CHAPTER 13

Terrestrial biodiversity

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13.1 Introduction

Biodiversity is the variety of life at all levels of organization, from genetically distinct populations to species, habitats, ecosystems, and biomes (Leopold 1949; Wilson 1992). While biodiversity influences the provision of all ecosystem services, and is the basis for many (Sekercioglu et al. 2004; Díaz et al. 2005), it also inspires conservation for its own sake (e.g., Ehrlich and Ehrlich 1982, Chapter 2). To protect what remains of declining biodiversity (Hughes et al. 1997; Dirzo and Raven 2003; Worm et al. 2006) conservationists seek to identify habitat conservation networks that maximize habitat or species persistence. The design of these networks typically uses species distribution maps (e.g., Ceballos et al. 2005) and an understanding of the factors that affect species presence and persistence on the landscape (e.g., Sekercioglu et al. 2007). More recently, the design of conservation networks have considered the financial and opportunity cost of network conservation and implementation (Ando et al. 1998; Wilson et al. 2007; Polasky et al. 2008). Systematic conservation planning (SCP) (Margules and Pressey 2000) marries many of these network design principles and conservation organizations implement SCP principles in their work (Groves et al. 2002).

We present three relatively simple biodiversity models that spring from this conservation planning literature. The models are straightforward to implement and are designed for analysis at landscape scales. Our simplest model, tier 1, combines basic information about land cover and threats to biodiversity to produce habitat-quality and habitat rarity maps. In tier 1 we assume that protection of a variety of high-quality habitats will confer protection to their component species and populations (Groves et al. 2002). Because the tier 1 biodiversity model uses data that are available virtually everywhere in the world and empirical data on the status of rare, endemic, and other species of conservation concern are unavailable for many places, a habitat analysis, instead of a species-based approach is commonly implemented as the first phase of a conservation assessment.

In tier 2 we assume data on potential distributions or ranges of species and on habitat suitability (as gauged by breeding and foraging activity) are available to us. We present two tier 2 models that rely on this species-specific data. The first model combines these data to calculate the relative contribution of a parcel’s habitat to the overall quantity of suitable habitat across a landscape or region. This approach is similar to deductive species distribution modeling (Stoms et al. 1992), the rarity-weighted richness methodology (Williams et al. 1996), and the Biological Intactness Index (BII) system (Scholes and Biggs 2005). The second tier 2 model aggregates information on species distributions and habitat suitability into a single landscape score. This score is derived using species–area relationships to translate habitat area into a measure of landscape-wide biodiversity status, based on work by Sala et al. (2005) and Pereira and Daily (2006). In addition, we can incorporate tier 1 output into tier 2 modeling in order to weight suitable habitat area by quality. Such quality weighting of habitat is common in algorithms that are used to select networks of areas for conservation (e.g., Schill and Raber 2008).

13.2 Tier 1: habitat-quality and rarity model

Habitat-quality depends on its proximity to human land uses and the intensity of these land uses...
Generally, habitat-quality is degraded as the intensity of nearby human land use increases (Nelleman et al. 2001; Forman et al. 2003). For example, a forest near a city in a developing country may be stripped of much of its timber and other non-timber forest products while forests isolated from people will tend to be less disturbed (see Chapter 8). Or a wetland near agricultural lands may have greater water quality issues then a wetland surrounded by other wetlands. These are both examples of the “edges” that human land use creates on the boundaries of near-by habitat. In general, edges facilitate entry of various degraders into habitat including predators, competitors, invasive species, toxic chemicals, and humans. In addition, a high density of human land use in an area means that any near-by habitat will tend to be isolated, further reducing the habitat’s ability to contribute to species persistence. Our definition of habitat-quality is similar to the notion of habitat integrity as used by many conservation organizations. Habitat with high integrity, like high-quality habitat, is relatively intact and has structure and function within the range of historic variability.

This tier 1 model assumes that habitat areas with higher quality scores are better able to maintain their full complement of biodiversity over time than those areas with lower scores. This does not mean, however, that areas with lower quality scores are bereft of rare species or are not important sources of biodiversity (see Box 13.1). For example, in the U.S. some of the last remaining populations of the most threatened species are on or are immediately adjacent to

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**Box 13.1 Integrating biodiversity and agriculture: a success story in South Asia**

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What is the long-term prospect for harmonizing food production and biodiversity conservation? Recent work in the Neotropics shows that native species across a wide range of taxa can persist in farming countryside, decades after land clearing, if critical landscape features are maintained (e.g., Medellín et al. 2000; Daily et al. 2003; Horner-Devine et al. 2003; Ricketts 2004; Mayfield and Daily 2005; Sekercioglu et al. 2007).

But will these agricultural landscapes continue to support native species over centuries to millennia? We surveyed bird diversity in an ancient agricultural landscape, cultivated continuously for over 2000 years and inhabited by people for at least 20,000 years (Ranganathan et al. 2008). On the fringes of the Western Ghats in southwest India, the area retains many habitat features known to be important for biodiversity (landscape heterogeneity, vegetative structural complexity, and native vegetation). Most of the land covers—rice, peanut, cashew, arecanut palm, extremely degraded shrublands, and native forest—have been present for well over 200 years. The native forests are designated either as Reserve Forest (relatively intact, no extraction officially allowed) and Minor Forest (extraction of non-timber products permitted).

We found a rich bird fauna, of which only 4% of species were restricted to Reserve Forest. Arecanut palm plantations and Minor Forest together harbored a distinct bird community, including 90% of the forest-affiliated species of most conservation concern, such as the Great Hornbill and the Malabar Grey Hornbill.

Arecanut is consumed by over 10% of people, concentrated in south and south-east Asia. In traditional cultivation practices of the area, arecanut is intercropped (with pepper, vanilla, coffee, banana, cacao, etc.), increasing the economic return to farmers and the structural complexity so critical for forest birds. Further, as arecanut palm plantations have high water demands, they displace rice production, in effect trading a low conservation value land cover with a much higher one. There is a strong economic incentive to maintain the Minor Forests of the region as forest, since they provide a critical component for traditional arecanut cultivation: leaf litter, used as mulch in plantations (Figure 13.A.1).

