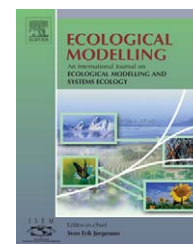


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# Subjective uncertainties in habitat suitability maps

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## ABSTRACT

Habitat suitability maps are very useful for planning management and conservation priorities. Epistemic uncertainty usually is an intrinsic part of the mapping process and yet, subjective uncertainties have rarely been addressed. Subjective uncertainty arises from subjective judgments, generally by experts, on how to interpret data and translate them into a model. This study examines how to encapsulate subjective uncertainty in a pair of 'bounding' habitat suitability maps. These maps represent extremes of the range of plausible maps obtained from alternative ways to model habitat suitability. Sambar deer (*Cervus unicolor*) was used to illustrate the process within the spatial context of the alpine areas of Victoria in southern Australia. Four habitat variables (presence of forest, distance to forest edge, presence of gullies, and amount of solar radiation) and three models were retained. A total of 22 equally plausible habitat suitability maps were compared with three different statistics (sum of suitability index, connectance and least-cost distance) to obtain bounding maps, each of them linked to a potential application of habitat suitability maps for this species. The three statistics gave different results, emphasizing the importance of considering how habitat suitability maps are used in subsequent analyses. Very large bounds were found when estimating Sambar population size through the sum of suitability values. With the connectance index, different pairs of bounding maps were found when the Alpine area or the State as a whole was considered. Using least-cost distances, we found that the uncertainty surrounding the choice of the suitability model was much more important than the uncertainty surrounding the ways of computing the habitat variables. Subjective uncertainty can be effectively propagated into subsequent analyses through the use of bounding habitat suitability maps, if the potential use of the maps in subsequent analysis is known. The importance of subjective uncertainties could therefore be assessed and decision-making in conservation ecology would be better informed.

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## 1. Introduction

A habitat suitability index (HSI) is a conceptual model that relates measurable environmental variables to the suitability of a site for a species (USFWS, 1996; Burgman et al., 2001). HSI values are combinations of environmental variables, each represented by a suitability index (SI), typically scaled from 0 (unsuitable habitat) to 1 (suitable habitat). Spatially explicit

HSI maps are created by discretizing a landscape into equal-sized subunits (pixels or cells) and calculating an HSI value for each. HSI maps are useful for planning management and conservation priorities, examining trade-offs and assessing potential impacts from human activities (Rand and Newman, 1998).

When sufficient field data are available for a species, an empirical approach can be used to derive HSIs from observa-

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tions (e.g. Hirzel et al., 2002). Alternatively, HSIs can be created from a process-oriented, conceptual model based on expert knowledge (e.g. Dettki et al., 2003; Yamada et al., 2003; Ruger et al., 2005). This conceptual approach is often used when the lack of sufficient field data is coupled with an imperative to proceed with some course of action (e.g. landscape alteration). Experts are an important source of knowledge for building habitat maps and HSIs provide a structured means of creating them. Geographic Information Systems (GIS) have been useful in eliciting knowledge of relationships between species and their environments from experts in a form that can be mapped (Radeloff et al., 1999; Zhu, 1999; Yamada et al., 2003).

Broadly defined, uncertainty is the lack of sureness or confidence about something. In biological systems, uncertainty falls into two main groups (Regan et al., 2002): epistemic uncertainty (uncertainty about a determinate fact) and linguistic uncertainty (uncertainty that arises because our natural language is vague, ambiguous, and context dependent). Regan et al. (2002) further classified epistemic uncertainty into five main types: measurement error, systematic error (e.g. bias in the measuring equipment), natural variation, subjective judgment and model uncertainty. All these types of uncertainty affect models in ecology (Elith et al., 2002). HSI models are particularly affected by subjective judgment and model uncertainty, which is why we concentrate on these two types of uncertainty in this study. Uncertainty due to subjective judgment occurs as a result of interpretation of data, especially when data are scarce and error prone. This is particularly the case when expert knowledge is the primary means of informing a HSI, and when experts estimate facts (e.g. the type of environmental factor a species is sensible to) or classifications (e.g. the relative importance of factors). Model uncertainty occurs as a result of our representation of physical and biological systems, and because models are simplifications of real processes.

Different methods have been developed to treat some form of uncertainty associated with HSI models. Burgman et al. (2001) included model uncertainties about the form of relationships between environmental variables and suitability in a HSI model to explore options for managing a threatened species' habitat. Larson et al. (2004) used a simplified application of the method of Burgman et al. (2001). They created upper and lower limits for ovenbird habitat suitability and propagated this uncertainty through a Population Viability Analysis to obtain bounds around probabilities of population quasi-extinction. Ottaviani et al. (2004) proposed a method to treat the uncertainty associated with spatial and temporal variability of presence-only field observations. The spatial uncertainty associated with the delineation of suitable and unsuitable habitat patches is also pervasive in spatially explicit ecological models (Jager and King, 2004). Jager et al. (2005) assessed the variations in model predictions that resulted from the spatial uncertainty associated with a given landscape reference map. To model this type of uncertainty, they used stochastic simulation to generate alternative landscapes that shared the spatial-statistical qualities of the reference landscape. This gives more realistic alternative landscapes than other techniques using for example fractal models (e.g. Gardner and Gustafson, 2004).

However, uncertainties associated with habitat models are broader than those discussed above. For example, experts usually select from among many alternatives a single set of habitat variables and a single way of combining them. Moreover, another, less visible, source of subjective judgment in GIS-based HSI models is linked to the fact that the GIS modeler decides among several different, plausible ways of computing habitat variables nominated by an expert. The modeler's choice generally depends on his or her experience and understanding of the problem, which may lead to a subjective interpretation of the task and to modeling choices that are often not communicated (but see Meer, 2001). This may have important consequences in decision-making for conservation, especially if the decision-maker is unaware of the modeler's subjective decisions and their effect on a HSI map. This lack of transparency could be particularly detrimental when a map is used by other people and in new contexts. For example, studies in statistical phylogeography (Knowles, 2004) and landscape genetics (e.g. Manel et al., 2003) make increasing use of HSI maps as surrogates for habitat permeability to model gene flow. In the absence of an appropriate treatment of uncertainty, inferences about links between genetic data and habitat variables will be error prone. Subjective judgments made by a GIS modeler can often fall into the "model uncertainty" category, because of the decision on how to model a habitat variable. We will therefore adopt in the following the broader term "subjective uncertainty" to refer to uncertainties emerging from subjective judgments and/or model uncertainty.

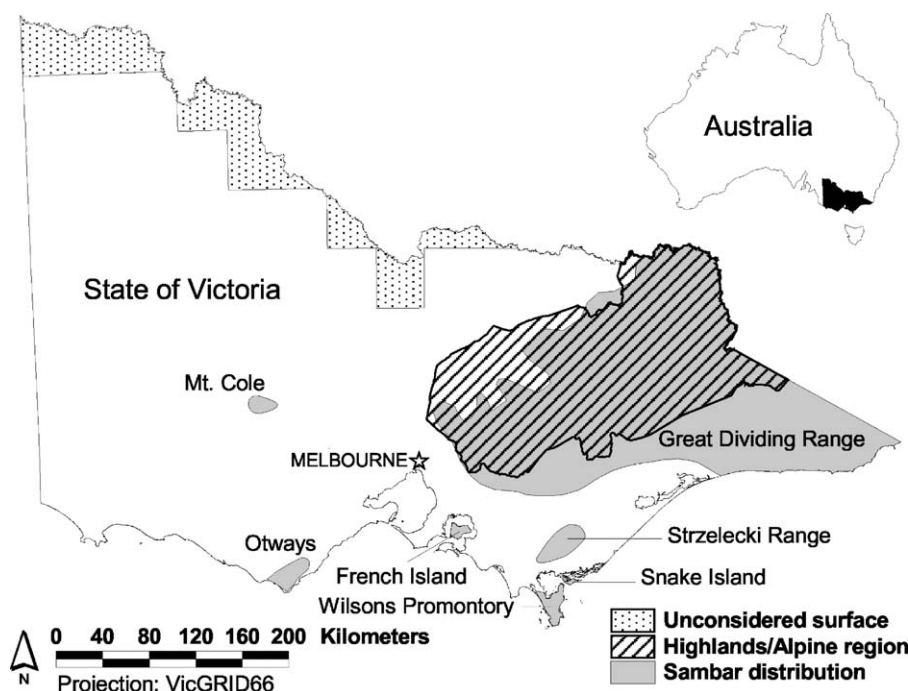
The GIS modeler's subjective uncertainties are not statistical. They represent a qualitative interpretation of ecological ideas. In many cases, the uncertainty is a discrete decision rather than a continuous function, making a continuous representation of uncertainty (a fuzzy number) inappropriate. Thus, these subjective uncertainties cannot be easily propagated into subsequent analysis or decision-making processes.

The purpose of this paper is to examine how subjective uncertainty of a model can be included in habitat suitability mapping. We propose GIS modelers generate 'bounding maps' defined by a set of alternative realistic choices in modeling HSIs that result in the most extreme, plausible maps possible, among the choices available. Given a set of plausible HSI maps, the task is to find the pair of HSI maps that encapsulates the broadest range of subjective uncertainty. We apply this approach to a habitat model for Sambar deer, an invasive species in the alpine areas of Victoria in southern Australia. The example will illustrate the potential for bounds to be influenced by the purpose of the map and the type of subsequent analysis. We will compare three statistics linked to a potential use of habitat suitability maps for Sambar deer and discuss the importance of uncertainty-informed HSI maps and how they may be used to model the population dynamics of the species.

