of 2002.

chose to use these indicators because they were shown to respond to land use disturbance gradients during the initial EHMP pilot study (Smith & Storey, 2001). The EHMP also collects indicators describing ecosystem processes (metabolism), but these indicators were omitted because they are less driven by landscape characteristics and more by local site conditions than other indicators (Bunn, Davies & Mosisch, 1999; Mosisch, Bunn & Davies, 2001). In addition, the EHMP does not collect ambient nutrients, which are generally low across SEQ (Schmitt, 2005; Udy & Dennison, 2005), because the correlation with land use disturbance gradients was shown to be weak when they were tested as part of the EHMP pilot study (Smith & Storey, 2001). The measurements taken on each sample date represent a snapshot of indicator condition, which may vary on a diel, seasonal or inter-annual basis because of climatic factors. In an effort to reduce this temporal variability, we chose to use the median indicator value at each site. If a site was not sampled at least twice, it was not assigned a median value and was considered missing.

Table 2 Ecological Health Monitoring Programme (EHMP) indicator categories, abbreviated indicator names and measurement units considered as response variables in this study. An explanation of each indicator is also provided

Indicator category	Indicator abbreviation	Unit	Indicator explanation
Fish	FishOE	Ratio	Fish assemblage observed/expected (modelled)
	PropAlien	%	% alien individuals
	PONSE	%	% of native species expected (modelled)
Invertebrates	PET	Count	Plecoptera-Ephemeroptera-Trichoptera: No. of macroinvertebrate families belonging to three ecologically sensitive orders: Plecoptera (stoneflies), Ephemeroptera (mayflies), and Trichoptera (caddisflies)
	MacroRich	Count	Macroinvertebrate richness: No. of macroinvertebrate families
	SIGNAL	Average score (1–10)	Average macroinvertebrate sensitivity/tolerance score: A score ranging between 1 (most tolerant) and 10 (most sensitive) assigned to macroinvertebrate families based on their tolerance/sensitivity to pollution
Nutrients	δ^{15}N	Ratio	Ratio of ^{15}N to ^{14}N stable isotopes within submerged filamentous algae
Physicochemical	Cond	μS cm^{-1}	Conductivity: Ability of water to carry an electrical charge based on the concentration of ions present in water
	pH	NA	Concentration of free hydrogen ions [H+] in the water
	DORange	mg L^{-1}	Diel dissolved oxygen range
	DOMin	%	Minimum % diel dissolved oxygen saturation
	TempRange	°C	Diel water temperature range
	TempMax	°C	Maximum diel water temperature

GIS methods

The per cent 'Grazing' and 'Mid-dense forest' (MDF) land uses in each EHMP catchment (i.e. the catchment upstream of the EHMP survey site) were calculated based on the seven metric types: lumped, iEucO, iEucS, iFLO, iFLS, HA-iFLO and HA-iFLS (see *Metric description* above for an explanation). Customised scripts written in PYTHON version 2.4.1 (Van Rossum & Drake, 2005) were used to process the input GIS datasets and to calculate the land use metrics. A general description of the GIS methodology is presented below.

We generated the spatial data necessary for modelling in a GIS using ARCGIS version 9.2 software (Environmental Systems Research Institute, Inc. (ESRI), Redlands, CA, U.S.A.). The stream data were provided by the Moreton Bay Waterways and Catchments Partnership (2005). The data were in vector format, but were originally delineated based on a 20 m digital elevation model (DEM). The stream lines were converted to a raster layer with a spatial resolution of 25 m so that it matched the other datasets used in this study. EHMP survey sites were manually 'snapped' to the appropriate stream line to ensure that a sample location coincided with a stream. The survey sites were also converted to a raster layer with a 25- m spatial resolution and used to represent the catchment outlet. The catchment boundaries for each EHMP survey site were delineated based on a DEM with a 25- m spatial resolution (Queensland Natural Resources and Water, 2000), the streams raster layer and the catchment outlet raster. The DEM was hydrologically corrected and the stream lines were 'burned in' 10 m prior to catchment delineation. The DEM was also used to calculate an eight-directional (D8) flow direction raster, which represents the direction of flow out of each cell (ESRI). A flow accumulation raster was then generated based on the flow direction raster, with each cell assigned a weighting equal to 1.

The flow accumulation raster was used to calculate the HA-iFLO metric. However, flow accumulation values in cells that intersected the streams were reclassed as NoData values before they were used to calculate the HA-iFLS metric. This was necessary because the flow accumulation for in-stream cells represents the terrestrial overland flow *plus* the in-stream flow contribution from further up in the stream network. We made the decision to remove the stream cells from the analysis for the HA-iFLS metric since we were attempting to represent hydrologically active areas in the terrestrial environment.

We acknowledge that using a D8 algorithm, which assigns flow from each cell into a single adjacent or diagonal grid cell, may introduce grid bias into the analysis (Tarboton, 1997). We chose to use this algorithm because it is the most commonly used flow direction algorithm and would probably be familiar and available to most users. However, the metrics described here could be calculated using alternative flow direction, flow accumulation and flow length algorithms, such as those provided in the Terrain Analysis Using Digital Elevation Models toolset (Tarboton, 1997). We also recognise that hydrologically correcting the DEM could potentially produce false ridgelines that parallel the stream, although these errors were expected to be relatively minor since the spatial resolutions of the two datasets were similar. We chose to 'burn in' the streams because we had more confidence in the locational accuracy of the streams data than in the flow paths produced by the coarser-scale DEM. This ensured that information concerning land use adjacent to the stream was as accurate as possible.

Two types of distances were generated and used to calculate the land use metrics: Euclidean distance and flow length distance. In the flow length function, the flow direction raster is used to identify the flow path, while the stream or the catchment outlet raster layers are used to represent the destination cells. This process resulted in four raster layers for each survey site, which contained the Euclidean and flow length distance between each catchment cell and the stream or the catchment outlet. A value of 1 was added to each cell to ensure that land uses directly adjacent to streams did not receive a distance equal to 0.