Arecanut may be key to conservation in south and southeast Asia, a region with critical conservation challenges on the planet. This example shows that agricultural landscapes can sustain high levels of biodiversity over centuries to millennia, and offers hope that other such production systems can be found. More generally, a likely key to sustainable protection of biodiversity is harmonizing its protection with the delivery of as many other ecosystem services as possible, so that people reap rewards far beyond the iconic species and endemic species that have been the more traditional focus of conservationists.
heavily modified landscapes (this proximity to human activity may be why they are rare in the first place; Scott et al. 2006).

13.2.1 Calculating a parcel’s habitat-quality score

The tier 1 model builds a habitat-quality score for each parcel \( x \) on the landscape \( (x = 1, 2, \ldots, X) \) where a parcel can be any user-defined land unit, including a grid cell, a hexagon, a polygon, etc.) by mapping the location and intensity of all human land uses in the neighborhood of the parcel and then estimating the impact of this human land use on the parcel’s habitat.

We index land-use types that can have a major impact on habitat by \( r = 1, 2, \ldots, R \). These land-use types can be coarsely defined, such as roads, built areas, croplands, and so forth, and can be supplemented as warranted by much more refined land-use categories, such as high vegetation density forests due to fire suppression, different classes of roads (e.g., primary versus secondary), or different densities of development. The maps of land uses \( R \) do not have to be comprised of the same parcel units as the parcel map but all maps need to overlap in space. We use generic spatial units \( y = 1, 2, \ldots, Y \) to allocate land uses that can impact habitat-quality across the landscape. Let \( D_{yr} \) indicate the amount or density of land-use type \( r \) in spatial unit \( y \). For example, \( D_{yr} \) can measure kilometers of road ha\(^{-1}\) in grid cell \( y \), people ha\(^{-1}\) in parcel \( y \), or the hectares of cropland in hexagon \( y \).

The impact of \( D_{yr} \) on habitat-quality in parcel \( x \) depends on several factors. First, some human land-use types have more impact per unit than others. Let \( w_r \) be the relative impact weighting for \( r \). For example, if built areas have been estimated to have twice the impact of roads on habitat-quality, then \( w_{\text{built}} / w_{\text{roads}} = 2 \). An equal weight can be used across
all land uses R if information on the relative impact of each source on habitat-quality is not known.

Second, D\(_r\)'s influence on habitat in parcel x is affected by x's institutional and structural features. For example, a fence along the edge of a protected parcel might reduce the impact of nearby human land uses on habitat in the area. Or extreme slopes may prevent the entry of predator and competitor species (the protection accorded by institutional and/or structural features in x will vary by land-use r). Let the resistance to r in parcel x due to the parcel's institutional and structural features be given by the parameter \(\beta_{xr}\) with \(\beta_{xr} = 1\) indicating maximum resistance to influence.

Third, D\(_r\)'s influence on habitat in parcel x is affected by the distance between x and y; generally, D\(_r\)'s affect on habitat in x declines with distance. Let \(d_{yr}\) represent the distance between parcel x and spatial unit y on the map of land-use type r as measured by Euclidean distance, road network, or any other relevant distance measure and let \(\alpha_{yr}\) be the parameter that determines how quickly r's influence on habitat in parcel x decays with distance, all else equal.

To determine the potential impact of all land-use types R on habitat in parcel x, given by D\(_r\), we consider all three factors that affect D\(_r\)'s relationship with habitat in parcel x,

\[
D_x = \sum_{r} \sum_{y} w_{yr} \times f_r(\beta_{yr}, \alpha_{yr}, d_{yr}) \times D_{yr}, \tag{13.1}
\]

where \(w_{yr}f_r(\beta_{yr}, \alpha_{yr}, d_{yr})\) translates the value of D\(_r\) into an impact on parcel x. The higher \(D_x\) is, the greater the potential of human land uses on the quality of habitat in x. A standard way to model \(f_r(\beta_{yr}, \alpha_{yr}, d_{yr})\), but by no means the only way, is with an exponential decay function,

\[
f_r(\beta_{yr}, \alpha_{yr}, d_{yr}) = e^{-\alpha_{yr}d_{yr}}. \tag{13.2}
\]

In Eq. (13.2), \(f_r\) declines, and therefore, the impact of \(D_r\) on habitat in parcel x declines, as \(\alpha_{yr}\) \(\beta_{yr}\), and/or \(d_{yr}\) increases. A parcel with a \(D_x\) score near 0 is relatively unaffected by human land use within the context of the landscape while a \(D_x\) near \(\max_{x \in \mathbb{R}} \{D_x\}\) indicates that a parcel is greatly affected by human land use within the context of the landscape.

When translating \(D_x\) into a habitat-quality score in parcel x we assume that not all habitat types are equally susceptible to sources of disturbance. Let \(j = 1, \ldots, J\) index habitat types on the landscape where habitat can include land covers and uses highly modified from their natural state, e.g., urban areas, high-intensity croplands, roads. In general, not every land use/land cover type found on the map has to be included in the set of \(J\); the modeler is free to choose the subset of land use/land cover types in set \(J\) based on their definition of habitat. We scale habitat type \(j\)'s resistance to human land uses by \(L_j \in [0, 1]\), where higher values of \(L_j\) means \(j\) is more resistant and \(L_j\) is close to or equal to 0 for \(j\) that are highly modified from their natural state. The values of \(L_j\), for all \(j\) need to be gauged empirically, ideally based on biodiversity response. The habitat-quality score for each habitat type \(j\) in a parcel, \(Q_{xj}\), and the parcel’s aggregate habitat-quality score, \(Q_x\), is given by

\[
Q_{xj} = q(L_j, D_x) \tag{13.3}
\]

and

\[
Q_x = q\left(\sum_{j=1}^J \frac{A_j}{A_x} L_j, D_x\right), \tag{13.4}
\]

where \(q\) is any function that is increasing in \(L_j\) and decreasing in \(D_x\); \(Q_{xj} = 0\) when \(L_j = 0\), \(A_j\) is the area of parcel \(x\) in habitat type \(j\), and \(A_x\) is the area of parcel \(x\) (land use/land cover types that are not part of the habitat set \(j\) are not given habitat-quality scores). A parcel with a \(Q_x\) score near 0 includes little habitat area and/or contains habitat that is severely degraded within the context of the landscape while a \(Q_x\) score near \(\max_{x \in \mathbb{R}} \{Q_x\}\) indicates that a parcel is replete with habitat and is approximately of the highest quality within the context of the landscape.

