Conservation Biology

Contributed Paper

# Conservation Businesses and Conservation Planning in a Biological Diversity Hotspot

ENRICO DI MININ,*† ** DOUGLAS CRAIG MACMILLAN,* PETER STYAN GOODMAN,‡ BOYD ESCOTT,‡ ROB SLOTOW,§ AND ATTE MOILANEN†

*School of Anthropology and Conservation, Durrell Institute of Conservation and Ecology, University of Kent, CT2 7NR, Canterbury, United Kingdom

†Department of Biosciences, Finnish Centre of Excellence in Metapopulation Biology, P.O. Box 65, FI-00014 University of Helsinki, Finland

‡Biodiversity Information Reporting and Management Division, Ezemvelo KwaZulu-Natal Wildlife, P.O. Box 13053, Cascades 3202, South Africa

§Amarula Elephant Research Programme, School of Life Sciences, University of KwaZulu-Natal, Durban 4041, South Africa

**Abstract:** *The allocation of land to biological diversity conservation competes with other land uses and the needs of society for development, food, and extraction of natural resources. Trade-offs between biological diversity conservation and alternative land uses are unavoidable, given the realities of limited conservation resources and the competing demands of society. We developed a conservation-planning assessment for the South African province of KwaZulu-Natal, which forms the central component of the Maputaland–Pondoland–Albany biological diversity hotspot. Our objective was to enhance biological diversity protection while promoting sustainable development and providing spatial guidance in the resolution of potential policy conflicts over priority areas for conservation at risk of transformation. The conservation-planning assessment combined spatial-distribution models for 646 conservation features, spatial economic-return models for 28 alternative land uses, and spatial maps for 4 threats. Nature-based tourism businesses were competitive with other land uses and could provide revenues of >US$60 million/year to local stakeholders and simultaneously help meeting conservation goals for almost half the conservation features in the planning region. Accounting for opportunity costs substantially decreased conflicts between biological diversity, agricultural use, commercial forestry, and mining. Accounting for economic benefits arising from conservation and reducing potential policy conflicts with alternative plans for development can provide opportunities for successful strategies that combine conservation and sustainable development and facilitate conservation action.*

**Keywords:** biological diversity hotspot, investment, land uses, opportunity costs, sustainable development, Zonation software

Negocios de Conservación y Planificación de la Conservación en un Sitio de Importancia para la Biodiversidad

**Resumen:** *La asignación de tierras para la conservación de biodiversidad compite con otros usos de suelo y las necesidades de desarrollo, alimento y extracción de recursos naturales. Los pros y contras de la conservación biológica y de las formas alternativas de uso de suelo son inevitables, en función de la realidad de recursos limitados para la conservación y la competencia de demandas sociales. Desarrollamos una evaluación de la planificación de la conservación para la provincia sudafricana de KwaZulu-Natal, que constituye el componente central del área de importancia para la Conservación Maputaland-Pondonoland-Albany. Nuestro objetivo fue reforzar la protección de la diversidad biológica al tiempo de promover el desarrollo sustentable y proporcionar orientación para la resolución de potenciales conflictos políticos en áreas prioritarias para la conservación que estén en riesgo de transformación. La evaluación de la planificación de la conservación combinó modelos de distribución espacial de 646 atributos de conservación, modelos espaciales de retorno*

***Current address: Department of Biosciences, Finnish Centre of Excellence in Metapopulation Biology, P.O. Box 65, FI-00014, University of Helsinki, Finland, email enrico.di.minin@helsinki.fi*
*Paper submitted July 27, 2012; revised manuscript accepted November 5, 2012.*



DOI: 10.1111/cobi.12048

*económico de 28 usos alternativos de suelo y mapas espaciales de 4 amenazas. Los negocios de turismo basado en naturaleza fueron competitivos con otras formas de uso de suelo y aportaron ganancias de >$60 US millones/año a accionistas locales y al mismo tiempo ayudan a alcanzar las metas de conservación para casi la mitad de los atributos de conservación en la región bajo planificación. La consideración de los costos de oportunidad disminuyó sustancialmente los conflictos entre la diversidad biológica, el uso agrícola, la silvicultura comercial y la minería. La consideración de los beneficios económicos de la conservación y la reducción de potenciales conflictos políticos mediante planes alternativos de desarrollo puede proporcionar oportunidades para estrategias exitosas que combinan la conservación y el desarrollo sustentable y facilitan las acciones de conservación*