We chose to use Grazing and MDF land use in this study because grazing and native bushland are the predominant land use types in SEQ (Abal *et al.*, 2005) and both are correlated with in-stream indicators (Bunn *et al.*, 1999). In addition, the relative size of land use percentages (0–100) affects the lumped, iEucO and iFLO metric performance (King *et al.*, 2005). Therefore, we also examined the distribution of per cent land use in the 126 EHMP catchments using each of the metrics to ensure that we were accounting for small, intermediate and high land use percentages. Grazing and MDF land use met these requirements, with lumped Grazing ranging between 0 and 99.99% and with lumped MDF accounting for 15.3–88.6% in the EHMP catchments (Table 1, Fig. S1). We considered other land use types, including urban, crop, conservation and other forested types, but these land use percentages tended to be low and did not adequately represent medium and large proportions of the catchments. Hence, all analyses were performed using Grazing and MDF land use.

We used the Queensland Land Use Mapping Programme (QLUMP) dataset (BRS, 2002) to generate a raster dataset where 1 indicated Grazing land use and 0 represented other land uses present in 1999. The QLUMP dataset was in vector format and was resampled to create a raster dataset with a 25 m spatial resolution. This seemed reasonable since the minimum mapping unit was 1 hectare and the minimum feature width was 50 m. Grazing land use included native, introduced and modified pastures.

The MDF raster dataset was based on the Statewide Landcover and Trees Study Derived 2001 Foliage Projective Cover dataset (Kuhnell *et al.*, 1998). The foliage projective cover (FPC) represented the percentage of ground area occupied by the vertical projection of foliage and branches in 2001. The MDF class included wooded areas with FPC values between 30 and 70% as specified by Specht, Roe & Boughton (1974). Note that, since MDF was based on a different dataset than Grazing, the two categories were not mutually exclusive. The MDF cells were allocated a value equal to 1, while other cells were given a value of 0. Land use cells that intersected streams and survey sites were not removed from either land use raster substratum when the catchment metrics were calculated.

The Grazing and MDF land datasets represent a snapshot in time because we did not have access to multiple temporally variable land use datasets. We believe that this was reasonable since we were modelling the medians of the indicator data rather than indicator measurements collected during separate years. Also, the effects of land use change may take some years to become apparent and, in some cases, past land use has a stronger relationship with in-stream condition than present land use (Harding *et al.*, 1998; Strayer *et al.*, 2003).

Statistical methods

We questioned whether medians based on measurements collected in dry and post-wet seasons could be combined to form a single dataset and analysed. We tested the equality of seasonal variances using the classical Levine's test (Levene, 1960) for continuous indicators and the Browne–Forsythe test (Brown & Forsythe, 1974) for counts. Then, Student's *t*-tests were used to test for equality of seasonal means (with either equal or unequal variances), while Mann–Whitney tests (Hollander & Wolfe, 1973) were used to test for equality of medians for counts.

We generated scatter plots and calculated Spearman's rank correlation coefficients, which were used to compare per cent Grazing and MDF produced using each of the metrics. The data were also assessed to determine whether the correlation between metrics changed with catchment area. Each site was assigned a catchment size class based on the 33rd and 66th percentile of the EHMP catchment area data. This resulted in small (<29.3 km^2), medium (≥29.3 and ≤99.86 km^2) and large (>99.86 km^2) categories; correlations were then assessed for each size class. Note, hereafter these size classes will simply be referred to as small, medium and large. Sites that did not contain Grazing or MDF land uses in the catchment were not included in these analyses. Metrics that were found to be strongly correlated with other metrics were removed from further analyses.

Three sets of general linear models were fitted to each of the 13 indicators to compare the ability of landscape representation metrics to explain variability in the EHMP indicators. The first set of models contained a response variable (median EHMP ecosystem health indicator), two explanatory variables (per cent Grazing and per cent MDF) and one explanatory factor (EHMP region). The EHMP region was used to account for natural variability in the indicators and was derived by classifying streams into four regions based on altitude, mean annual rainfall, stream order and stream gradient (Fig. 2; Bunn *et al.*, 2010). We acknowledge that there was probably additional natural variability that could not be accounted for in this study. Models were fitted separately by metric type (lumped, iFLO, iFLS, HA-iFLO and HA-iFLS), meaning that each model contained a per cent Grazing and per cent MDF variable that was calculated using a single metric, such as lumped Grazing and lumped MDF or iFLS Grazing and iFLS MDF.

The relationship between in-stream response variables and land use metrics has been shown to vary with catchment area (King *et al.*, 2005); therefore, two additional model sets were fitted to determine whether area had a significant effect here. The construction of the second model set was identical to the first (described above), except that an explanatory variable representing catchment area was also included. Two additional interaction terms between catchment area and the land use metrics (Grazing and MDF) were included in the construction of the third model set. This resulted in three model sets that could be used to explore the influence of catchment area: model set (1) no explanatory variables for catchment area, model set (2) one explanatory variable for catchment area and model set (3) an explanatory variable for catchment area and interaction terms for land use metrics (Grazing and MDF) and catchment area. In total, 390 models were fit to the data (13 indicators × two seasons × five metrics × three model sets). The model residuals were checked for normality and transformations were applied where necessary. Outliers were removed only if they were considered outliers in every metric model.

Two analysis of variance (ANOVA) tests (Ott & Longnecker, 2001) were used to investigate whether catchment area affected the model results. The ANOVA test between model sets 1 and 2 was used to factor out the correlative relationship between catchment area and the response variable. Then, the ANOVA test between model sets 2 and 3 was used to evaluate whether the ability of a land use metric to explain variability in the response varied in relation to catchment area. When multiple comparisons are conducted on a dataset, it increases the probability of a type I errors (Ott & Longnecker, 2001). Since we compared five models for each of the seasonal indicators (one model for each land use metric type), a Bonferroni correction (α/n, where $n = 5$) was used to set the overall error rate at $\alpha = 0.05$. Consequently, individual tests were performed using a significance level of $\alpha = 0.01$.