### 13.2.2 Calculating a parcel's rarity score

While mapping habitat-quality can help identify the areas where biodiversity is likely to be more or less threatened on the landscape, it is also important to prioritize habitat types based on their relative rarity. We define a habitat type’s rarity as the amount of the habitat type currently found on the landscape relative to the amount of that habitat type that existed on the landscape at some reference time. The ideal reference landscape would be from a period prior to substantial anthropogenic conversion of land (Scholes and Biggs...
For example, a description of the distribution of major habitat types in the Willamette Basin of Oregon, USA, from the year 1850 (Christy et al. 2000) would meet this criterion (even though Native Americans shaped their landscapes in many ways as well, see Mann 2005). If a habitat type that was relatively abundant on the reference landscape is now rare on the modern landscape, then species dependent on that habitat type will likely have declined.

Assuming we have a reference landscape, we calculate the relative rarity of habitat type $j$ on a modern landscape as

$$Y_j = I_j \left(1 - \frac{\sum_{x=1}^{X} A_{xj}}{A_j}\right),$$

where $Y_j = 0$ if $A_{xj} = 0$, $I_j$ is equal to 1 if $j$ is a natural land cover (as opposed to a $j$ that is significantly managed) and is equal to 0 otherwise, and $A_j$ is the area of habitat type $j$ on the reference landscape. The closer $Y_j$ is to 1, the rarer the habitat type $j$ is on the modern landscape vis-à-vis the reference landscape.

If appropriate reference maps are not available (and as a useful check even when they are), another option is to weight the relative scarcity of habitat types on the modern landscape according to a rarity metric from NatureServe. NatureServe measures the status of habitat types with a metric that ranges from 1 through 5 where a 1 indicates critical imperilment across a region or the globe, and a 5 indicates that the habitat type is abundant and secure (NatureServe 2008). In this approach, the relative rarity of habitat type $j$ on the modern landscape is given by

$$NS_j = \left(6 - \frac{NS_j}{5}\right) \left(1 - \frac{\sum_{x=1}^{X} A_{xj}}{A}\right),$$

where $NS_j$ is NatureServe’s conservation status of habitat type $j$ and $A$ is the area of the landscape. Set $NS_j = 6$ for all $j$ that are significantly managed. If possible, we use NatureServe’s regional scores for $NS_j$ instead of their global scores because a habitat type that is relatively secure from a global perspective may be relatively scarce in the particular landscape.

Once we have calculated $Y_j$ for each habitat type, we quantify the overall rarity of habitat types in parcel $x$ on the modern landscape by taking the area-weighted average of $x$’s $Y_j$ scores,

$$Y_x = \sum_{j=1}^{J} Y_j \left(\frac{A_{xj}}{A_x}\right).$$

where the more rare the habitat area in $x$ the closer $Y_x$ is to 1.

We can combine data on habitat-quality and rarity to provide a measure that can be used to prioritize conservation efforts. Rare habitats with high quality could represent one conservation priority. Such areas are identified by parcels with high $V_x \in [0,1]$ scores where

$$V_x = \frac{Q_x}{\max_{m=1,\ldots,M} \{Q_m\}} \times \frac{Y_x}{\max_{m=1,\ldots,M} \{Y_m\}},$$

where $m = 1, 2, \ldots, M$ also index parcels. Another simple composite habitat-quality and rarity score is given by $VW_x \in [0,1]$, where

$$VW_x = \gamma \frac{Q_x}{\max_{m=1,\ldots,M} \{Q_m\}} + (1 - \gamma) \frac{Y_x}{\max_{m=1,\ldots,M} \{Y_m\}},$$

where $\gamma \in [0,1]$ determines the weight given to quality versus rarity when tracking the conservation value of each parcel.

### 13.3 Tier 2 models of terrestrial biodiversity

The major drawback with the tier 1 approach is that it does not necessarily indicate how well the landscape is meeting the specific needs of species of concern. For example, if the species of concern are generally located in areas of low-quality habitat then conserving the remaining patches of high-quality habitat may not generate as great a conservation return as restoring valuable degraded habitat. In tier 2 we complement tier 1 results by assessing how species react to and use the landscape and their spatial relationship with habitat-quality patterns.

To this end we consider two alternative formulations of tier 2 models that measure biodiversity patterns and status using species-specific data. The first tier 2 model measures the marginal contribution of each parcel to biodiversity on the entire landscape. The model can also track the change in a parcel’s marginal contribution to biodiversity as the land use/land cover (LULC) pattern on the landscape changes over time. The second tier 2 model summarizes an entire landscape’s ability to support a suite of species.
### 13.3.1 Parcel-level contribution to biodiversity conservation on the landscape

For each parcel $x$ on the landscape we calculate a marginal biodiversity value ($MBV_x$) that measures the proportion of the landscape’s total modeled biodiversity supplied by that parcel. The $MBV$ of a parcel is a function of: (1) the number of modeled species whose potential ranges overlap with that parcel, and (2) the fraction of each species’ suitable habitat area that the parcel contains. We deem a habitat type suitable for a species if the species has been observed intermittently or consistently using the habitat for breeding, foraging, migration, or other life-sustaining purposes. To understand $MBV$, consider a simple example for a single species. Five equally sized parcels on a landscape of 100 parcels comprise the species’ geographic range. Each of the five parcels in the species’ range is completely covered by equally suitable habitat. Then, in our $MBV$ model, each of these five parcels has an $MBV$ of 0.2, and all other parcels have an $MBV$ of 0. Computing $MBV$ on a large landscape with multiple species is a straightforward generalization of this simple example that allows for different parcel areas, species-specific weights, multiple habitat types within a parcel, and incorporation of tier 1 habitat-quality model scores.