## 2. Methods

### 2.1. Sambar deer in the study area

Sambar deer (*Cervus unicolor*) were originally introduced to Victoria from Sri Lanka and India in the 1860s (Harrison, 1998).



**Fig. 1 – Limits of the Highlands/Alpine region, approximate boundaries of the current distribution of Sambar in Victoria (after Lucas, 2001; Moriarty, 2004), and unconsidered surface (due to lack of data).**

They have an adaptable diet and high fecundity and are rapidly expanding their range. Currently, they are present throughout the Great Dividing Range of eastern Victoria and in the southern part of the adjacent State of New South Wales. Occasional sightings of Sambar have been reported in forest patches including the Mt. Cole-Pyrenees group, Wilsons Promontory, Strzelecki Range, French Island, Snake Island and the Otways (Fig. 1).

Sambar are the largest of Australia's six feral deer species. Adult stags can weigh over 300 kg, are solitary and possess large territories that encompass the range of several hinds. Hinds do not tend to form herds (Karanth and Sunquist, 1992) and commonly occur in small family groups of three to four individuals including calves and yearlings. Mating can occur throughout the year and hinds can produce calves annually (Downes, 1983; Bentley, 1998; Harrison, 1998). The characteristic wariness and predominantly nocturnal habits of Sambar, along with their low population density, contribute to a lack of awareness of their existence in forest in Victoria.

Sambar deer and their effects on the environment are not formally monitored or managed in Victoria although hunting in some areas is thought to control their numbers. Peoples' beliefs about the type and severity of their impacts conflict (Lucas, 2001). In its native range in India, the species damages crops (Udaya Sekhar, 1998) but substantial impacts in Victoria have not been formally documented (Stockwell, 2003). If future studies show significant impacts on the native flora of the State of Victoria, it is possible that management strategies (e.g. fencing, culling) may be enforced to limit these impacts. Lucas (2001) used a population model to explore the viability of populations at Lake Eildon National Park (LENP, north-east of Melbourne; Lucas, 2001) under alternative management sce-

narios. One of the key elements was a habitat suitability map. The extension of this work to the scale of the State depends on habitat maps at appropriate scales. The maps developed so far (Downes, 1983; Mays, 2003; Yamada et al., 2003) do not account for the subjective uncertainties in the habitat mapping process.

This study focuses on the Highlands/Alpine region (HAR; Fig. 1) of Victoria for which National Park management plans are being developed. Opportunistic sightings and anecdotal records suggest Sambar are increasing in numbers in these conservation areas (I. Mansergh, personal communication, 2003). Lucas (2001) used nine local experts to estimate a mean Sambar population density of 2.7 deer/km<sup>2</sup> (with an interquartile range of [1–7.5]) in forest habitat of Lake Eildon National Park. This is within the range of Sambar population densities recorded in their native habitat (0.5–10.7 deer/km<sup>2</sup>) (Harikumar et al., 1999; Biswas and Sankar, 2002; Jathanna et al., 2003). Other considerations about Sambar ecology are discussed below in relation to the environmental variables retained for this study.

## 2.2. Environmental variables and subjective uncertainties

Yamada et al. (2003) elicited conceptual models for Sambar habitat in LENP from 12 local experts. These experts identified four environmental variables consistently: presence of forest, distance to forest edge, presence of gullies, and amount of solar radiation.

These terms are vague and ambiguous, so that several different, precise definitions could represent them adequately. This means that a subjective judgment needs to be made by

someone (often the GIS modeler) about: (i) how to derive these environmental variables from existing GIS layers, and (ii) how to relate each derived variable to habitat suitability values. Table 1 describes the nature of subjective judgments required for several types of uncertainties associated with our data and models, along with the decisions made to handle these uncertainties (details are given below).

### 2.2.1. Forest (FOR)

Sambar are less specialized in food requirements than are other ungulates (Schaller, 1967). There are no known plants or floristic groups essential for their welfare (Downes, 1983), although selective browsing has been observed (Stockwell, 2003). In their native Asian range, Sambar are found in semi-arid deciduous (Bagchi et al., 2003), tropical moist deciduous and tropical dry deciduous forests in India (Udaya Sekhar, 1998; Biswas and Sankar, 2002; Jathanna et al., 2003), and cool moist mountain forests in Sri Lanka (Padmalal et al., 2003). In New Zealand, where the species was introduced during the 19th century, Sambar occupy remnant indigenous forest, swamps, pine plantations and other exotic forest/scrub (Douglas, 1990; Forsyth and Duncan, 2001).

In south-eastern Australia, Sambar are found mainly in the eastern part of the tall open-forest (wet sclerophyll forest) and open forest region of the central highlands and alpine area (Downes, 1983) (Fig. 1). They use a mosaic of forest types although, according to Downes (1983), a central feature of their habitat is the presence of “wet sclerophyll understorey”, moist gully vegetation best developed in tall open-forest.

Forests are thought to be important for the security they provide Sambar. Although alert, wary and usually staying at long distances from human activities, Sambar have been observed to bed down within sight and sound of farm and forestry workers (Douglas, 1990). In Yarra Range National Parks (YRNP), Sambar are increasingly seen browsing on private gardens, next to houses and roads (YRNP Rangers, personal communication, 2003). However, it is not known whether these observations are due to population growth, habituation, or the attraction of food and water close to inhabited areas (Houston, 2003).

Sambar inhabit a wide array of forest types in their native range and in introduced areas, making the specification of forest types as habitat in Victoria uncertain. To account for this, we used the ecological vegetation classes (EVC) map of Victoria (NRE, 2001), a composite of 1:100,000 and 1:25,000 local vegetation maps, currently the most accurate and detailed vegetation map of the State. We produced two forest maps, one narrowly defined and the other broadly defined. These two “extreme” maps represent uncertainty by encompassing the full array of plausible vegetation surfaces that are or may become Sambar habitat. This process is similar to an interval with values around a point estimate (not known), and our two forest maps can therefore be called “bounding maps”.

The narrowly defined forest map was built by selecting the EVC categories that best matched Downes (1983) forest map of tall open-forest and open-forest with canopy greater than 30 m high. These two forest types contain a wet sclerophyll understorey. The usually dense undergrowth and difficult terrain minimize hunting, and this map therefore represents ideal breeding habitats for Sambar (Downes, 1983).

The broadly defined forest map was constructed by adding to the narrowly defined map the areas of open-forest with canopy less than 30 m high. This forest type has less wet sclerophyll understorey and the open nature of the vegetation makes human access easy and hunting pressure is greater. However, this is still considered to be good breeding habitat for Sambar (Downes, 1983). Because there is no direct relationship between Downes’ categories and EVC categories, we reclassified the EVC categories according to their description to match Downes’ forest categories. In several cases, we used the GIS to check visually that the geographic area of a reclassified EVC category corresponded to Downes’ map.

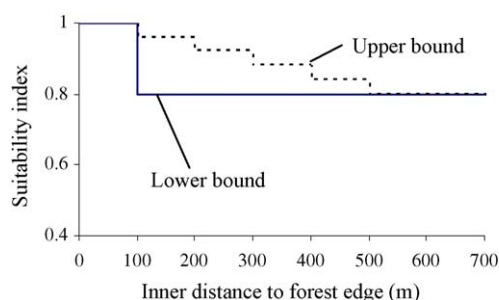
### 2.2.2. Distance to forest edge (EDG)

Forest edge is an important habitat component for a majority of deer species, including Sambar (Harrison, 1998; Mason, 2001). Sambar prefer forest for cover, foraging and breeding (Boroski et al., 1996), but also need to remain close to open areas where browsing is easy. The ecotone also provides a wider variety of food plants than either adjacent community (Yamada et al., 2003).

In this model, we are interested primarily in a suitability function that depends on distance from the forest edge inside forest, because we want HSI maps to reflect breeding capacities and the carrying capacity of the environment (unlike Yamada et al. who calculated distances inside and outside the forest). Open areas outside forest are not suitable for breeding. Yamada et al. (2003) derived the suitability of the forest edge in LERP with a linearly decreasing function of suitability from the edge to a distance to forest edge inside forest of 200 m. However, the distance and shape of the suitability function inside the forest are very uncertain. We used an interval of 100–500 m to bound this estimate. We used the Euclidean distance function in ARCGIS Ver. 8.3 (ESRI, Inc., Redlands, USA) to compute inner distances to forest edge for both bounds. We then used the suitability functions illustrated in Fig. 2 to translate distance to habitat suitability.

### 2.2.3. Gullies (GUL)

All 12 of Yamada et al.’s (2003) experts considered gullies to be important for browse, shelter, water and breeding (Downes, 1983; Lewis et al., 1990; Bovill, 2000). Gullies are also corridors for Sambar movements between forest and adjacent open feeding sites (Douglas, 1990).