When the second ANOVA test was shown to be significant (i.e. the ability of a land use metric to explain variability in the response varied in relation to catchment area), the data were split into three groups based on catchment size class (small, medium and large), and three separate linear models were fitted to the data. The models were similar to model set 1; they contained a response variable (median EHMP ecosystem health indicator), two explanatory variables (per cent Grazing and per cent MDF) and one explanatory factor (EHMP region).

Models were compared using an information-theoretic approach (Burnham & Anderson, 2004) to determine which landscape representation metric explained the most variability in the indicators. The Corrected Akaike's Information Criterion (AICc) (Hurvich & Tsai, 1989) was used to estimate the Kullback–Leibler (K-L) information loss (Kullback & Leibler, 1951) for each model.

$$\mathrm{AICc} = -2\log(L(\hat{\theta})) + 2K + \frac{2K(K+1)}{n-K-1} \tag{3}$$

where θ is a K-length vector of regression parameters relating each indicator to the explanatory variables, $L(\hat{\theta})$ is the maximum likelihood estimate of θ based on the candidate model and the data, and K is the number of parameters being estimated.

We rescaled the AICc values to create a relative AICc value, Δ_i (Burnham & Anderson, 2004):

$$\Delta_i = \mathrm{AICc}_i - \mathrm{AICc}_{\min}. \tag{4}$$

The model with the lowest AICc value was assigned a Δ_i equal to 0 and all other models a value greater than 0. The Δ_i values provide a simple statistic that can be used to interpret the strength of evidence for each candidate model; as the Δ_i value increases, the amount of support for the alternative model decreases. In addition, Burnham & Anderson (2004) provide simple rules of thumb that can help in their interpretation. For example, a $\Delta_i \le 2$ indicates that there is considerable support for a second model, $4 \le \Delta_i \le 7$ suggests that there is substantially less support for the second model and a $\Delta_i > 10$ indicates that there is in effect no support for the second model.

The likelihood of each model given the data (Akaike, 1981), $L(g_i|\mathrm{data})$, was generated by transforming the rescaled AICc values given in (4):

$$L(g_i|\mathrm{data}) = \exp(-\Delta_i/2). \tag{5}$$

The likelihoods were then normalised and used to calculate a weight of evidence statistic, ω_i, for each model

$$\omega_i = \frac{e^{(-\Delta_i/2)}}{\sum_{r=1}^{R} e^{(-\Delta_r/2)}}, \tag{6}$$

where R is the full set of candidate models for each indicator (Burnham & Anderson, 2004). The ω_i for a model set sum to one and the larger the ω_i, the greater the evidence that a model is the best K-L model in the model set (Burnham & Anderson, 2004).

Results

Exploratory analysis

Student's *t*-test and the Mann–Whitney tests showed that eight of the 13 indicators had unequal means ($\alpha = 0.05$) and two indicators had unequal variances in the dry and post-wet seasons. Interestingly, all of the invertebrate indicators had equal means and variances. For the fish indicators, the seasonal means and variances for the observed versus expected fish assemblage (FishOE) indicator were equal, while the means for the proportion of native species expected (PONSE) and the proportion of alien species (Prop-Alien) indicators were unequal and the variances equal. The only nutrient indicator, δ^{15}N (the ratio of δ^{15}N to δ^{14}N stable isotopes within filamentous algae), also had unequal seasonal means, but equal variances. The physicochemical indicators showed the greatest seasonal variation, with all of the indicators except conductivity (Cond) having unequal means. In addition, two of the indicators (Cond and maximum temperature – TempMax) produced unequal variances. Therefore, we decided to evaluate all of the indicators separately for the dry and post-wet seasons. Summary statistics for each of the indicators are provided in Tables S1 & S2.

The Spearman rank correlation coefficients for the Grazing and MDF metrics showed that all of the metrics were somewhat correlated (Tables 3 & 4), but that the HA-IDW metrics tended to be less correlated with the other metrics. The correlations between the lumped metric and the HA-IDW metrics were noticeably smaller than those of the lumped and pure IDW metrics. In addition to inter-metric type correlations, the IDW metrics were strongly correlated with each other (Tables 3 & 4). The correlation between the iEucO and iFLO, as well as the iEucS versus iFLS metrics, produced correlation coefficients >0.99 for both Grazing and MDF. There was no evidence that any of the correlative relationships differed across catchment size classes; these results are not shown here. Finally, there was no consistent tendency for Euclidean or flow length metrics to be greater or

Table 3 Spearman's rank correlation coefficients for each of the catchment metrics using Grazing land use. The metrics include the lumped, inverse-distance-weighted Euclidean distance to the survey site (iEucO) and the stream (iEucS), the inverse-distance-weighted flow length to the survey site (iFLO) and the stream (iFLS), and the hydrologically active inverse-distance-weighted flow length to the survey site (HA-iFLO) and the stream (HA-iFLS)

Metric	Lumped	iEucO	iEucS	iFLO	iFLS	HA-iFLO	HA-iFLS
Lumped	1						
iEucO	0.921	1					
iEucS	0.979	0.933	1				
iFLO	0.910	0.999	0.924	1			
iFLS	0.978	0.934	>0.999	0.925	1		
HA-iFLO	0.524	0.707	0.557	0.732	0.559	1	
HA-iFLS	0.844	0.898	0.897	0.895	0.897	0.638	1

Table 4 Spearman's correlation coefficients for each of the catchment metrics using Mid-dense forest (MDF) land use. The metrics include the lumped, inverse-distance-weighted Euclidean distance to the survey site (iEucO) and the stream (iEucS), the inverse-distance-weighted flow length to the survey site (iFLO) and the stream (iFLS), and the hydrologically active inverse-distance-weighted flow length to the survey site (HA-iFLO) and the stream (HA-iFLS)

Metric	Lumped	iEucO	iEucS	iFLO	iFLS	HA-iFLO	HA-iFLS
Lumped	1						
iEucO	0.877	1					
iEucS	0.877	0.837	1				
iFLO	0.859	0.997	0.831	1			
iFLS	0.889	0.857	0.996	0.850	1		
HA-iFLO	0.158	0.397	0.254	0.445	0.250	1	
HA-iFLS	0.664	0.707	0.842	0.706	0.839	0.292	1

smaller than the other. Given that the metrics were so strongly correlated in all catchment size classes, we removed the iEucO and iEucS metrics from further analysis.