The calculation of $MBV$ requires a potential range map for each modeled species and a compatibility score for each species/LULC combination that indicates the degree of suitability of LULC $j$ for species $s$ ($s = 1, 2, \ldots, S$) (in tier 1 $j$ indexed the more narrowly defined habitat types). We set $H_{xs} = 1$ if parcel $x$ is in the potential range of species $s$, and equals 0 otherwise. Ideally, each species’ potential range map is based on its estimated geographic range in the pre-modern era. However, such data are only available for a limited subset of species and may not be particularly reliable. Therefore, we most often define $H_{xs}$ with recently observed patterns of species distribution (however, see Rondinini et al. (2006) for a discussion of the biases introduced in biodiversity modeling and mapping when using maps of recently observed ranges).

We incorporate the degree to which LULC $j$ supports species $s$ by setting $C_{sj} = 0$ for unsuitable habitat and $C_{sj} > 0$ for suitable habitat where $C_{sj} = 1$ indicates the most preferred habitat. The per-unit-area marginal value of each LULC type $j$ for species $s$ on the landscape is,

$$\hat{C}_{sj} = \frac{C_{sj}}{\sum_{x=1}^{X}\sum_{s=1}^{S} C_{sj} A_{sx} H_{xs}} \tag{13.10}$$

where $k$ indexes LULC types as well, $A_{sx}$ is the area of LULC $k$ in parcel $x$, and the denominator gives species $s$’ total suitable habitat area on the landscape.

Next, we use $\hat{C}_{sj}$ to calculate the $MBV$ score on parcel $x$,

$$MBV_x = \sum_{s=1}^{S} w_s H_{xs} \left( \sum_{j=1}^{J} A_{sx} \hat{C}_{sj} \right), \tag{13.11}$$

where $MBV_x$ is an estimate of each parcel’s contribution to the landscape’s total supply of biodiversity, biodiversity consists of the $S$ modeled species, and $w_s$ is the weight assigned to species $s$. If we disregard $w_s$ temporarily, a parcel will score highly on the $MBV$ metric if it contains suitable habitat for the species that have little suitable habitat elsewhere on the landscape or if it contains reasonable shares of suitable habitat for many species. Not all species need be weighted equally. For example, threatened and endangered species may be given greater weight in conservation planning and implementation. If $\sum_{s=1}^{S} w_s = 1$ then $\sum_{s=1}^{S} MBV_s = 1$.

Alternative formulations of the per-unit-area marginal value that incorporates habitat-quality scores from tier 1 are

$$\hat{C}_{sj} = \frac{C_{sj}}{\sum_{x=1}^{X}\sum_{s=1}^{S} Q_{sj} C_{sj} A_{sx} H_{xs}} \tag{13.12}$$

if we have habitat-quality scores for each LULC (habitat) type $j$ in each parcel $x$ or

$$\hat{C}_{sj} = \frac{C_{sj}}{\sum_{x=1}^{X} Q_{sx} \sum_{s=1}^{S} C_{sj} A_{sx} H_{xs}} \tag{13.13}$$

if we only have or prefer to use parcel-level habitat-quality scores. We assume quality affects suitable habitat in a linear manner; alternative rates of suitable habitat modification can be used if we have the data to support such relationships. If we use a version of $\hat{C}_{sj}$ given by Eq. (13.12) or (13.13) we calculate habitat-quality-adjusted $MBV_x$ with a modified version of Eq. (13.11),
To obtain the year associated with the baseline landscape. In this new landscape, the species in four of these parcels is lost, while half of its range, each entirely covered with habitat preferred by the species, the biodiversity value of the species potential range can change over time due to climate change or other landscape-level disturbances, and \( A_{x,t} \) is the area of LULC \( j \) in a parcel \( x \) at time \( t \).

Finally, for each time \( t \), we calculate the ratio \( RMBV_{x,t}/MBV_{x,t} \) for each parcel \( x \). This so-called ratio is greater than 1 if parcel \( x \)'s LULC and habitat-quality composition (if included in \( RMBV \)) has changed vis-à-vis the base landscape in a manner that produces a net increase in the parcel's suitable habitat across all species \( S \).

### 13.3.2 Landscape level biodiversity model

The MBV and RMBV models described above are intended primarily for evaluating and comparing the biodiversity supplied by individual parcels, either within a landscape (the MBV model) or across time on the landscape (the RMBV model). The above methodologies do not yield a single, satisfactory landscape score, however, that can be used for assessing the trade-offs between landscape-level measures of biodiversity and ecosystem services under different landscape scenarios. To remedy this shortcoming of the MBV model, we use species–area relationships (SAR) to develop a landscape-level biodiversity score that requires many of the same data inputs used in the MBV or RMBV models.

The SAR of biogeography (MacArthur and Wilson 1967) specifies the following relationship between total habitat area \( A \) and species richness \( S \):

\[
S = c A^z, \quad (13.19)
\]

where \( c \) is a constant and \( z \) indicates the rate of species accumulation as \( A \) increases and is typically

\[
MBV_x = \sum_{i=1}^S w_i H_i \left( \sum_{j=1}^I Q_{ij} A_{ij} \hat{C}_{ij} \right) \quad (13.14)
\]

or

\[
MBV_x = Q_x \sum_{i=1}^S w_i H_i \left( \sum_{j=1}^I A_{ij} \hat{C}_{ij} \right), \quad (13.15)
\]

where Eq. (13.14) uses the \( \hat{C}_{ij} \) from Eq. (13.12) and Eq. (13.15) uses the \( \hat{C}_{ij} \) from Eq. (13.13).

### 13.3.1.1 Tracking changes in parcel-level marginal biodiversity value

The MBV score compares the biodiversity value of parcels on a landscape for a given point in time, but it can be misleading to compare MBV scores of a particular parcel across time. Recall the simple example above for one species with five equally sized parcels in its range, each entirely covered with habitat preferred by the species, the MBV score for each parcel is 0.2. Consider a scenario in which all suitable habitat for the species in four of these parcels is lost, while half of the fifth parcel’s area is converted to unsuitable habitat. In this new landscape, the MBV score of the fifth parcel would increase to 1 despite the loss of half of its suitable habitat. This change in score may provide useful information in terms of the parcel’s contribution to remaining habitat, but it obscures determination of whether the amount of biodiversity supported by a parcel has increased or decreased over time.