**Fig. 2 – The functions used to convert distance to forest edge to the suitability index. Inner distance refers to within forest distance. The stair-like form of the functions is due to the 100 m resolution of the maps.**



**Table 1 – Range of uncertainty in Sambar deer habitat suitability maps in Victoria**

Type of uncertainty <sup>a</sup>	Parameter	Nature of subjective judgment required	Considerations and decision <sup>b</sup>
Measurement error	Delineation of vegetation boundaries in EVC map	Determine what other parameters will be affected by the error; determine whether to consider the error, or at what scale it will be considered	Depending on location, errors can range from 100 m to 1 km (NRE, 2001), but were not considered here
	Assignment of vegetation categories in EVC map	Determine what other parameters will be affected by the error; determine whether to consider the error, or at what scale it will be considered	Errors are possible, but depend on the source in the composite EVC map, and were therefore not considered here
	DEM vertical error	Determine what other parameters will be affected by the DEM error; determine whether to consider the error, or at what scale it will be considered	Depending on location, errors can range from 1 m to 10 m (NRE, 2002), but were not considered here
Subjective judgment	Presence of gullies (GUL)	Determine combination of altitude thresholds and neighborhood widths that represent extreme, but plausible, presence of gullies. Determine whether a threshold value or a continuous function is used to represent suitability index (SI)	GUL1: altitude threshold = –10 m; neighborhood size = 100 m (Mays, 2003)  GUL2: altitude threshold = –20 m; neighborhood size = 200 m (Yamada et al., 2003) A threshold value was chosen
	Amount of solar radiation (ASR)	Determine what type of solar radiation Sambar are sensitive to (e.g. morning radiation, mean seasonal radiation); determine what statistics will be used for ASR; determine the function linking ASR to SI	ASR1: sun index (aspect and slopes) (Wilson et al., 2003)  ASR2: DEM-based solar irradiation (NSW/NPWS, 1998) A linear relationship between ASR and SI was chosen
	Forest/non-forest (FOR)	Determine what type of vegetation is considered as forest for Sambar; determine the plasticity of the term forest by considering broadly defined and narrowly defined forest types	FOR1: narrowly defined—only tall open-forest and open forest from Downes (1983)  FOR2: broadly defined—extrapolation from the work of Yamada et al. (2003) by using the complete map from Downes (1983)
	Inside distance to forest edge (EDG)	Determine bounding values that encompass the best estimate; determine the function linking EDG to SI	EDG1: distance decay function up to 100 m  EDG2: distance decay function up to 500 m A linear relationship between EDG and SI was chosen
	Resolution of the final HSI map	Determine what minimum resolution will be used; determine what aggregation method will be used (e.g. mean, median)	Due to the area of Victoria and computer constraints, a resolution of 100 m was chosen, by using mean values as aggregation method
Model uncertainty	Variables to be considered	Determine what variables will be considered in the model	Considered variables: GUL, ASR, FOR, EDG
	HSI model structure	Determine the weight that will be given to each parameter and the function linking them; determine how many models will be considered as equally plausible	Three models were chosen  1. HSI = FOR 2. HSI = (FOR + EDG)/2 3. HSI = (FOR/2) + (2GUL + ASR + EDG)/8

<sup>a</sup> According to the taxonomy of uncertainty of Regan et al. (2002).

<sup>b</sup> Bold names define scenario for each variable, and are used later in the text and figures.

There was no map of gullies at the scale of the State so we created one from the 20-m Digital Elevation Model (DEM; NRE, 2002), as follows:

- for each cell, we subtracted from its altitude the mean altitude of all cells within a given circular neighborhood ( $r$ );
- if the resulting value was lower than a given threshold ( $t$ ), the cell was classified as a gully.

The values given to  $r$  and  $t$  have a substantial effect on the resulting maps of gullies in a landscape. Elith et al. (1997) used  $r=80$  m and  $t=-12$  m, Yamada et al. (2003) used  $r=200$  m and  $t=-20$  m, while Mays (2003) used  $r=100$  m and  $t=-2$  m. For the latter, the parameter combination results in a very high density of gullies in the landscape, and we doubt that this parameter combination is appropriate to capture gullies when used at the scale of the State. All combinations of parameter values were chosen subjectively (for example, with reference to known landscape features), but the subjective basis for the decision is not necessarily consistent between models. For Sambar, there are no field data that can help a modeler to set these values objectively. It is possible that only major deep gullies affect the presence and abundance of Sambar. It is also possible that smaller, shallower gullies are important where food resources are scattered or during droughts. We accounted for these uncertainties by using two sets of values representing plausible extremes. We chose  $r=100$  m and  $t=-10$  m, and  $r=200$  m and  $t=-20$  m. Suitability was given a value of 1 where gullies were present, and 0 elsewhere. We decided to use a threshold value rather than applying a continuum of habitat suitability linked to the depth of gullies. Experts indeed perceive landscape elements as either a gully or not a gully, and we lack knowledge on whether Sambar perceive suitability of gullies in a continuous manner.

#### 2.2.4. Amount of solar radiation (ASR)

Yamada et al.'s (2003) experts all agreed on the importance of solar radiation for Sambar, reflecting a thermal requirement (Moore, 1994; Bovill, 2000). Yamada et al. (2003) used specially developed scripts (NSW/NPWS, 1998) to compute an annual solar radiation index that takes into account aspect, hillshade and latitudinal effects on the incoming direct and diffuse radiation. However, there are other ways to calculate solar radiation. Two common methods are to use the cosine of the aspect to obtain an insulation index, which is at maximum for north-facing slopes (Shafii et al., 2003), or to obtain a so-called sun index by combining aspect with slope (Wilson et al., 2003; Gibson et al., 2004). A sun index is obtained from:

$$SI = \cos(\text{aspect}) \times \tan(\text{slope}) \times 100$$

There are no data to identify the most appropriate way to measure ASR. We accounted for this uncertainty by computing two plausible suitability indices for ASR: one with the annual solar radiation index, the other with the sun index. For each resulting GIS layer, ASR values were rescaled to vary from 0 to 1 to obtain a habitat suitability map. The choice of a continuous variable is justified by the judgment that Sambar are likely to respond physiologically to a range of different intensities of solar radiation.

### 2.3. Combination and comparison of HSI maps

Fig. 3B provides, for each of the four habitat variables, an example of the extent of the difference between the two alternative ways of representing the variable. To further investigate the differences between them, we computed a simple linear correlation coefficient, on a pixel-by-pixel basis, over all forest pixels. We also computed an asymmetric distance version of Kulczynski's coefficient (Legendre and Legendre, 1983). The Kulczynski's coefficient for comparison of map  $j$  versus  $k$ ,  $D_{jk}$ , is

$$D_{jk} = \frac{\sum_{i=1}^n X_{ij} - \sum_{i=1}^n \min(X_{ij}, X_{ik})}{\sum_{i=1}^n X_{ij}},$$

where  $X_{ij}$  and  $X_{ik}$  are the habitat suitability for cell  $i$  for maps  $j$  and  $k$ , respectively, and  $n$  is the number of cells. Similarly,  $D_{kj}$  can be calculated for  $k$  versus  $j$ , and  $D_{kj}$  is not, in general, equal to  $D_{jk}$ . Asymmetric Kulczynski's coefficients are not influenced by agreement of zeros. We used them here to measure how HSI values relate to each other within a pair of HSI maps. The asymmetric Kulczynski coefficient is zero when all values in a given HSI map are lower than or equal to their corresponding values in another HSI map.

Due to computation limitations, all habitat suitability maps were aggregated to 100 m resolution. Other technical considerations for creating HSI maps are summarized in Table 2.

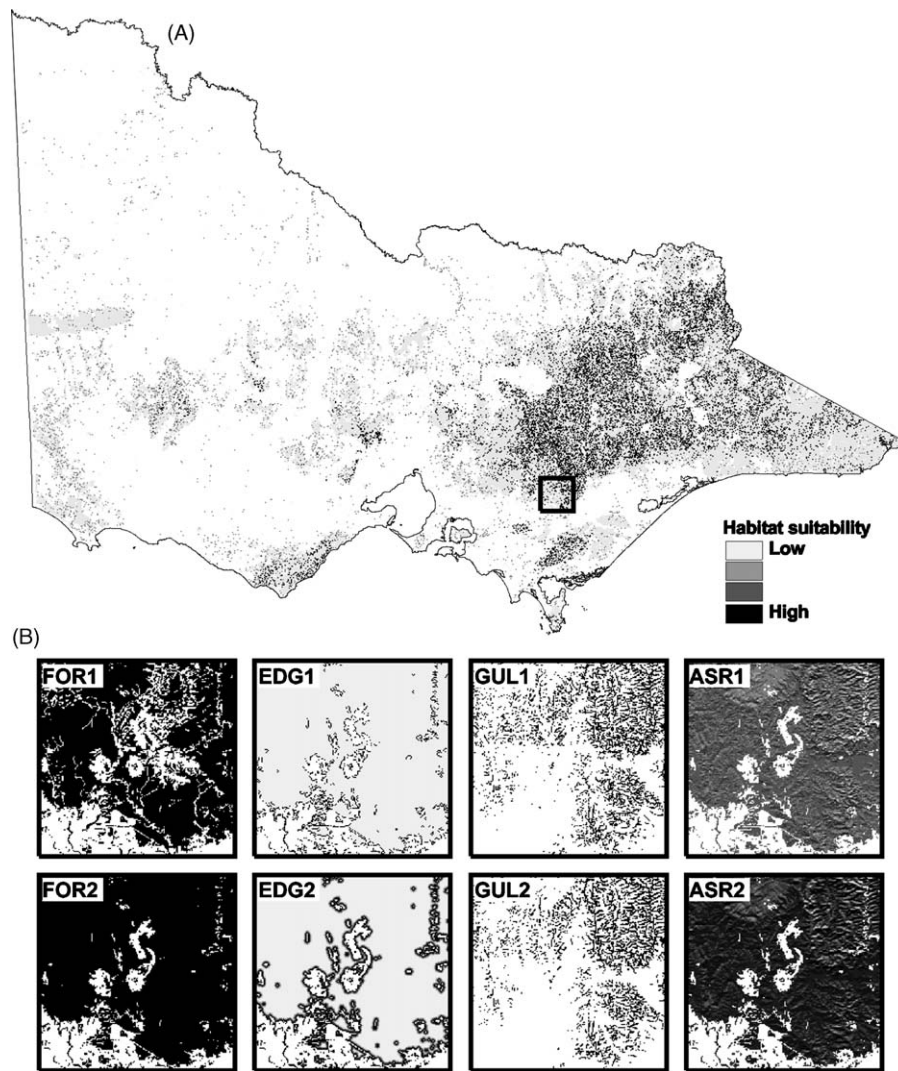
Apart from uncertainty in each SI, model uncertainty was present in the form of alternative HSI models. We specified three possible alternatives. The simplest assumed suitability was uniform within forest areas. The second acknowledged the potential suitability of forest edges through the function of distance to forest edges. The third combined the four variables in the way recommended by Yamada et al. (2003) as

$$HSI = \frac{2 \times SI_{GUL} + SI_{ASR} + SI_{EDG}}{4}$$

We assumed that findings at the small scale of LENP by Yamada et al. (2003) can be extrapolated to the whole State. These three alternative models are described in Fig. 4A.