The linear model residuals indicated that many of the indicators required transformations (Tables S1 & S2). We also considered fitting the macroinvertebrate richness (MacroRich) and Plecoptera-Ephemeroptera-Trichoptera (PET) indicators with a Poisson model since they were based on counts. However, we chose instead to fit a Gaussian model since both sets of model residuals were normally distributed. Very few outliers were removed; these included two dry season conductivity measurements, one dry season pH measurement and two post-wet season conductivity measurements. In addition, there were missing values for each of the indicators (Tables S1 & S2).

Three sets of models were tested using an ANOVA so that we could separate the effects of catchment area on the response versus the effect of catchment area on land use and the relationship to the response. The *P*-values for the ANOVA test results between model sets 1 and 2 (ANOVA 1, Tables S3 & S4) showed that there was little evidence of a catchment area effect in either the post-wet or dry season. In addition, there was no consistent evidence that a significant catchment area⁄land use metric interaction occurred in either season (ANOVA 2, Tables S3 & S4). In the post-wet season, only 4.6% of the models contained statistically significant interaction terms (PONSE HA-iFLS, the δ^{15}N iFLO and δ^{15}N HA-iFLO models), while only 7.7% of the spring models had a significant interaction term (TempMax iFLS, TempMax HA-iFLS, temperature range (TempRange) HA-iFLO, δ^{15}N HA-iFLO, and δ^{15}N HA-iFLS). When there was a significant catchment area⁄land use interaction, it was not consistent across season, with the exception of δ^{15}N.

Based on the weight of evidence from AICc, Δ_i and ω_i values, there was no one metric model type that could be considered the K-L best model (hereafter referred to as the 'best model') for all indicator categories (Figs 3 & 4; Tables S3 & S4). Rather, we found that the best model varied by indicator category, indicator and season.

Fish indicators

Metric types based on flow length to the stream (iFLS and HA-iFLS) tended to be the best models for the fish indicators (Figs 3 & 4; Tables S3 & S4). The weight of the evidence for an HA-iFLS metric model for FishOE and PONSE was substantial in both dry and post-wet seasons ($\omega_i \geq 0.69$). Although there was a significant catchment area⁄land use interaction occurring in the post-wet PONSE models ($\alpha = 0.003$), the HA-iFLS had more than twice the support of the next best model (HA-iFLO) in small and medium catchments ($\omega_i = 0.43$ and 0.44, respectively). In large catchments, the HA-iFLO model had the most support in the data ($\omega_i = 0.37$), but the HA-iFLS also had strong support ($\omega_i = 0.31$). In contrast, there was little evidence that

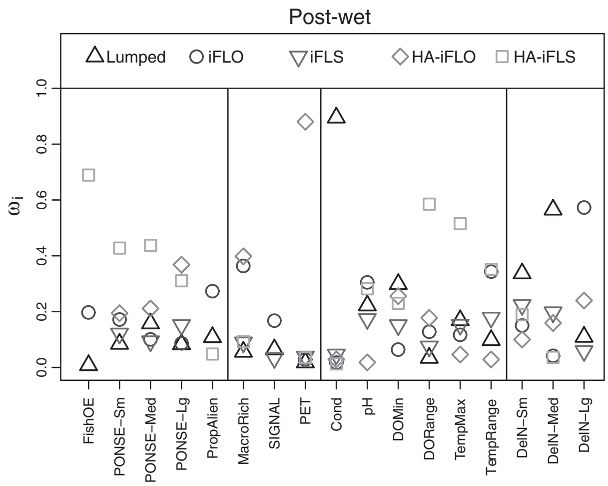

Fig. 3 Weight of evidence statistics (ω_i) for the post-wet season indicator data.

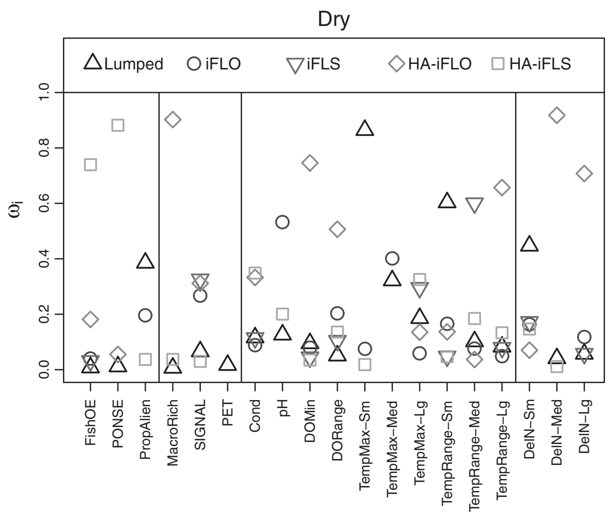

Fig. 4 Weight of evidence statistics (ω_i) for the dry season indicator data.

the HA-iFLS model was the best for the PropAlien indicator. In the post-wet season, the best model for PropAlien was based on a different flow length to stream metric (iFLS; ω_i = 0.56) although there was also considerable evidence for an iFLO metric model (ω_i = 0.27). In the dry season, the weight of evidence for the lumped and iFLS metric models was similar (ω_i = 0.39 and 0.37, respectively), while the iFLO model could not be ruled out (ω_i = 0.20).