We therefore use an alternative biodiversity statistic, the relative marginal biodiversity value (RMBV), to track the contribution of a parcel to the landscape’s level of biodiversity through time. Calculation of RMBV scores and associated RMBV ratios use the same input data as MBV. The calculation of RMBV uses the per-unit-area value of each LULC type \( j \) as evaluated in the base landscape. This quantity is then applied to a future specification of the landscape.

Using a base landscape map (i.e., the first map in a chronological series of maps for the landscape), we calculate \( \hat{C}_{ij} \) as in Eq. (13.10), (13.12), or (13.13). This statistic is denoted as \( \hat{C}_{ij} \), where the \( b \) subscript indicates the year associated with the baseline landscape.

To obtain RMBV scores for parcel \( x \) at time \( t \) (where \( t > b \)), we plug \( \hat{C}_{ij} \) and \( x \)'s LULC mix from year \( t \) into,

\[
RMBV_{x,t} = \sum_{i=1}^S w_i H_i \left( \sum_{j=1}^I A_{ij} \hat{C}_{ij} \right) \quad (13.16)
\]

or

\[
RMBV_{x,t} = Q_x \sum_{i=1}^S w_i H_i \left( \sum_{j=1}^I A_{ij} \hat{C}_{ij} \right) \quad (13.17)
\]

where we use Eq. (13.16) if \( \hat{C}_{ij} \) was calculated with Eq. (13.10), Eq. (13.17) if \( \hat{C}_{ij} \) was calculated with Eq. (13.12), Eq. (13.18) if \( \hat{C}_{ij} \) was calculated with Eq. (13.13), indexing \( H_i \) by \( t \) acknowledges that species potential range can change over time due to climate change or other landscape-level disturbances, and \( A_{x,t} \) is the area of LULC \( j \) in a parcel \( x \) at time \( t \).
between 0.1 and 0.7. Ideally, the values of the parameters \( c \) and \( z \) are calibrated to observed patterns on the studied landscape. This relationship between richness and habitat area has proven to be one of the most empirically robust patterns in all of ecology, though with important nuances (Rosenzweig 1995).

While the SAR is typically used to predict species richness, we use it to determine how well a landscape supports species. Each species receives a SAR score based on the proportion of area in that species’ potential geographic range that is suitable habitat. The SAR score for species \( s \) at time \( t \) is

\[
SAR_{st} = \gamma_s \frac{\left( \sum_{x=1}^{X} \sum_{j=1}^{J} Q_{xj} A_{xj} H_{xj} C_{xj} \right)^{\gamma_s}}{\left( \sum_{x=1}^{X} A_{xj} H_{xj} \right)^{\gamma_s}}, \quad (13.20)
\]

where \( \gamma_s \) is a species-specific constant (the \( c \) in Eq. (13.19)), \( z_{st} \) is the species–area function power parameter for species \( s \) and all other variables are as before. We index \( s \), \( H \), \( C \), and \( z \) with \( t \) to allow for changes in these parameters and variables over time. In Eq. (13.20) we normalize the observed species-area relationship value (the numerator) with the species–area relationship value that would hold if the species’ entire potential range were in perfectly suitable habitat (the denominator). Therefore, \( SAR_{st} \) is a measure of the fraction of total potential support that the landscape provides for species \( s \) at time \( t \) where complete support on the landscape at time \( t \) is given by \( SAR_{st} = 1 \) (assuming \( \gamma_s = 1 \)).

Species that have lost a greater proportion of their suitable habitat across their reference-era range are at a greater risk of extinction than species that have lost a smaller proportion, regardless of the absolute size of habitat loss (Channell and Lomolino 2000; Abbitt and Scott 2001; Scholes and Biggs 2005). Therefore, just like our MBV and RMBV models, our SAR model may be more accurate if each species’ potential range map (i.e., \( H \)) is based on its estimated spatial distribution in the pre-modern era in lieu of recently observed ranges (though reliable estimates of pre-modern ranges are not available for most species and places).

Regardless of the potential range map used, research has also shown that, all else equal, range-restricted species tend to have higher extinction risks than large-range species (Newmark 1995; Purvis et al. 2000; Pimm and Brooks 2000; Parks and Harcourt 2002; Cardillo et al. 2006). \( SAR_{st} \) reflects this tendency as a one-unit decrease in suitable habitat for a species (the numerator of Eq. (13.20)) with small range (a small denominator value) reduces \( SAR_{st} \) more than a similar one-unit decrease for a geographically widespread species.

We can modify Eq. (13.20) to include the habitat-quality as calculated in tier 1,

\[
SAR_{st} = \gamma_{s} \frac{\left( \sum_{x=1}^{X} \sum_{j=1}^{J} Q_{xj} A_{xj} H_{xj} C_{xj} \right)^{\gamma_{s}}}{\left( \sum_{x=1}^{X} A_{xj} H_{xj} \right)^{\gamma_{s}}}, \quad (13.21)
\]

\[
SAR_{st} = \gamma_{s} \frac{\left( \sum_{x=1}^{X} Q_{xj} A_{xj} H_{xj} C_{xj} \right)^{\gamma_{s}}}{\left( \sum_{x=1}^{X} A_{xj} H_{xj} \right)^{\gamma_{s}}}, \quad (13.22)
\]

where again habitat-quality modifies suitable habitat in a linear manner and the reference species range (the denominators of Eqs. (13.21) and (13.22)) assumes habitat of the highest quality is uniformly present across \( s' \) range (\( Q_{xj} = 1 \) for all \( x, j \), and \( t \) combinations and \( Q_{xj} = 1 \) for all \( x \) and \( t \) combinations). These equations are such that, all else equal, a smaller area of high-quality suitable habitat can generate a higher \( SAR_{st} \) score than a larger area of low-quality suitable habitat.