Given model uncertainty and alternative ways of computing each SI, it is not possible to select a priori the combination of SIs that will result in the most extreme HSI maps. The only sure way was to compute all possible combinations of parameter values. Fig. 4B shows the binary tree used to output the 22 HSI maps reflecting subjective uncertainty. Maps were obtained through standard cartographic algebra in the GIS. An example (HSI map no. 15) is depicted in Fig. 3A.

We used three statistics to explore discrepancies among HSI maps. Each of these represents possible (though not necessarily advisable) interpretations of the maps. First, we calculated the total suitability (TS) of each map by summing suitability values of all cells. By assuming a linear relationship between Sambar density and habitat suitability, we can use TS as a surrogate for the total carrying capacity or population size of the area. A typical use of this statistic is the comparison of potential Sambar densities among regions, which may be valuable for monitoring programs or culling strategies.

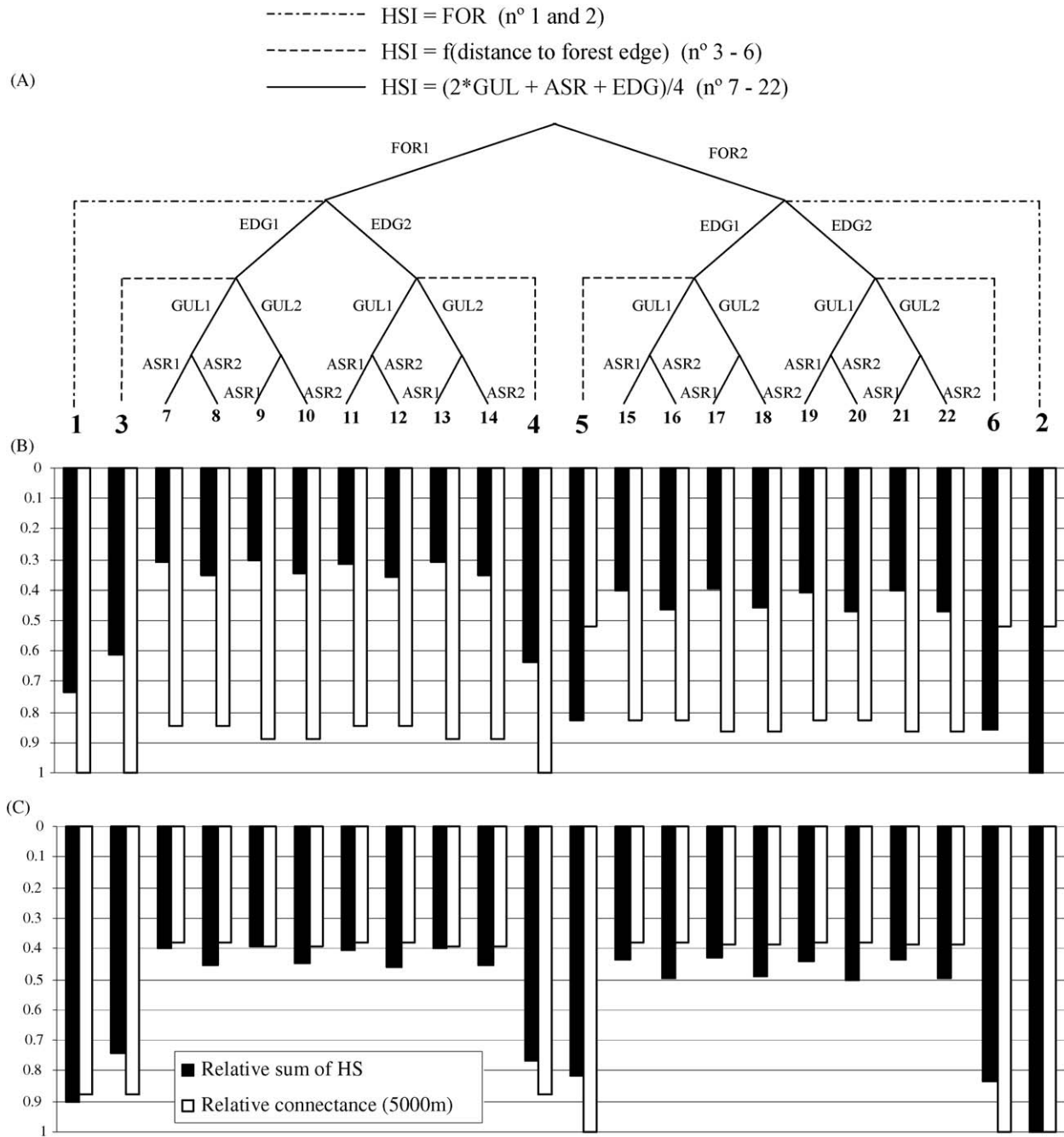


**Fig. 3 – (A) Example of habitat suitability map from HSI map no. 15 (described in Fig. 4A). (B) Illustration of the differences in habitat suitability between the two alternative representations of the four individual habitat variables: presence of forest (FOR1 and FOR2), distance to forest edge (EDG1 and EDG2), presence of gullies (GUL1 and GUL2) and amount of solar radiation (ASR1 and ASR2).**

**Table 2 – Technical considerations for creating habitat suitability maps**

Habitat suitability component	Initial resolution/format	Data manipulation <sup>a</sup>
Forest habitat	Shapefile	FOR1 and FOR2: reclassification, fusion of forest polygons and aggregation to 100 m grid
Distance to forest edge	Shapefile	EDG1 and EDG2: distance computation, and aggregation to 100 m grid through a mean value kernel
Presence of gullies	20 m DEM	GUL1 and GUL2: circular filter to find gullies, and aggregation to 100 m grid
Amount of solar radiation	20 m DEM	ASR1: computation of aspect and slope, combination through cartographic algebra, and aggregation to 100 m grid ASR2: aggregation to 100 m grid, computation of DEM-based solar irradiation
Final habitat suitability map	Habitat suitability components at 100 m resolution	HSI: cartographic algebra to combine habitat suitability components

<sup>a</sup> All aggregation functions were done in ARCVIEW using the mean of aggregated values. Model acronyms refer to Table 1.



**Fig. 4 – (A) Binary tree of subjective uncertainty describing how parameters (indicated on tree branch) were combined to obtain the 22 alternative habitat suitability (HS) maps. The number at the end of a tree branch identifies the HSI map and is used in the text. Results for each statistic are relative to the highest value of this statistic (value of 1). The relative sum of habitat suitabilities and relative connectance (within a radius of 5000 m) are depicted for each HSI map for the State of Victoria (B) and for the Highlands/Alpine region (C).**

We also computed a connectance index (CT) on each HSI map using FRAGSTATS (McGarigal et al., 2002), as

$$CT = \left[ \frac{\sum_{j \neq k}^n c_{jk}}{(n(n-1))/2} \right] \times 100,$$

where  $n$  is the number of patches,  $c_{jk} = 1$  when patches  $j$  and  $k$  are within a threshold Euclidean distance  $t$  of each other, and

$c_{jk} = 0$  when the distance between patches  $j$  and  $k$  is greater than  $t$ . CT equals the number of functional joinings between all habitat patches, divided by the number of possible joinings between all patches. CT characterizes the connectivity (or connectance) of the landscape. In the context of the management of Sambar populations, a connectance index based on HSI maps may predict the ease with which Sambar disperse within the landscape. If management actions are enforced



in the future to limit range expansion of Sambar in Victoria, alternative management options could be compared by calculating the connectance of the landscape under alternative habitat management scenarios. The connectance index has been shown to perform much better than other connectivity measures based solely on the nearest patch (Moilanen and Nieminen, 2002). Because patches of suitable habitat need to be defined to compute CT, we reclassified all cells in the maps by assigning a value of 0 (unsuitable) where  $HSI < 0.5$ , and a value of 1 (suitable) where  $HSI \geq 0.5$ . There is clearly a high degree of uncertainty associated with the mean dispersal distance of Sambar, and on how far they would venture into non-habitat to reach a habitat patch (Lucas, 2001). We used a threshold distance  $t$  of 5000 m.