Invertebrate indicators

In contrast to the fish data, the best models for invertebrate indicators appeared to be based on flow length to the outlet (iFLO and HA-iFLO) in both dry and post-wet seasons (Figs 3 & 4; Tables S3 & S4). In the post-wet season, the weight of evidence for an HA-iFLO metric model for PET and the macroinvertebrate sensitivity⁄tolerance score (SIGNAL) was strong (ω_i = 0.88 and 0.73, respectively). However, the evidence for the HA-iFLO and iFLO metric models was nearly equal for MacroRich in the post-wet season (ω_i = 0.40 and 0.36, respectively). In the dry season, there was little evidence for any model except the HA-iFLO for the MacroRich indicator (ω_i = 0.90), but the iFLO and HA-iFLO models had almost equal evidence for PET (ω_i = 0.53 and 0.44, respectively). The iFLS metric model for dry season SIGNAL was the only case where a flow length to the stream metric performed on par with the flow length to the outlet distance-weighted metrics (ω_i = 0.33). However, the weight of evidence for the iFLO and HA-iFLO metric models was almost equal (ω_i = 0.27 and 0.32, respectively). Interestingly, when we consider the results for both seasons, the HA-iFLO model could never be ruled out as the best model (Figs 3 & 4).

Physicochemical indicators

Analysis of the physicochemical indicators showed different responses by indicator and season (Figs 3 & 4; Tables S3 & S4). There was some evidence that one model was better than the others for three of the post-wet indicators: Cond (Lumped, ω_i = 0.90), TempMax (HA-iFLS, ω_i = 0.52) and dissolved oxygen range (DORange) (HA-iFLS, ω_i = 0.59). In contrast, three or more models based on different general metric types and distance measures demonstrated significant support in the data for the pH, dissolved oxygen minimum (DOMin) and TempRange indicators (Fig. 3). Interestingly, none of the post-wet physicochemical indicator models showed evidence of a significant catchment area⁄land use interaction.

In the dry season, five of the six indicators showed considerable support for at least two models (Fig. 4). The exception was the DOMin indicator, where there was substantial support for the HA-iFLO model over the others (ω_i = 0.75). Metrics based on flow length to the outlet also performed well for the DORange indicator; the two models with the strongest weight-of-evidence were the HA-iFLO (ω_i = 0.51) and iFLO (ω_i = 0.20) metric models. The two temperature indicator models demonstrated a significant catchment area⁄land use interaction effect. When TempRange was analysed separately for each catchment size class, there was strong support for a unique metric model in each class. In small catchments, the lumped model had the most support (ω_i = 0.60), while the iFLS model was the best model in medium catchments (ω_i = 0.60) and the HA-iFLO model in large catchments (ω_i = 0.66). When the TempMax data were analysed separately by catchment size class, the lumped model clearly had the most support in the data for small catchments (ω_i = 0.86). However, separating the data into size classes did not reduce the number of competing models at all scales; three or more models based on different general metric types and distance measures demonstrated significant support in both medium and large catchments. Finally, the pH indicator was the only physicochemical indicator to show somewhat similar results across seasons. The iFLO model was most likely to be the best model in both dry and post-wet seasons (ω_i = 0.30 and 0.53, respectively), but other metric models based on different distance measures could not be ruled out in either season.

When we examined the results by season, there was some evidence of differences in the metric model performance for physicochemical indicators. The HA-iFLS metric had considerable support ($\Delta_i \leq 2$) as the best model for five of the six of the physicochemical indicators in the post-wet season (Fig. 3; Table S3), while HA-iFLS only had considerable support for three of the six indicators in the dry season (Fig. 4; Table S4). In contrast, there was considerable support for metrics based on flow length to the outlet (iFLO and HA-iFLO) for all six indictors during the dry season (Fig. 4; Table S4), but only three of six indicators in the post-wet season (Fig. 3; Table S3).

Nutrient indicator

The δ^{15}N indicator models showed that there was a significant catchment area/land use interaction in both seasons and no one metric type was suitable for all catchment size classes or seasons (Figs 3 & 4; Tables S3 & S4). When models were fitted separately to data from each class, there were three or more models with considerable support for small catchments in the post-wet and dry seasons, although the lumped model was the absolute best model for each season (post-wet ω_i = 0.33 and dry ω_i = 0.45). In the dry season, the lumped model had also considerable support (ω_i = 0.56) for medium catchments, while both the iFLO and HA-iFLO models had considerable support in large catchments (ω_i = 0.57 and ω_i = 0.24, respectively). In the post-wet season, there was strong support for an HA-iFLO model for both medium and large catchments (ω_i = 0.92 and ω_i = 0.71, respectively).

Discussion

Data and metric considerations

The spatial resolution of the stream network dataset has been shown to have a strong influence on IDW metrics; as the resolution of the dataset increases, the near-stream catchment area increases and mean distance to the stream network decreases (Baker, Weller & Jordan, 2007). In addition, the seasonal expansion and contraction of the stream network (Junk *et al.*, 1989; Malard *et al.*, 1999; Wigington *et al.*, 2005) makes it unlikely that a relatively coarse and static stream resolution will accurately represent temporally dynamic to-stream distances (Baker *et al.*, 2007). Interestingly, the HA-IFLO and HA-IFLS metrics may be less dependent on the spatial resolution of the stream network dataset than IDW metrics that are based purely on Euclidean distance or flow length. Accounting for the hydrological activity in addition to the proximity to the stream (eqn 2) assigns larger weights to preferential flow pathways that are not included in the streams dataset, where water may have the potential to flow at various times of the year (Fig. 1). This characteristic may be particularly useful during the wet season, since a greater area within the catchment has a direct connection with the stream network compared to the dry season (Wigington *et al.*, 2005). Nevertheless, a thorough investigation is needed to determine the degree to which the HA-IDW metrics are influenced by the spatial resolution of the stream network dataset.