We can generate a single \( SAR_{st} \) score for the collection of modeled biodiversity on the landscape by taking a weighted sum of all \( SAR_{st} \) scores,

\[
SAR_{i} = \sum_{s=1}^{S} w_{s} SAR_{st}, \quad (13.23)
\]

where \( w_s \) is the weight attached to species \( s \).

### 13.4 Tier 1 and 2 examples with sensitivity analysis

We illustrate the tier 1 and 2 models with projected LULC change in the region covered by the Sierra Nevada Conservancy (a California state agency) (see Figure 13.1). The 101,000 km² region encompasses the Sierra Nevada ecoregion and includes portions of six other ecoregions, with elevation ranging from 100 to 4421 m, including the highest peak in the contiguous United States. The region has approximately 3500 species of vascular plants,
including more than 400 endemics (Shevock 1996); 293 birds, 135 mammals, 46 reptiles, 37 amphibians, and 61 fish (CDFG-CIWTG 2007).

We used Sierra Nevada housing-density projections for 2030 from the Spatially Explicit Regional Growth Model (Theobald 2005) to create two 2030 landscape scenarios. The Conservation scenario assumes that new development will have a minimum housing density of one unit per 0.6 ha. The developed land footprint increases 140% (from 78,389 ha in 2000 to 187,769 ha in 2030) under this scenario. The Growth scenario includes lower density housing development options (a minimum of one unit per 4 ha). The developed land footprint increases 927% (from 78,389 ha in 2000 to 805,362 ha in 2030) under this scenario. The region’s LULC map in 2000 is the base landscape. (See Davis et al. (2006) for a much more complex and thorough mapping of conservation priority areas in the Sierra given the spatial distribution of habitats, species, land tenure, and the predicted spatial pattern of development in the region, i.e., a tier 3 approach.)

For the purposes of the examples below, the areas that develop housing in these scenarios are always referred to as “urban,” though this will overstate the impact of low density development as exemplified by the Growth scenario on species that can tolerate lower density residential development. Further, we assume for simplicity’s sake that no other land-use changes occur in either scenario, including no expansion of the region’s transportation network. Obviously, no matter the actual future, new roads will be built in the region as its population and urban footprint expands.

13.4.1 Tier 1

We conducted twelve separate tier 1 habitat-quality mapping analyses; in each case we used a different combination of $w_r$ and $L_j$ values to map parcel-level habitat-quality scores, $Q_x$ (the set of 1 habitat types remain constant across all analyses). In this illustrative example, human land uses that affect habitat-quality are roads, urban areas, and agricultural fields. In Figure 13.2 (Plate 6) we present tier 1 results for two such unique combinations of $w_r$ and $L_j$ values. In general the greatest difference between the two is the relative weight assigned to the human land uses of roads, urban areas, and agriculture. In the “Roads” parameter combination we assume roads are more deleterious to habitat-quality than urban areas and agriculture and in the “Urban” parameter combination we assume urban areas are more disruptive than the other two land uses. See the chapter’s supplementary online material (SOM) for model details.

The “Roads” and “Urban” parameter combinations produce the two most extreme distributions of habitat-quality scores on the baseline and two future maps. Specifically, of the twelve parameter combinations, the Roads parameter combination produces a distribution of $Q_x$ values that is most skewed to the left on the unit scale (low values) under both future scenarios whereas the Urban parameter combination produces a distribution of $Q_x$ values that is the most skewed to the right under both future scenarios (high values).

Not surprisingly, regardless of the parameter combination used, the Growth scenario landscape consistently, because of its larger footprint change, produces lower $Q$ scores when compared to the Conservation scenario landscape. Only a handful of parcels have lower $Q$ scores under the Conservation scenario landscape than they do under the Growth
that the habitat-quality trade-off between the two future scenarios seems starker when using the Urban parameter combination rather than the Road parameter combination (see Figure 13.52 in the SOM).

Spatially, the Urban parameter combination leaves many more large patches of relatively high-quality habitat (the darkest green on the maps) than the Roads parameter combination (Figure 13.2; Plate 6). Given our uncertainty regarding the direction of development in the future and the relative impact of these sources of human land use on habitat-quality, it is appropriate to conclude that the areas that are the darkest green (high-habitat-quality) on all four future scenario-parameter combination variations in Figure 13.2 (Plate 6) are the areas most likely to contain high-quality habitat in the future.

13.4.2 Tier 2 analyses

We calculated MBV, $RMBV$, and $RMBV$ ratio scores (without considering habitat-quality) for various subgroups of herpetofauna—federally endangered herpetofauna (FE), federally threatened herpetofauna (FT), California herpetofauna of special concern (CSC), amphibians (A), and reptiles (R)—that have at least part of their range in the Sierra Nevada Conservancy. In Figure 13.3 histograms of the distribution of parcel $RMBV$ ratio values across the landscape (i.e., the relative change in parcels’ MBV scores from 2000 to 2030) under each scenario for each subgroup of herpetofauna using mean $C_{sj}$ values for each $s$ and $j$ combination are given. The FT ($N = 5$), FE ($N = 3$) and CSC ($N = 25$) subgroups experience severe reductions in effective habitat area in many parcels under the Growth scenario (recall that a $RMBV$ ratio value near 0 indicates a significant loss of habitat in the parcel over time for the modeled species). These histograms also show that the reduction in habitat under the Conservation scenario most acutely affects the same subgroups.

We map the FT subgroup species year 2000 MBV and $RMBV$ ratio values under both scenarios using minimum and maximum $C_{sj}$ values in Figure 13.4 (Plate 7). The MBV maps (Figure 13.4; Plate 7) indicate that the most important habitat for FT

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**Figure 13.2** Maps of parcel habitat-quality scores when the “Roads” and “Urban” parameter combinations are used in the Sierra Nevada illustrative example. We ran the tier 1 model on a grid map with a cellular resolution of 400 m × 400 m (16-ha grid cells). In these maps we present the mean habitat-quality score ($Q$) of all grid cells within 500 hectare hexagons. There are 23,042,500 ha hexagons in the Sierra Nevada Conservancy. In both future LULC scenarios the majority of residential development is centered on Sacramento, and generally along the western foothills. In the Growth scenario, montane hardwood is the land cover type that loses the most area to development (158,268 ha). In the Conservation scenario, annual grassland is the land cover type that loses the most area (17,798 ha). See the chapter’s SOM for all tier 1 model details. (See Plate 6.)
species in 2000 were in the western foothills. It is in this area that most urbanization is expected to occur by 2030 under both scenarios, albeit to a much greater extent in the Growth scenario. The maps appear to be fairly insensitive to the range in $C_{s,j}$. Finally, these maps explain why the $A$ ($N = 35$) subgroup has the most right-skewed histogram of parcel $RMBV$ ratio scores: species in subgroup $A$ are more likely than any other subgroup of species to be found in the higher elevation areas, the areas experiencing the least development.