The third statistic was developed to characterize the degree to which the landscape facilitates or impedes movements of Sambar (functional connectivity; Tischendorf and Fahrig, 2000, 2001; Moilanen and Hanski, 2001). The statistic is based on the least-cost distance (LCD) algorithm, which computes a deterministic trajectory (or least-cost path) between a source point and a target point by using a friction (or resistance) layer. A least-cost path minimizes the sum of frictions of all cells along the path, and this sum is the least-cost distance (for detailed description and discussion of the algorithm; see Adriaensen et al., 2003). Least-cost distances may give a more realistic ecological measure of connectivity than statistics based on Euclidean distances (e.g. Chardon et al., 2003; Coulon et al., 2004). This measure of connectivity may be translated into probabilities of migrations among individuals or subpopulations, or into some measure of isolation (e.g. Coulon et al., 2004). In this context, HSI maps are important to inform models such as Population Viability Analysis (e.g. Lucas, 2001; Reed et al., 2002).

For the sake of computational efficiency, we only considered the extent of Highlands/Alpine region for this third statistic. Suitability values were transformed into friction values ( $F_i$ ) that express the relative difficulty of moving through each cell by assuming an inverse relationship between HSI and  $F_i$  (Coulon et al., 2004) according to the function:

$$F_i = \begin{cases} 101 - (\text{trunc}[100 \cdot HSi]), & \text{if } HSi > 0 \\ 200, & \text{if } HSi = 0 \end{cases}$$

where 'trunc' is the decimal truncation. This function generates friction values between 1 and 101 in forested areas, and 200 outside forests, values comparable with those used in a

study of Roe deer in France (Coulon et al., 2004). LCD assumes animals maximize their use of high suitability areas when moving between two locations. To characterize the general LCD-based connectivity of the Highlands, we drew 100 points at random on the broadly defined forest map using the Animal Movement extension to ARCVIEW (Hooge and Eichenlaub, 2000). Points were constrained to fall in forested areas. For each HSI map, we computed a matrix of pair-wise LCD among these points with PATHMATRIX Ver. 1.0 (Ray, 2005). The differences between these matrices were then assessed using Mantel's test of matrix correspondence in MANTELN (Ray and Excoffier, 2003), with a permutation procedure (10,000 permutations) to obtain  $p$ -values. The resulting pair-wise correlation matrix was used as input for non-metric multidimensional scaling ordination (MDS) (Kruskal, 1964a, b), to represent the multivariate data in two dimensions. This analysis was performed with SYSTAT Ver. 10 (SPSS Inc., Chicago, USA). In this context, the pair of HSI maps whose corresponding matrices of pair-wise LCDs exhibited the lowest correlation were considered to be the bounding HSI maps for the LCD analysis, encompassing subjective uncertainty on habitat suitability.

### 3. Results

At the scale of the State of Victoria, correlations between each pair of alternative SI variables range from 0.72 to 0.83 (Table 3). Apart from the SI maps linked to gullies, the four other pairs of variables have Kulczynski's coefficients of 0 (from the point of view of the first member of each pair, FOR1, EDG1 and ASR1). This results from the fact that the spatial extent of FOR1 is a subset of FOR2. For the pairs EDG1/EDG2 and ASR1/ASR2, it indicates that the suitability values of EDG1 and ASR1 are always lower than or equal to their corresponding alternative EDG2 and ASR2. Positive values for both Kulczynski's coefficients of the pair GUL1/GUL2 reveal that a member of the pair is not a subset of the other, and that presence or absence of gullies is therefore computed differently, depending on the surrounding topography.

The results of comparisons for the Highlands/Alpine region are similar to those for the State, apart from a higher correlation and a lower Kulczynski's coefficient for the pair FOR1/FOR2. This indicates that the ratio of broadly defined to narrowly defined forest is lower in the Highlands/Alpine

**Table 3 – Comparisons between pairs of alternative SI variables**

	FOR1 FOR2	EDG1 EDG2 (FOR1) <sup>a</sup>	EDG1 EDG2 (FOR2) <sup>a</sup>	GUL1 GUL2 <sup>b</sup>	ASR1 ASR2 <sup>b</sup>
Pair of variables (State of Victoria)					
Correlation	0.812	0.725	0.741	0.806	0.828
Kulczynski's coefficient <sup>c</sup>	0.000 0.268	0.000 0.041	0.000 0.035	0.212 0.156	0.000 0.353
Pair of variables (Highlands/Alpine region)					
Correlation	0.851	0.700	0.711	0.787	0.891
Kulczynski's coefficient <sup>c</sup>	0.000 0.100	0.000 0.037	0.000 0.026	0.202 0.150	0.000 0.345

<sup>a</sup> Comparisons of EDG1/EDG2 HSI maps are made within each alternative definition of the forested area (indicated in brackets).

<sup>b</sup> Comparisons of ASR1/ASR2 and GUL1/GUL2 HSI maps are made by considering only the extent of the broadly defined forest map (FOR2).

<sup>c</sup> Due to its asymmetry, a pair of coefficients is shown for a given pair of variables.

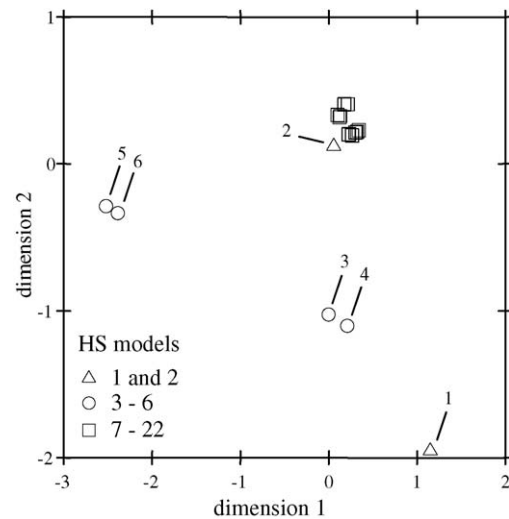
region. The uncertainty in the extent of forested habitat for the Sambar is lower in Highlands/Alpine region than it is in the State as a whole.

Results of the differences of the first two descriptive statistics (relative sum of habitat suitabilities and connectance) applied to the 22 HSI maps are shown in Fig. 4B for the State, and in Fig. 4C for the Highlands/Alpine region. As expected, the HSI map with the highest HSI sum is the broadly defined uniform forest map (no. 2), for which all forested areas are considered equally and highly suitable for Sambar. At the scale of the State, HSI maps derived solely from the distance to forest edge (nos. 3–6) have a lower HSI sum, while the combined HSI maps (nos. 7–22) have sums between 30% and 47% of the value from HSI map no. 2. For the Highlands/Alpine region, the sum of HSI of the maps derived from the narrowly defined forest map (nos. 1, 3, 4 and 7–14) are higher than corresponding HSI maps for the State. The HSIs for the Highlands/Alpine region are less variable than those of the State.

For both scales (State and Highlands/Alpine), map no. 9 has lowest sum of HSI values, making it the lower bound for the set of maps. Map no. 2 is the upper bound.

The absolute sum of HSI values provides an estimate of the uncertainty associated with the number of Sambar deer, if we assume that there is a linear relationship between habitat suitability and density or carrying capacity. By using the estimated density interval of 1–7.5 deer/km<sup>2</sup> (0.01–0.075 deer/ha) from Lucas (2001), we can estimate the number of deer (*N*) if all suitable habitat is inhabited. Using interval arithmetic, the lower bound for *N* is obtained by multiplying the sum of HSI values from map no. 9 by the lower bound of the population density interval. Similarly, the upper bound for *N* is obtained by multiplying the sum of HSI values from map no. 2 by the upper bound of the population density interval. The potential Sambar population is estimated to be [42,949–1,060,706] for the State and [10,311–196,994] for the Highlands/Alpine region.

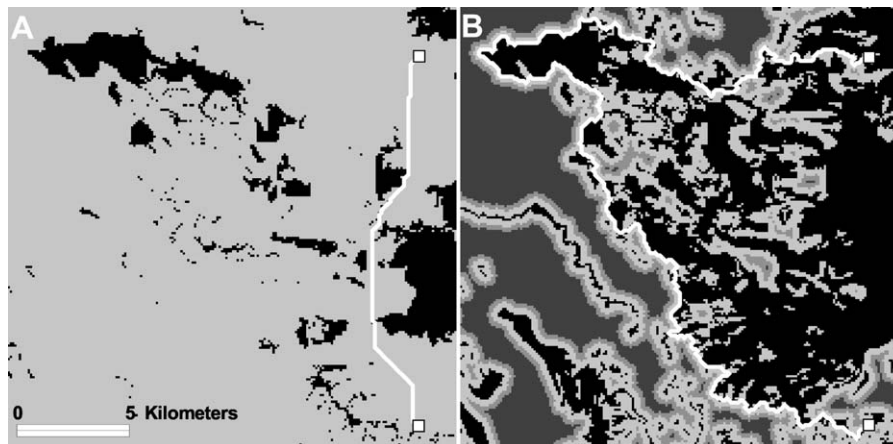
Results for the connectance index CT for the State of Victoria (Fig. 4B) contrast with those for the Highlands/Alpine region (Fig. 4C). For the State, the highest CT (an absolute value of 0.229) was found for maps nos. 1, 3 and 4, while for the Highlands/Alpine region, maps nos. 2, 5 and 6 had the highest CT



**Fig. 5 – Reduced-space plot of first two dimensions from non-metric multidimensional scaling (MDS) of the correlation matrix. The distance between a given pair of models is inversely proportional to the correlation of the corresponding matrices of least-cost path distances. Model numbers correspond to those in Fig. 4. The final stress of the MDS after 100 iterations is equal to 0.01, suggesting that reduced-space scaling is a good representation of the data.**

(an absolute value of 0.876). For the State, the lowest CT value was found for maps nos. 2, 5 and 6 (an absolute value of 0.119), and for the Highlands/Alpine region it occurred on maps nos. 7, 8, 11, 12, 15, 16, 19 and 20 (absolute value of 0.334). When HSI maps derived from the distance to forest edge (nos. 3 and 4 and nos. 5 and 6) were reclassified into a binary patch/non-patch landscape, they were similar to maps nos. 1 and 2. CT is therefore equal for these sets of maps and the statistic cannot be used to differentiate them.