The spatial resolution of the land use data has also been shown to affect the ability to represent riparian areas (Gergel *et al.*, 2007). Many of the EHMP sites have riparian widths that are <30 m (F. Sheldon, unpublished data) and this may have been too coarse to provide a true representation of riparian areas, which are heavily weighted in many of the metrics based on inverse distance. In addition, the distance-decay function must be carefully considered in conjunction with the spatial resolution of the data. For example, the sharp decline in influence dictated by the d^{-1} weighting may be suitable for data with a 30 -m spatial resolution, but might not be appropriate for data with a 1- m resolution. Nevertheless, all of the metrics were based on the same land use datasets and we do not believe that this would negatively impact one metric over another.

The results presented here represent the statistical relationship between in-stream indicators and a major land use (in this case Grazing or MDF). As such, it is unclear whether the metrics would perform in a similar manner for other land use types, such as intensive horticulture or urban. In general, we believe that land use processes involving the transportation and attenuation of material via overland flow will probably be better represented by a metric that incorporates distance to the source, such as an IDW (King *et al.*, 2007) or HA-IDW metric. However, these metrics may not perform as well when connectivity is controlled by non-natural mechanisms, as is the case with point-source discharges. In addition, the hydrological connectivity between the catchment and the stream may be strongly altered in urban catchments with a high percentage of impervious substrata and an extensive storm water drainage network. In these situations, riparian areas may be bypassed and distance to the source should be based on factors other than proximity (Walsh, Fletcher & Ladson, 2005).

Prior to this study, we hypothesised that the size of the catchment might affect the ability of metrics based on different distance measures (i.e. Euclidean or flow length) to represent land use. For example, we expected the Euclidean distance to be shorter than the flow length to the outlet and that the difference between the measurements would increase with catchment area. However, we found no evidence to suggest that it is necessary to calculate both IDW based on Euclidean and flow length distance when a weighting of $(d + 1)^{-1}$ is used. When the stream intersects a land use cell, that cell is allocated a flow length and a Euclidean distance weight equal to 1. Since these cells have such a strong influence on the final catchment land use percentage, it may explain why the differences between IDW flow length and Euclidean metrics were so small. Although the two types of metrics were essentially redundant in this study, this might not be the case if another weighting scheme was used.

EHMP indicators and landscape representation metrics

Catchment area did not appear to affect strongly the relationship between in-stream indicators and land use metrics in SEQ. However, when there was a catchment effect, lumped models tended to perform well in small catchments, with the exception of the post-wet season PONSE models. This was most strongly observed in the dry season, where the lumped model was the best model for all indicators. As catchment size increased, the IDW and HA-IDW (HA-iFLO) models tended to outperform the lumped models. This is not surprising, since all land use within a small catchment would be expected to be in close proximity to a survey site and would probably affect the conditions found there. However, these results contradict those of King *et al.* (2005), who found that the per cent cropland derived using an iEucO metric explained more variability in nitrate-N concentrations than a lumped metric in small catchments (<6 km^2), but that models based on lumped cropland out-performed iEucO models in medium (6–26 km^2) and large (>26 km^2) catchments.

There were a number of differences in the study performed by King *et al.* (2005) that may account for this apparent inconsistency in the results. First, we did not test ambient nutrients because they do not have a strong correlation with land use gradients in SEQ (Smith & Storey, 2001). In addition, cropland was not included in any of the models since it does not account for a large percentage of land use in SEQ. As such, it is impossible to make a direct comparison between the two studies. Second, catchment size classes were based on the 33rd and 66th percentiles of the data in both studies, which ensured that each size class retained enough observations to fit a balanced set of models. Although the EHMP catchments appear to cover the full range of catchment size classes used in King *et al.* (2005), the EHMP catchments tended to be much larger (Table 1), with a maximum of 10 320 km^2. This may have disadvantaged the lumped models, which allocate equal weights to all land use areas, regardless of proximity to the stream or survey site. Finally, and possibly most importantly, our study was undertaken in a subtropical environment (Pusey *et al.*, 1993; Abal *et al.*, 2005). Clearly, variability in rainfall and runoff would be substantially different than the conditions found in Maryland, U.S.A., and this may have contributed to the disparity in the results. Despite these differences, both studies show that patterns in metric model performance related to catchment size may occur; though they were relatively uncommon for most indicators in the EHMP dataset. Our study also shows that the catchment size effect has the potential to vary by season since it was only present in the models for TempMax, TempRange and PONSE during a single season.

There was more seasonal variation observed in the models for the fish indicators than for the invertebrate indicators, but less than the physicochemical indicators. Our results suggest that metric types based on flow length to the stream (iFLS and HA-iFLS) may be more appropriate for the fish indicators than other metric types, regardless of season, and similar results have been found in other studies (see King *et al.*, 2004; Van Sickle & Johnson, 2008). As we mentioned previously, the area of influence represented by a metric based on flow length to the stream makes sense from an ecological perspective; fish distribution generally reflects multi-scale environmental conditions from the landscape, to the riparian zone and in-stream habitat (Gregory *et al.*, 1991; Pusey & Arthington, 2003; Allan, 2004; Kennard *et al.*, 2006a) and includes the temporal aspects of broad-scale habitat availability, configuration and connectivity (Fausch *et al.*, 2002; Isaak *et al.*, 2007; Stewart-Koster *et al.*, 2007).

The two modelled fish indicators, FishOE and PONSE, demonstrated less seasonal variability than the PropAlien indicator and seemed to be more strongly influenced by hydrologically-active areas. The multivariate predictive models used to generate the FishOE and PONSE indicators contained explanatory variables, such as mean wetted width and maximum water depth, which would be expected to reduce seasonality in the indicators (see Kennard *et al.*, 2006a,b for a detailed description of the methods and explanatory variables used). However, the model inputs were not spatially explicit and did not specifically represent hydrologically active areas. Therefore, we do not believe that the strong performance of the HA-iFLS metric is a result of the model inputs. This metric allocates a relatively strong weighting to potential flow pathways, such as intermittent channels, compared to the iFLS metric. If the magnitude and duration of flow is adequate, fish may be using these channels seasonally. The differences observed in the PropAlien indicator results could be due in part to the nature of alien fish distribution, with their presence possibly reflecting conditions or events unrelated to land use. For example, the presence of alien fish may simply reflect their physical introduction or the existence of weirs and culverts affecting dispersal, which were not accounted for in our data (Kennard *et al.*, 2005).