Data in Figure 13.5 corroborates the decrease in FT and CSC subgroup suitable habitat as suggested by the $RMBV$ ratio histograms. These two subgroups experience the greatest relative decrease in their SAR scores (without considering habitat-quality) under both scenarios no matter which $C_{s,j}$ and $z$ values we use (low, mean, or high for the $C_{s,j}$ scores for each $s$ and $j$ combination and 0.11, 0.25, 0.64, and 1 for the $z$ scores). Again, this is due to the fact that many of the taxa included in these subgroups are primarily found in the foothill areas and the Central Valley to the west, the zone in which most of the projected development is expected to occur. At what point a decline in SAR indicates an immediate and imminent threat to the persistence of a subgroup is an empirical question. See the chapter’s SOM for tier 2 model details.

### 13.4.3 Incorporating tier 1 results in a tier 2 analysis

In many cases we will not be able to perform a tier 2 analysis due to a lack of species-specific data. However, if we do have the wherewithal to perform a tier 2 analysis, as we do in this example, if would be judicious on our part to perform it twice, once with tier 1 output incorporated and another time without (e.g., the results above). Such an analysis will indicate some of the spatial relationships between habitat-quality, species habitat, and the pattern of habitat loss on the landscape over time.

By definition, $MVB_{xt}$ and $SAR_{st}$ scores calculated with habitat-quality scores will always be equal to
or lower than those without. However, habitat-quality-modified $RMBV_{st}$ ratio scores and the change in habitat-quality-modified $SAR_{st}$ scores over time may be more or less than their unmodified counterparts. In general, habitat-quality-modified $RMBV$ ratio scores will be higher and decreases in habitat-quality-modified $SAR$ scores will be less severe than their unmodified counterparts if the habitat that is lost over time tends to be of low quality on the base landscape.

In Table 13.1 we present the change in the CSC and FT herpetofauna subgroups’ SAR statistics when and when not incorporating $Q_x$ scores from the Roads and Urban parameter combinations (using mean $C_{sj}$ values for all $s$ and $j$ combinations). The inclusion of $Q_x$ scores in the SAR calculations suggests: (1) that habitat conversion under the Growth scenario tends to occur more frequently on higher quality habitat than is does under the Conservation scenario, (2) if we use the Urban parameter combination to measure the relative impact of human land uses on habitat-quality then a greater proportion of higher quality habitat is developed by 2030 under either scenario than if we used the Roads parameter combination, and (3) a greater fraction of CSC subgroup’s high-quality habitat is developed than that of the FT subgroup’s.

While we do not perform the analysis for this illustrative example, we expect a comparison of the
Table 13.1  Percent change in SAR statistic from 2000 to 2030 where $z = 1$

<table>
<thead>
<tr>
<th>2030 LULC scenario</th>
<th>Conservation</th>
<th></th>
<th></th>
<th>Growth</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Q scores from tier 1 are not included (%)</td>
<td>Q scores from the tier 1 “Roads” parameter combination are included (%)</td>
<td>Q scores from the tier 1 “Urban” parameter combination are included (%)</td>
<td>Q scores from tier 1 are not included (%)</td>
<td>Q scores from the tier 1 “Roads” parameter combination are included (%)</td>
<td>Q scores from the tier 1 “Urban” parameter combination are included (%)</td>
</tr>
<tr>
<td>Herpetofauna subgroup</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>California herpetofauna of special concern (CSC)</td>
<td>$-1.11$</td>
<td>$-0.88$</td>
<td>$-1.11$</td>
<td>$-8.26$</td>
<td>$-9.95$</td>
<td>$-10.14$</td>
</tr>
<tr>
<td>Federally threatened herpetofauna (FT)</td>
<td>$-2.35$</td>
<td>$-1.76$</td>
<td>$-2.15$</td>
<td>$-15.58$</td>
<td>$-17.91$</td>
<td>$-18.16$</td>
</tr>
</tbody>
</table>
RMBV ratio scores with and without habitat-quality scores to corroborate our initial finding that the Growth scenario converts a greater portion of high-quality habitat and that under either scenario a greater portion of high-quality CSC subgroup habitat than high-quality FT subgroup habitat is developed between 2000 and 2030.

13.4.4 Sensitivity analyses and analysis limitations

A parcel’s habitat-quality scores are explained by variables \( w_r, a_r, \beta_r, \) and \( L_j \) that are uncertain and functions, \( f_r \) and \( q \), that are simplistic and in many cases, unverifiable representations of complicated ecological processes. In tier 2 analyses, the data used in the \( H \) and \( C \) matrices and to set the \( z \) exponents are often derived from a limited number of field-based studies.

In this illustrative example we attempt to quantify some of the ramifications of this uncertainty with a limited data sensitivity analysis. First, for the baseline and the two scenario maps, we used 12 different combinations of \( w_r \) and \( L_j \) values to find the combinations that produced the most left-skewed and right-skewed distributions of \( Q_x \) across all 3 maps, respectively (Figure 13.2; Plate 6). We did not vary the values of \( a_r \) or \( \beta_r \) nor did we experiment with the structures of \( f_r \) and \( q \); otherwise, we would have calculated an even greater range in habitat-quality results.