**Palabras Clave:** costos de oportunidad, desarrollo sustentable, inversión, sitios de importancia para la biodiversidad, software para zonación, usos de suelo

## Introduction

Recent rates of species extinction and habitat loss through anthropogenic activities are unprecedented (Butchart et al. 2010). Given limited conservation budgets, resources need to be allocated so as to maximize the conservation return on investment (Murdoch et al. 2007). Maximizing conservation return requires assessment of expected benefits and costs of alternative conservation strategies and selection of the most cost-effective strategies (Polasky 2008). Conservation-resource allocation has mainly focused on the biological benefits of representing current patterns of biological diversity in as little area as possible (Naidoo et al. 2006). However, conservation plans that include economic costs conserve equal or greater levels of biological diversity with dramatically fewer resources than plans that do not consider costs (Richardson et al. 2006; Bode et al. 2008; Carwardine et al. 2008). Furthermore, including economic benefits from biological diversity and ecosystem services can show where conservation can be more profitable than alternative land uses (Naidoo & Ricketts 2006). Including data on vulnerability (the likelihood or imminence of loss of an important biological feature from current or future threats) is also important when conducting spatial conservation prioritization (Wilson et al. 2005).

The allocation of land to conservation of biological diversity competes with other land uses and the needs of society (Carpenter et al. 2006). Trade-offs between biological diversity conservation and alternative land-uses are unavoidable given the realities of limited conservation resources and the demands of society (Wilson et al. 2010). Thus, methods need to be developed to facilitate compromise, especially in developing, biological diversity-rich countries, where conservation resources are particularly scarce (Faith & Walker 2002). A range of social, economic, and political factors that define opportunities for implementing conservation action in complex social-ecological systems need to be considered (Knight & Cowling 2007; Knight et al. 2011). In conservation planning, data on conservation value and vulnerability are combined with data on human, social, and economic factors to determine the appropriateness, feasibility, and effectiveness of conservation actions (Knight & Cowling 2007). Economic costs of land acquisition (Polasky et al. 2001) and implementation of conservation action (Wilson et al. 2007); human and social dimensions (Knight et al. 2010, 2011); and policy instruments (Theobald et al. 2000; Pierce et al. 2005) have been included in conservation plans. Because many priority areas for conservation are on unprotected private and communal land, including the economic potential arising from enterprise-based activities focusing on conservation in conservation plans could reveal further opportunities to protect biological diversity.

We developed a conservation-planning assessment that accounts for conservation opportunities and examines the trade-offs among biological diversity conservation, threats, opportunity costs, and the financial benefits derived from conservation. We focused on the South African province of KwaZulu-Natal, which forms the central component of the Maputaland–Pondoland–Albany biological diversity hotspot. Our objective was to enhance biological diversity protection while promoting sustainable development through conservation businesses and reducing potential policy conflicts over priority areas for conservation that are at risk of transformation. In particular, we were interested in the potential of conservation businesses to help meet conservation-planning goals for the area. We considered conservation businesses those that are run with the objective of maximizing economic return from nature-based tourism (hunting, live sales of wildlife species, and ecotourism) (Di Minin et al. 2013). We integrated spatial-distribution models for 646 conservation features, spatial economic-return models for 28 alternative land-uses, and spatial maps for 4 threats.