In comparison, the lack of seasonality in the invertebrate indicators was at first surprising since invertebrate counts elsewhere respond to fine-scale conditions that are seasonally variable (Wood & Petts, 1994; Cox & Rutherford, 2000; Mykra, Heino & Muotka, 2004). This may be the result of a prolonged drought and a reduction in catchment runoff, which occurred during this time period. In addition, the invertebrate indicators used in this study were based on assemblage indices (MacroRich and PET) and sensitivity scores (SIGNAL) rather than individual counts (Table 2), which may be less sensitive to seasonal changes (Chessman, 1995). In contrast to fish indicators, metrics based on distance to the stream outlet clearly outperformed other metric types for invertebrates in all but one case and could never be ruled out as the best model. These results are somewhat similar to those of King *et al.* (2005), who found that an iEucO developed land metric explained more variability in invertebrate assemblage than a lumped metric. In this study, the HA-iFLO model always had considerable support in the data, while the iFLO metric only had considerable support for one of three indicators in the post-wet season and two of the three indicators in the dry season. This suggests that land use in hydrologically active areas directly adjacent to the survey site may have a disproportionate influence on invertebrate indicators.

The superior performance of land use metrics based on distance to the stream outlet is somewhat intuitive. Invertebrates generally have a shorter lifespan and a more limited ability to migrate than fish (Rosenberg & Resh, 1993); though some species can escape undesirable conditions via upstream flight or downstream drift (Allan, 1995). Large-scale landscape conditions do affect invertebrates, but it is thought to be an indirect relationship through their influence on local-scale conditions (Biggs *et al.*, 1990) and the hydrologic response from the catchment (Allan, 2004). As a result, the local conditions directly adjacent to the outlet that are also located within hydrologically active areas appear to have the strongest influence on invertebrate indicators. Since the HA-iFLO metric model could never be ruled out as the best model, we suggest using it to calculate land use characteristics for invertebrate indicators based on assemblage indices, regardless of season.

There was more seasonal variation in the physicochemical indicator values and model performance than in any other indicator category. To our knowledge, no other study has used distance-weighted metrics to investigate the effect of land use on freshwater physicochemical indicators during a wet or post-wet season (but see Comelo *et al.*, 1996 for an example from an estuarine environment). In this study, the HA-iFLS metric model was regularly a candidate for the best metric in the post-wet season (Fig. 3), while metrics based on flow length to the outlet (iFLO and HA-iFLO) had considerable support as the best model in the dry season (Fig. 4). In addition, metric model performance tended to vary by catchment area in the dry season (TempMax and TempRange) compared to the post-wet season. All this suggests a seasonal shift in influence from the broader landscape-scale in the post-wet to local-scale conditions during the dry season, which is probably the result of temporally variable lateral and longitudinal connectivity in the stream network. As such, a metric giving greater influence to hydrologically active areas in close proximity to the stream may be more suitable during the post-wet season, while the areas directly adjacent to the survey site may be more suitable for physicochemical indicators during the dry season.

Interestingly, there was strong evidence that the lumped model outperformed other metric types in post-wet conductivity data. As we have mentioned previously, the increase in both lateral and longitudinal connectivity occurring in the post-wet season is likely to strengthen the relationship between landscape-scale and in-stream conditions (Johnson *et al.*, 1997; Robertson *et al.*, 1999; Olivie-Lauquet *et al.*, 2001; Pan *et al.*, 2004). In-stream conductivity is influenced by vegetation type and catchment condition (Kawakami, Honoki & Yasuda, 2001) and all locations within a catchment may contribute to in-stream conductivity values when there is a high degree of connectivity. In the dry season, the reduction in lateral and longitudinal connectivity (Junk *et al.*, 1989; Malard *et al.*, 1999; Wigington *et al.*, 2005) causes constriction of the stream network and increases the influence of local-scale conditions (Fellows *et al.*, 2009). Reductions in lateral connectivity have also been shown to reduce the impact of land use on in-stream condition (Johnson *et al.*, 1997; Pan *et al.*, 2004). This may explain why the lumped model had considerable support for both the pH and conductivity indicators in the post-wet season, when a high degree of connectivity would be expected, but not in the dry season.

Clearly, our conclusions concerning the physicochemical indicators are much more tentative than those of the fish and invertebrate indicators. Multiple models for physicochemical indicators tended to have substantial support in the data. As such, we do not recommend a single metric over another, but suggest thoroughly evaluating each indicator, identifying particularly influential processes and then selecting the most appropriate land use metric. It may also be worthwhile to compare multiple land use metrics to determine which metric(s) is most suitable for a particular physicochemical indicator.

Catchment area appeared to have a significant influence on the relationship between δ^{15}N and land use in both seasons. In small catchments, the lumped metric model always explained the most variability in δ^{15}N; though numerous IDW and HA-IDW models also performed well. These results are not unexpected since a large proportion of land is found in close proximity to the survey site in small catchments compared with large; these areas are probably to have a strong influence on in-stream conditions in either season. In contrast, we observed seasonal differences in metric model performance in medium catchments, with the lumped metric performing well in the post-wet season and the HA-iFLO performing well in the dry. These differences are also probably the result of seasonal differences in lateral connectivity between the catchment and the stream (Junk *et al.*, 1989; Malard *et al.*, 1999; Wigington *et al.*, 2005); when lateral connectivity is high in the post-wet season, a greater proportion of the catchment would be expected to have an influence on in-stream conditions than in the dry season. The results for large catchments also support this conclusion, since iFLO and HA-iFLO metrics were the only models with considerable support during both seasons. The iFLO and HA-iFLO metrics allocate the largest weighting to the area directly adjacent to the survey site and this would essentially shrink the area of influence in a large catchment. The superior performance of these metrics in large catchments may mean that many land use areas are simply too far away from the survey site to have a direct effect on δ^{15}N, even when those areas are directly adjacent to the stream.