In our tier 2 illustration we found \( MBV, RMBV, \) and \( RMBV \) ratio scores for all parcels and SAR values on all three landscapes using a range of \( C_s \) values for each \( s,j \) combination. For example, in Figures 13.53 and 13.54 in this chapter’s SOM we illustrate which subgroup’s distribution of \( RMBV \) ratios is most sensitive to uncertainty in \( C_s \) scores under both the Growth and Conservation scenarios. In Figures 13.4 and 13.5 the ramifications of some of this uncertainty is mapped and graphed, respectively.

Placing reasonable bounds on model outputs is the simplest uncertainty analysis we can perform. A more thorough method for determining how sensitive a model’s output is to variable and parameter value and functional form uncertainty is to run a Monte Carlo simulation analysis. Under the Monte Carlo method, one or more variable and parameter values are randomly drawn from distributions that describe the variables and parameters range of possible values. In addition, functional forms can also be varied in a random manner. The process of randomly drawing variable and parameter values or functional forms and then running the model is repeated many times. Thus, this method calculates a distribution of potential solutions, including, if the process is iterated enough times, approximations of the worst and best case scenarios. The more variables, parameters, and functions that are simultaneously varied, the more robust the uncertainty analysis.

See the SOM for all data used in this illustrative example.

13.5 Limitations and next steps

13.5.1 Limitations

Tier 1 and 2 models should be viewed as complements and not as alternatives. Because of data limitations, we presume that tier 1 modeling will be much more widely implemented. If species-level data on habitat compatibility and potential ranges are available, however, we believe it is important to determine if both tiers suggest the same trends and spatial patterns of biodiversity. If tier 1 and 2 analyses produce spatially correlated results (e.g., areas with high \( Q \) scores also have high \( MBV \) scores; the parcels that exhibit the greatest decline in habitat-quality over time have the lowest \( RMBV \) ratio scores; the relative change in SAR scores over time are the same with and without habitat-quality included; etc.), then the quality of habitat can be used as a proxy for the status of species of concern on the landscape.

The sources of anthropogenic threat that we have presented here as candidates for use in the tier 1 habitat-quality model are all land use related, but many factors affect biodiversity that are difficult to map, such as the presence of exotic species or an altered disturbance regime. Further, our tier 1 model could be extended to allow habitat resistance \( L_j \) to vary across the \( R \) sources of human land uses (i.e., we could use \( L_j \) instead of \( L_{jr} \)). For example, some forested areas may be resistant to the chemicals applied to nearby farm...
fields but particularly affected by a nearby road’s provision of easy access to gatherers of timber and non-timber forest products. In addition, the source of human land use and its ecological impact may be thousands of miles apart. This is most strikingly demonstrated by the pronounced effect of fertilizer use on farm fields of the upper Midwest US on water quality in the Gulf of Mexico. Such broad-scale impacts will not be characterized by our tier 1 model.

Integrating landscape structure and connectivity analyses in the tier 2 model would allow for more explicit population viability modeling (for examples of such modeling see Hanski and Ovaskainen 2000; Vos et al. 2001, Schumaker et al. 2004). Other than the spatial relationship between potential range space and habitat type, the tier 2 biodiversity models presented here do not consider how the spatial configuration of suitable habitat on a landscape may affect species. Further, the models do not consider the size of habitat patches or the ability of animals to move from patch to patch (see Polasky et al. 2005; Winfree et al. 2005; Nelson et al. 2008; Polasky et al. 2008 for examples of species conservation models that do consider species movement among patches). In addition, issues of minimum viable population size, population stochasticity, competition and other species interactions, are not addressed in our models.

By treating a landscape as an island surrounded by terra incognito we may under- or overestimate species status in the broader region. For example, a species with a small amount of suitable habitat in its potential range on the studied landscape will have a low SAR score. However, if the species has effective habitat in a significant portion of its potential range outside of the landscape in question then a low SAR score may not be indicative of the species’ overall status. On the other hand, a species can have a high SAR score in the studied landscape yet only have a small portion of its regional or global potential range space in suitable habitat.

13.5.2 Next steps

All of the models presented in this chapter can be extended in fruitful ways. For example, the set of habitat types $J$ and $L_j$ values in a tier 1 analysis can be defined according to the habitat needs and suitabilities of some specific objective of biodiversity conservation; for example, a species guild that shares habitat or ecological roles. We would then be calculating guild-specific $Q_{x_j}$ and $Q_{x}$ scores. For example, if mapping the habitat-quality of interior forest-dependent species, we would construct the set of habitat types $J$ and $L_j$ values according to their needs, suitabilities, and reaction to different sources of disturbance. Then a species MBV, RMBV, and RMBV ratio scores for these interior forest-dependent species, as well as the countryside SAR score for the entire landscape, could be modified by $Q_{x_j}$ or $Q_{x}$ scores that are more descriptive of the habitat limitations facing this particular guild.

Both tiers of the biodiversity model can be easily integrated with systematic conservation planning processes, such as ecoregional assessments or biodiversity visions. The habitat-quality model in tier 1 could be used to ensure that the portfolio of selected sites includes those features with the highest quality. In addition, ecosystem service planning processes can use these models to calculate the biodiversity “costs” or trade-offs, if any exist at all, associated with LULC changes designed to enhance or conserve ecosystem service provision where landscape-level biodiversity costs are given by changes in SAR values and spatial biodiversity costs by RMBV ratio maps (e.g., Chan et al. 2006; Nelson et al. 2008). In comparing spatial patterns of biodiversity and ecosystem services we may identify areas where conservation investments can benefit species and increase the supply and value of ecosystem services (Balvanera et al. 2001; Naidoo and Ricketts 2006; Turner et al. 2007).

Finally, the output from either tier could be used as input into a site-selection algorithm, such as Marxan, to design alternative conservation area networks (Ball and Possingham 2000). For example, a conservation objective could be to find LULC changes that increase as many RMBV ratio parcel scores, or alternatively minimize the number of RMBV ratio parcel scores below 1, subject to some conservation budget constraint (see Nelson et al. 2008 for details on an optimization model that maximized the gain in SAR across a suite of species for a given conservation budget). Then, once a network of conservation areas is selected to meet targets, the habitat-quality model could be used to conduct a threats assessment on proposed or existing protected areas.
References