Results for the least-cost path computation in the Highlands/Alpine region are represented visually in reduced space in Fig. 5. All correlations were highly significant (*p*-



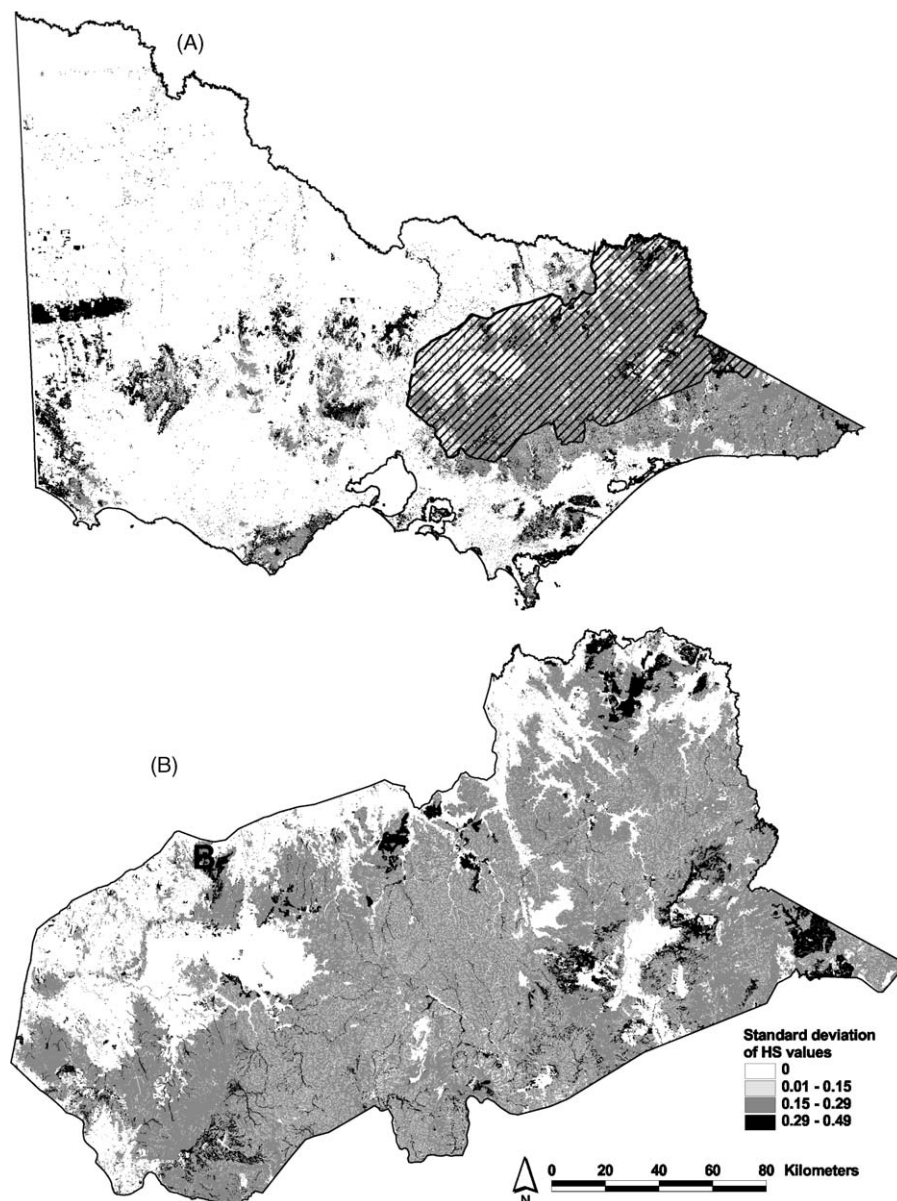
**Fig. 6 – Example of least-cost paths (white line) computed in HAR between two points, and using friction values derived from HSI map no. 1 (A) and HSI map no. 5 (B). Frictions are depicted as different intensities of grey, with highest friction (200) as black.**

values  $< 0.0001$ ). Correlations within pairs of maps nos. 3 and 4 and nos. 5 and 6 were very high (0.995 and 0.993, respectively), but correlations between map pairs were between 0.595 and 0.656. This indicates that the uncertainty associated with the width of the forest edge does not strongly influence least-cost path computation, while the choice of a broadly or narrowly defined forest map is important (cf., maps nos. 1 and 2 with a correlation of 0.740).

The choice of a way to compute a variable (EDG, GUL or ASR) has a small effect on the measure of connectivity among the set of random locations. Correlations within the cluster of maps nos. 7–22 are all greater than 0.99. The lowest correlation (0.354) between maps nos. 1 and 5 is due to the fact that

forest edges in map no. 5 act as corridors of high suitability (low friction), along which least-cost paths are preferentially computed. These least-cost paths may therefore be very different than those in the uniform habitat suitability map no. 1, as illustrated in Fig. 6. For a least-cost path analysis in the Highlands/Alpine region, maps nos. 1 and 5 represent the bounding maps encompassing the subjective uncertainty on habitat variables.

To represent the degree of subjective uncertainty associated with habitat suitability, we computed the standard deviation of HSI values on a cell-by-cell basis over the 22 HSI maps. At the scale of Victoria (Fig. 7A), the level of uncertainty is particularly high in the west part of the State, where broadly



**Fig. 7** – Maps of the State of Victoria (A) and the Highland/Alpine region (B) showing degrees of subjective uncertainty as the standard deviations of habitat suitability (HS) values, computed on a cell-by-cell basis among the 22 HSI maps. Areas in black show highest standard deviation and correspond to areas where broadly and narrowly defined forest maps differ. Areas with a medium and low degree of uncertainty constitute the rest of the forested zone, with standard deviation values depending on the interaction of the other habitat variables.



and narrowly defined forest maps differ substantially. Similar patches of high uncertainty are scattered throughout the Highlands/Alpine region (Fig. 7B), while most of the region has an intermediate level of uncertainty depending on the other habitat variables.

#### 4. Discussion

Subjective uncertainty in habitat suitability maps is usually neglected. Unacknowledged uncertainty may compromise the use of HSI maps in subsequent applications. The analysis shows how this kind of uncertainty may be incorporated in a modeling process, resulting in a pair of HSI maps that encompass the uncertainty.

The first step is to identify alternative model structures and parameters (Table 1). In our example, four habitat variables and the subjective judgments associated with their representations were considered. Model uncertainty was incorporated in three different habitat suitability models.

The second step is to reflect on the nature of the subjective judgments required to build a HSI map. The result is a set of plausible, alternative decisions that generate a set of alternative values. We believe that this process is an important part of HSI mapping because it leads to a better understanding of the extent of one's knowledge about the ecological process.

The third step is to calculate all combinations of parameters and values, in a search for maps that bound the extent of subjective uncertainty. It is important to note that, as the examples above show, the definition of 'extreme' depends on the end-use of the maps.

For example, when we used the sum of HSIs, we were interested in a relative measure of the habitat suitability of a region. Subjective uncertainty was encapsulated in the bounding HSI maps (nos. 2 and 9). This uncertainty was propagated in the calculation of the sums of HSIs with interval arithmetic, giving bounds for Sambar density. The intervals for Sambar populations were about three times wider than if subjective uncertainty was ignored. The upper bound represents a landscape "saturated" with deer. These large intervals reveal the extent of the lack of knowledge about Sambar density and distribution in Victoria, underlining the urgent need for field investigations to decrease this uncertainty. The lack of knowledge also currently limits the implementation of local management options (e.g. culling) that rely on a good knowledge of population densities. Note that these relatively large intervals are not in themselves an argument against the use of expert-based HSI maps, because without much information from the field these maps are presently the best way of summarizing the current state of knowledge about Sambar ecology. Conditional on a substantial field work effort, a sufficient amount of information on Sambar distribution and abundance in Victoria might be available in the future, which would then favor empirical data-based rather than expert-based HSI mapping.

The importance of considering the use of the maps is underlined by the fact that the pairs of bounding HSI maps for the connectance index CT were different for the State and the Highlands. The bounds were sensitive to other factors such as the degree of fragmentation of the landscape

(driven by the arbitrary rule for constructing suitable patches:  $HSI > 0.5$ ).

Results on the matrices of least-cost distances suggested that the subjective uncertainty surrounding the choice of an appropriate habitat suitability model is much more important than the uncertainty surrounding the ways of computing presence of gullies, the amount of solar radiation and forest edge effects (Fig. 5). The directions and lengths of the least-cost paths are defined through complex interactions between the absolute values of HSI and the autocorrelation of patches of similar HSI.