The δ^{15}N indicator represents the ratio of δ^{15}N to δ^{14}N stable isotopes within filamentous algae collected from each site (Udy *et al.*, 2006). As such, we would not expect the same strong seasonal fluctuations in δ^{15}N, which have been observed in ambient nutrient indicators (Johnson *et al.*, 1997). Given that we evaluated only one nutrient indicator, δ^{15}N, which behaves very differently than ambient nutrient indicators evaluated in similar studies (King *et al.*, 2005; Poor *et al.*, 2008), we cannot draw general conclusions about the relationship of nutrient indicators to spatial representation metrics here.

Management implications

Lumped metrics are used in many of the predictive models currently applied in freshwater and estuarine ecology (Hale, Paul & Heltshe, 2004; Kennard *et al.*, 2005; Peterson *et al.*, 2006). The models are used to evaluate an in-stream response to disturbance gradients (Johnson *et al.*, 1997; Strayer *et al.*, 2003; Norris *et al.*, 2007), to perform environmental classifications (Snelder & Biggs, 2002; Wardrop *et al.*, 2005), as part of environmental assessments (Wickham *et al.*, 1999; Jones *et al.*, 2001) and to make recommendations about land use thresholds that may cause in-stream degradation (Bunn & Davies, 2000; Wang *et al.*, 2001). In addition, lumped metrics may be used to target conservation or restoration efforts (Linke *et al*., 2006). The methods presented here are extremely general; the product is represented as a percentage, which means that spatially explicit metrics can be substituted for lumped metrics without altering the model form. As such, these metrics will generally be expected to improve the predictive ability of many models currently in use.

One of the disadvantages of a lumped representation method is the difficulty of establishing a causal relationship between catchment processes and in-stream condition (King *et al*., 2005). The cause-and-effect linkage is generally established using a process-based model, where the exchange of material or energy is mathematically modelled based on ecological knowledge and understanding. Nevertheless, process-based models are typically not generally applicable in practice; they may be unreliable when applied in dissimilar regions, may have considerable data requirements, tend to be complex and may be computationally intensive (Sivakumar, 2008). The spatially explicit landscape representation approaches presented here provide more information about a causal relationship than a non-spatial lumped approach, with the added advantage that they are generally applicable and can be easily implemented without regard to regional differences. The distance-decay function and hydrologically active weighting scheme are simplistic representations of mechanistic processes, attenuation rates and transport pathways between catchment and stream (King *et al*., 2007; Van Sickle & Johnson, 2008). Comparing the results of different weighting schemes and distance measures allows areas with a stronger influence on in-stream conditions to be identified, which provides clues about which processes contribute to the correlation. This is useful because we cannot return entire catchments to pristine condition to improve ecological health (Allan, 2004). Rather, a comparison of different metric models could be used to identify the spatial location of particularly influential areas, which could be further investigated and potentially targeted for restoration.

Our results add to the growing evidence that spatially explicit landscape representations explain more variability in freshwater and estuarine indicators than lumped metrics, regardless of indicator category or season. That being said, there does not appear to be one metric that is most suitable for all indicators types. However, some patterns did emerge, which allowed us to make two general recommendations: (i) for fish indicators, metrics based on inverse distance to the stream tend to perform better, regardless of season and (ii) metrics based on inverse distance to the outlet appear to be more suitable for invertebrates, regardless of season. Seasonal patterns may be less evident in modelled indicators (depending on the model inputs) and indicators that represent assemblages rather than individuals. As such, indicators from a single category, such as fish or invertebrates, may be strongly correlated with different metric types. This may also be true for other indicators from the same category, such as δ^{15}N and ambient nutrients, although we were unable to make that comparison. Therefore, the methods used to calculate the indicators and the processes likely to affect them must be taken into consideration before a landscape representation metric is selected for further use. The conclusions that we are able to draw for the physicochemical indicators are much more tentative, but there may be a seasonal pattern in metric performance associated with a hydrologic flushing effect.

We believe that these metrics are a step towards a more spatially explicit landscape representation. Yet they remain simple representations, leaving plenty of opportunities for future research. For example, it is unclear whether the spatial relationships observed here hold true for other land use types, such as urban or agricultural areas, and whether different processes would be better represented by another weighting scheme or distance measure. Also, the metrics used here simply represent influence as a function of distance, with the possibility of incorporating preferential flow pathways. Yet we know that the context of the land use (i.e. what lies *between* a particular land use cell and the stream) is extremely important (Turner *et al*., 2001). Hence, the challenge is to develop more effective landscape representation methods that are generally applicable so that they may be applied to a range of land use types across diverse regions.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. The distribution of per cent mid-dense forest (MDF) and Grazing in the 126 EHMP catchments based on the lumped landscape representation metric.

Table S1. Summary statistics for post-wet season fish, invertebrate and physicochemical indicators.

Table S2. Summary statistics for dry season fish, invertebrate and physicochemical indicators.

Table S3. Model results for post-wet season indicators: corrected Akaike Information Criteria (AICc), likelihood, change in AICc (Δ_i) and the weight of evidence statistic (ω_i) for each indicator category, indicator and metric model used to select the model with the most support in the data.

Table S4. Model results for post-wet season indicators: corrected Akaike Information Criteria (AICc), likelihood, change in AICc (Δ_i) and the weight of evidence statistic (ω_i) for each indicator category, indicator and metric model used to select the model with the most support in the data.

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