## Methods

### Planning Region

The KwaZulu-Natal province of South Africa is approximately 92,000 km$^2$. The province is internationally recognized for its high levels of species richness and endemism,

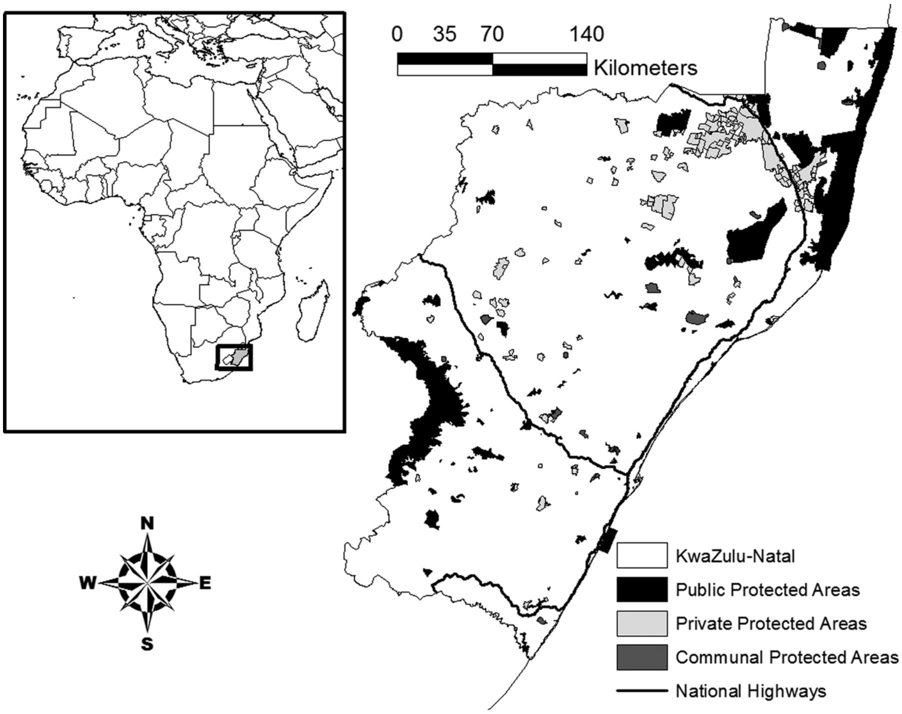


*Figure 1. Map of KwaZulu-Natal showing public, private, and communal protected areas.*

which are under different levels of threat (Steenkamp et al. 2004). The current protected-area network (Fig. 1) fails to adequately conserve a representative sample of the province's biological diversity or to maintain key ecological processes across the landscape (Goodman 2006). There is, therefore, a need to develop a conservation-planning assessment that can guide protected-area expansion and enhance persistence of biological diversity. Economic development and a rapidly growing human population are threatening biological diversity in the area (CEPF 2010). Transformation of land for agricultural use, commercial forestry, and mining is the biggest threat to biological diversity. Human population density, poverty, inequality among humans, and unemployment rates are very high in KwaZulu-Natal, and policy makers in the area are under extreme pressure to create jobs for the poor (KZNDAE 2011).

High rainfall, warm temperatures, and rich soils make extensive areas of KwaZulu-Natal particularly suitable for agriculture and commercial forestry (Camp 1999). Thus, the provincial government is prioritizing the development of agriculture and commercial forestry so as to alleviate poverty, create jobs, further economic development, and ensure food security (KZNDAE 2011). Mining also contributes substantially to poverty relief and job creation in the province and represents a daunting threat to biological diversity (CEPF 2010). Other threats to biological diversity include invasive plant species, unsustainable resource use, road development, and urbanization (Goodman 2006). Consumptive and nonconsumptive nature-based tourism that focuses on the 5 most charismatic mammal species (conservation businesses) is also being promoted as a means for sustainable development and poverty relief (Di Minin et al. 2013).

### Conservation Features

We used a data set of 646 conservation features for which accurate spatial-distribution models were available (Goodman 2006). Such features included ecosystems, vegetation types, species, and populations of species (Table 1 & Supporting Information). We used ecosystems and vegetation types as surrogates for specific ecological processes (for details see Goodman [2006]). The selection criteria for each conservation feature were based on endemicity, global and national rarity, population trends and degree of threat, importance of KwaZulu-Natal to the conservation of the feature; and economic potential of the feature (Goodman 2006). We modeled species distributions with a maximum entropy algorithm (the MaxEnt software) on the basis of presence records only (Di Minin 2012) or on the basis of cartographic models derived from several predictor variables (Goodman 2006).