It is important to recognize and document the types of uncertainty that were ignored in the mapping process. For example, in Table 1 we presented three parameters classified under "measurement error" uncertainty that were not considered further. One of them was the delineation of vegetation boundaries in the EVC map, which had an associated error of up to 1 km. While this uncertainty may be ignored when working at the extent of the State or even the Highlands region, it might be problematic if the same HSI maps were to be used for a much smaller extent. In such a case, the potential errors associated with locations of vegetation boundaries might be propagated in the modeling process (e.g. Zhang and Goodchild, 2002, Chapter 6).

Some of the important questions for the management of Sambar deer populations are: (i) how fast are Sambar expanding their range in the north-eastern part of Victoria, and (ii) what is the likely time of arrival at particular key locations in the State. These questions may be approached through a modeling technique such as cellular automata (CA; e.g. Hirzel et al., 2001; Currat et al., 2004). This type of spatially explicit modeling typically relies on estimates of carrying capacity (for local growth functions) and on a measure of connectivity between adjacent sub-populations (for dispersal functions). We have shown that bounding HSI maps for the carrying capacity and connectivity (CT or least-cost distances) may be different. To propagate subjective uncertainty through a population model, we cannot know a priori which two maps would better encompass subjective uncertainty.

To resolve this issue, we could assume that the output of interest (say, the time of arrival at a key location) depends mostly on one type of variable (say, connectivity), so that the bounding HSI maps for a connectivity index should be used. Another possibility is to compute all HSI maps to obtain intervals of values for the output of interest. However, an iteration of a CA model might require substantial computational power, and if uncertainty related to many parameters is considered, the total number of model iterations might be too high (see Ray, 2003, Chapter 4.6). A third possibility is to use a subset of the pairs of bounding HSI maps obtained through the method outlined above. The subset of say, four HSI maps will encompass the subjective uncertainty linked to carrying capacity and habitat connectivity, if we assume additive effects between the two variables in the CA model. In such case, the propagation of the subjective uncertainty will consist in running iterations of the CA model for each bounding HSI map, and reporting the extended confidence interval for simulated times of arrival of the Sambar expansion at key locations.

In this study, we have chosen two plausible alternatives for computing each SI variable. This binary structure derives from



the typical properties of an interval, for which the two bounds are extreme plausible values. However, this choice may itself be arbitrary in certain situations. Computational time may quickly become limiting when increasing the number of alternative values for each habitat variable. For example, for each additional value of either GUL or ASR in the tree in Fig. 4A, the total number of HSI maps almost doubles. Many maps may be manageable for simple statistics like the sum of HSIs, but may be problematic with computer-demanding statistics such as the correlation among least-cost path matrices. The tree of subjective uncertainties is therefore a trade-off between the full spectrum of perceived uncertainty and the time required to compute the statistics of interest.

While this paper has addressed HSI maps, several issues are relevant to the characterization of uncertainty across the broader range of predictive habitat distribution models (Guisan and Zimmermann, 2000). These models also rely on GIS-derived input data that are prone to subjective uncertainty. This uncertainty could be propagated in the predictive models in the form of pairs of maps for each habitat variable. Each map would be an alternative plausible way of representing the habitat variable. Confidence intervals around predictions could therefore be extended (for statistical details, see Appendix A in Elith et al., 2002) and would represent more of the true uncertainty. In this way, the uncertainty surrounding the predicted distribution maps could then be represented, and comparisons between predictive modeling methods (see, e.g. Elith and Burgman, 2002) would be more accurate.

Explicit representation of bounds provides a richer and more realistic context for decision-making. For example, if the arrival of Samba deer at a critical point represent a trigger for management intervention, planners may design monitoring systems to be effective for a lower bound for the time of arrival rather than relying on the midpoint or 'best estimate'. Such risk averse strategies are an example of a situation in which information about uncertainty allows planners to deal with it appropriately.

Visualizing the amount of subjective uncertainty associated with a HSI in a geographic map (as in Fig. 7B) may also influence decision-makers. Monitoring may be most effective if it focuses on areas with high expected densities and low uncertainty. Darker zones in Fig. 7B (high uncertainty) are candidate areas where field work could be relatively efficient.

As more geospatial information becomes available for ecologists, the role of meta-information (information that describes information) is essential to understand and minimize the uncertainty in using the data (Beard, 2001). Typical pieces of information such as scale of use, spatial resolution and projection provide the core of the meta-information description of a HSI map. We propose, in addition, that meta-information should be supported by equally plausible representations of the HSI map together with a description of the method that was used to generate the bounding maps. These additions to the meta-information framework would contribute to an "encapsulated uncertainty measurement process" (Goodchild et al., 1999) that can help to propagate uncertainty into subsequent analysis or applications. The importance of subjective uncertainties could be assessed and decision-making would be better informed.

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## REFERENCES

- Adriaenssens, F., Chardon, J.P., De Blust, G., Swinnen, E., Villalba, S., Gulinck, H., Matthysen, E., 2003. The application of 'least-cost' modelling as a functional landscape model. *Landscape Urban Planning* 64, 233–247.
- Bagchi, S., Goyal, S.P., Sankar, K., 2003. Prey abundance and prey selection by tigers (*Panthera tigris*) in a semi-arid, dry deciduous forest in western India. *J. Zool.* 260, 285–290.
- Beard, K., 2001. Roles of meta-information in uncertainty management. In: Hunsaker, C.T., Goodchild, M.F., Friedl, M.A., Case, T.J. (Eds.), *Spatial Uncertainty in Ecology. Implications for Remote Sensing and GIS Applications*. Springer-Verlag, New York, pp. 363–378.
- Bentley, A., 1998. *An Introduction to the Deer of Australia*. The Australian Deer Research Foundation, Melbourne.
- Biswas, S., Sankar, K., 2002. Prey abundance and food habit of tigers (*Panthera tigris tigris*) in Pench National Park, Madhya Pradesh, India. *J. Zool.* 256, 411–420.
- Boroski, B.B., Barrett, R.H., Timossi, I.C., Kie, J.G., 1996. Modelling habitat suitability for black-tailed deer (*Odocoileus hemionus columbianus*) in heterogeneous landscapes. *Forest Ecol. Manage.* 88, 157–165.
- Bovill, L., 2000. *Bunyip Deer Study: The Presence, Movement and Environmental Impact of Deer within Bunyip State Park*. Diploma Project. Natural Resource Management, Institute of TAFE, Holmesglen, Victoria.
- Burgman, M.A., Breininger, D.R., Duncan, B.W., Ferson, S., 2001. Setting reliability bounds on habitat suitability indices. *Ecol. Appl.* 11, 70–78.
- Chardon, J.P., Adriaenssens, F., Matthysen, E., 2003. Incorporating landscape elements into a connectivity measure: a case study for the Speckled wood butterfly (*Pararge aegeria* L.). *Landscape Ecol.* 18, 561–573.
- Coulon, A., Cosson, J.F., Angibault, J.M., Cargnelutti, B., Galan, M., Morellet, N., Petit, E., Aulagnier, S., Hewison, A.J.M., 2004. Landscape connectivity influences gene flow in a roe deer population inhabiting a fragmented landscape: an individual-based approach. *Mol. Ecol.* 13, 2841–2850.
- Curat, M., Ray, N., Excoffier, L., 2004. SPLATCHE: a program to simulate genetic diversity taking into account environmental heterogeneity. *Mol. Ecol. Notes* 4, 139–142.
- Dettki, H., Löfstrand, R., Edenius, L., 2003. Modeling habitat suitability for moose in coastal Northern Sweden: empirical vs process-oriented approaches. *Ambio* 32, 549–556.
- Douglas, M.J.W., 1990. Sambar deer. In: King, C.M. (Ed.), *The Handbook of New Zealand Mammals*. Oxford University Press, Auckland, pp. 477–483.
- Downes, M., 1983. *The Forest Deer Project*. The Australian Deer Research Foundation, Melbourne.
- Elith, J., Burgman, M.A., 2002. Predictions and their validation: rare plants in the Central Highlands, Victoria, Australia. In: Heglund, P.J., Scott, J.M., Morrison, M.L., Raphael, M.G., Wall, W.A., Samson, F.B. (Eds.), *Predicting Species Occurrences*:

- Issues of Accuracy and Scale. Island Press, Covelo, CA, pp. 303–314.
- Elith, J., Burgman, M.A., Minchin, P., 1997. Improved Protection Strategies for Rare Plants. Consultancy Report for Environmental Australia. University of Melbourne, Environment Australia, Melbourne.
- Elith, J., Burgman, M.A., Regan, H.M., 2002. Mapping epistemic uncertainties and vague concepts in predictions of species distribution. *Ecol. Modell.* 157, 313–329.
- Forsyth, D.M., Duncan, R.P., 2001. Propagule size and the relative success of exotic ungulate and bird introductions to New Zealand. *Am. Nat.* 157, 583–595.
- Gardner, R.H., Gustafson, E.J., 2004. Simulating dispersal of reintroduced species within heterogeneous landscapes. *Ecol. Modell.* 171, 339–358.
- Gibson, L.A., Wilson, B.A., Cahill, D.M., Hill, J., 2004. Spatial prediction of rufous bristlebird habitat in a coastal heathland: a GIS-based approach. *J. Appl. Ecol.* 41, 213–223.
- Goodchild, M.F., Shortridge, A., Fohl, P., 1999. Encapsulating simulation models with geospatial data sets. In: Lowell, K., Jaton, A. (Eds.), *Spatial Accuracy Assessment: Land Information Uncertainty in Natural Resources*. Sleeping Bear Press, Chelsea, MI, pp. 123–130.
- Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. *Ecol. Modell.* 135, 147–186.
- Harikumar, G., Thomas, B., Joseph, K.J., Zacharias, V.J., 1999. Population dynamics of Sambar *Cervus unicolor*, in Periyar Tiger Reserve. *Indian Forester* 125, 995–1003.
- Harrison, M., 1998. *Wild Deer of Australia*. The Australian Deer Research Foundation, Melbourne.
- Hirzel, A., Hausser, J., Chessel, D., Perrin, N., 2002. Ecological-Niche Factor Analysis: how to compute habitat-suitability maps without absence data? *Ecology* 83, 2027–2036.
- Hirzel, A., Hausser, J., Perrin, N., 2001. *Biomapper 1.0*. Laboratory for Conservation Biology, Lausanne.
- Hooze, P.N., Eichenlaub, B., 2000. *Animal Movement Extension to Arcview*. Ver. 2.0. Alaska Science Center-Biological Science Office, U.S. Geological Survey, Anchorage, AK, USA.
- Houston, E., 2003. The Use of Faecal Counts to Estimate Sambar Deer (*Cervus unicolor*) Populations Abundance in Victoria. Monash University, Clayton, Vic.
- Jager, H.I., King, A.W., 2004. Spatial uncertainty and ecological models. *Ecosystems* 7, 841–847.
- Jager, H.I., King, A.W., Schumaker, N.H., Ashwood, T.L., Jackson, B.L., 2005. Spatial uncertainty analysis of population models. *Ecol. Modell.* 185, 13–27.
- Jathanna, D., Karanth, K.U., Johnsingh, A.J.T., 2003. Estimation of large herbivore densities in the tropical forests of southern India using distance sampling. *J. Zool.* 261, 285–290.
- Karanth, K.U., Sunquist, M.E., 1992. Population structure, density and biomass of large herbivores in the tropical forests of Nagarhole, India. *J. Trop. Ecol.* 8, 21–35.
- Knowles, L.L., 2004. The burgeoning field of statistical phylogeography. *J. Evol. Biol.* 17, 1–10.
- Kruskal, J.B., 1964a. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrics* 29, 1–27.
- Kruskal, J.B., 1964b. Non metric multidimensional scaling: a numerical method. *Psychometrics* 29, 115–129.
- Larson, M.A., Thompson III, F.R., Millspaugh, J.J., Dijak, W.D., Shifley, S.R., 2004. Linking population viability, habitat suitability, and landscape simulation models for conservation planning. *Ecol. Modell.* 180, 103–118.
- Legendre, L., Legendre, P., 1983. *Numerical Ecology*. Elsevier, New York.
- Lewis, J.C., Flynn, L.B., Marchinton, R.L., Shea, S.M., Marchinton, E.M., 1990. Introduction, study area, description and literature review. In: *Ecology of Sambar Deer on St. Vincent National Wildlife Refuge, Florida*. The Station, Tallahassee, FL, USA, pp. 1–12.
- Lucas, P., 2001. A population model and habitat management for Sambar deer (*Cervus unicolor*) in Lake Eildon National Park. Honours Thesis. The University of Melbourne, Melbourne.
- Manel, S., Schwartz, M.K., Luikart, G., Taberlet, P., 2003. Landscape genetics: combining landscape ecology and population genetics. *Trends Ecol. Evol.* 18, 189–197.
- Mason, E., 2001. Secrets of the Sambar: farm fringe tactics. *Guns Game* 30, 76–80.
- Mays, C., 2003. The addition of environmental data and species records to the development of a suitability model for the Sambar deer in Lake Eildon National Park. Master of Environment. The University of Melbourne, Melbourne.
- McGarigal, K., Cushman, S.A., Neel, M.C., Ene, E., 2002. *FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps*. University of Massachusetts, Amherst.
- Meer, E., 2001. Using Comparative Risk to Set Pollution Prevention Priorities in New York State: A Formula for Inaction: A Critical Analysis of the New York State Department of Environmental Conservation Comparative Risk Project. A Report from the New York State Assembly Legislative Commission on Toxic Substances and Hazardous Wastes. Assemblyman Steve Englebright, Chair, New York.
- Moilanen, A., Hanski, I., 2001. On the use of connectivity measures in spatial ecology. *Oikos* 95, 147–151.
- Moilanen, A., Nieminen, M., 2002. Simple connectivity measures in spatial ecology. *Ecology* 83, 1131–1145.
- Moore, I.A., 1994. Habitat use and activity patterns of Sambar deer, *Cervus unicolor*, in the Bunyip Sambar enclosure. In: Bentley, A. (Ed.), *An Introduction to the Deer of Australia*. The Australian Deer Research Foundation, Melbourne.
- Moriarty, A., 2004. The liberation, distribution, abundance and management of wild deer in Australia. *Wildl. Res.* 31, 291–299.
- NRE, 2001. *Ecological Vegetation Classes at 1:100,000-Composite Information*. Department of Natural Resources and Environment.
- NRE, 2002. *Vicmap Elevation-20 Meter DEM for the State of Victoria*. Department of Natural Resources and Environment, Melbourne.
- NSW/NPWS, 1998. *Eden Fauna Modelling—A Report Undertaken for the NSW CRA/RFA Steering Committee Project Number NE24/EH*. New South Wales National Parks and Wildlife Service, Canberra.
- Ottaviani, D., Lasinio, G.L., Boitani, L., 2004. Two statistical methods to validate habitat suitability models using presence-only data. *Ecol. Modell.* 179, 417–443.
- Padmalal, U.K.G.K., Takatsuki, S., Jayasekara, P., 2003. Food habits of Sambar *Cervus unicolor* at the Horton Plains National Park, Sri Lanka. *Ecol. Res.* 18, 775–782.
- Radeloff, V.C., Pidgeon, A.M., Hostert, P., 1999. Habitat and population modelling of roe deer using an interactive geographic information system. *Ecol. Modell.* 114, 287–304.
- Rand, G.M., Newman, J.R., 1998. The applicability of habitat evaluation methodologies in ecological risk assessment. *Hum. Ecol. Risk Assess.* 4, 905–929.
- Ray, N., 2003. *Modélisation de la démographie des populations humaines préhistoriques à l'aide de données environnementales et génétiques*. Thèse de doctorat. Université de Genève, Genève.
- Ray, N., 2005. *PATHMATRIX: a GIS tool to compute effective distances among samples*. *Mol. Ecol. Notes* 5, 177–180.

- Ray, N., Excoffier, L., 2003. MANTELN 1.1. Software for the Computation of Mantel Tests for Multiple Matrices. Genetics and Biometry Laboratory. University of Geneva, Switzerland.
- Reed, J.M., Mills, L.S., Dunning, J.B., Menges, E.S., McKelvey, K.S., Frye, R., Beissinger, S.R., Anstett, M.-C., Miller, P., 2002. Emerging issues in population viability analysis. *Conserv. Biol.* 16, 7–19.
- Regan, H.M., Colyvan, M., Burgman, M.A., 2002. A taxonomy and treatment of uncertainty for ecology and conservation biology. *Ecol. Appl.* 12, 618–628.
- Ruger, N., Schluter, M., Matthies, M., 2005. A fuzzy habitat suitability index for *Populus euphratica* in the Northern Amudarya delta (Uzbekistan). *Ecol. Modell.* 184, 313–328.
- Schaller, G.B., 1967. The Deer and the Tiger. A Study of Wildlife in India. The University of Chicago Press, Chicago.
- Shafii, B., Price, W.J., Prather, T.S., Lass, L.W., Thill, D.C., 2003. Predicting the likelihood of yellow starthistle (*Centaurea solstitialis*) occurrence using landscape characteristics. *Weed Sci.* 51, 748–751.
- Stockwell, M., 2003. Assessing the levels and potential impacts of browsing by Sambar deer (*Cervus unicolor*) in the Upper Yarra catchment, Victoria. Honours thesis. Monash University, Clayton, Vic.
- Tischendorf, L., Fahrig, L., 2000. On the usage and measurement of landscape connectivity. *Oikos* 90, 7–19.
- Tischendorf, L., Fahrig, L., 2001. On the use of connectivity measures in spatial ecology. A reply. *Oikos* 95, 152–155.
- Udaya Sekhar, N., 1998. Crop and livestock depredation caused by wild animals in protected areas: the case of Sariska Tiger Reserve, Rajasthan, India. *Environ. Conserv.* 25, 160–171.
- USFWS, 1996. Habitat Evaluation Procedures Report 870 FW 1. United States Fish and Wildlife Service, Washington, DC, USA.
- Wilson, B.A., Lewis, A., Aberton, J., 2003. Spatial model for predicting the presence of cinnamon fungus (*Phytophthora cinnamomi*) in sclerophyll vegetation communities in south-eastern Australia. *Austral Ecol.* 28, 108–115.
- Yamada, K., Elith, J., McCarthy, M., Zenger, A., 2003. Eliciting and integrating expert knowledge for wildlife habitat modeling. *Ecol. Modell.* 165, 251–264.
- Zhang, J., Goodchild, M.F., 2002. Uncertainty in Geographical Information. Taylor & Francis, London.
- Zhu, A.X., 1999. A personal construct-based knowledge acquisition process for natural resource mapping. *Int. J. Geogr. Inf. Sci.* 13, 119–141.