### Economic Features

We developed spatial economic-return models for 28 individual land uses in 4 broad land-use categories, such as agriculture, commercial forestry, conservation businesses, and mining (Table 1 & Supporting Information). We calculated the spatial distribution of economic returns at full equity as gross revenue less all variable and fixed costs of production (Crossman et al. 2011). We did not consider interest payments on loans or income

**Table 1. List of conservation and economic features included in the prioritization scenarios for KwaZulu-Natal.**

| *Conservation feature* | *Number included* | *Economic feature* | *Number included* |
|---|---|---|---|
| Ecosystems | 2 | agriculture | 16 |
| Vegetation types | 55 | conservation businesses | 2 |
| Plant species | 225 | commercial forestry | 8 |
| Annelid species | 66 | mining | 2 |
| Arachnid species | 3 | total | 28 |
| Beetle species | 23 | | |
| Butterfly species | 21 | | |
| Diplopoda species | 33 | | |
| Grasshopper species | 10 | | |
| Millipede species | 85 | | |
| Mollusc species | 42 | | |
| Termite species | 3 | | |
| Velvet worm species | 2 | | |
| Amphibian species | 10 | | |
| Reptile species | 43 | | |
| Bird species | 16 | | |
| Mammal species | 7 | | |
| Total | 646 | | |

generated by other activities (Hajkowicz & Young 2005). Comparing returns from alternative land uses is complicated by the fact that returns usually differ in size and in length of time over which expenditures have to be made and benefits returned (Polasky et al. 2008). Thus, so we could make a direct comparison between alternative land uses, we discounted the costs and returns incurred over an investment period to a present-day value. Generally, the net present value (NPV) for land use *i* on parcel *j* was calculated as

$$\mathrm{NPV}^i_j = \sum_{t=0}^{\infty} \frac{A_j\left(b^i_j - c^i_j\right)}{(1+\delta)^t}, \qquad (1)$$

where $i = 1, 2, 3, 4, .., 28$, $t$ (time) $= 0, 1, 2, 3, \ldots, 35$ (indexes years), $A_j$ is the area of parcel $j$, $b^i_j$ is the per unit area gross revenue for land use $i$ on parcel $j$, $c^i_j$ is the per unit area production or management costs of land use $i$ on parcel $j$, and $\delta$ is the annual discount rate (5.5%) on the basis of cost of borrowing money in South Africa in 2011 (OECD 2011).

For agriculture, commercial forestry, and mining, we calculated gross revenue per unit area ($b^i_j$) by combining data on commodity prices with estimates of yields (ton per hectare). We based spatial-yield models on climatic conditions, soil quality, and management practices, such as the parcel being irrigated or not, and validated them independently from this study. (See Smith [1996], Dye et al. [2004], and Bezuidenhout [2005] for a full explanation of these methods.) For mining, we developed a yield-map based on suitable geological substrates and validated it with geo referenced information on current mines and prospecting in the area (EKZNW 2011). For coal mining, we divided the study area into a grid composed of cells ranked according to their distance from the coal seams (e.g., decreased yields with increased distance from the seam). For hunting and live sales of wild animals, we used georeferenced data from annual game counts to estimate the density of 34 species in 5 land-cover types and then predicted long-term sustainable off-take levels of each species per unit area on the basis of harvesting models or published information (Blignaut & Moolman 2006; Di Minin 2012). We then calculated gross revenue per unit area ($b^i_j$), by combining the monetary value of each species with the sustainable off-take levels. In the models, we assumed 80% of the animals were sold alive and 20% were hunted for trophies (Aylward & Lutz 2003).

Ecotourism in the study area generates profit from overnight stays and park-entrance fees (Aylward & Lutz 2003). In general, the value of an ecotourism site increases as the quantity or quality of environmental attributes at the site increases (Adamowicz et al. 2011). Thus, we used a choice-modeling approach to determine what drove tourists' preference for experiences in nature (environmental attributes) in the study area (Di Minin et al. 2013). We focused solely on species of big game because they are thought to be a primary motivator for tourist decision making and the key factor to financial competitiveness for protected areas in sub-Saharan Africa (Di Minin et al. 2013). We generated a biological diversity supply map by overlaying individual habitat-suitability models for tourists' favorite species (e.g., lion, elephant, leopard, black rhino) (Di Minin 2012; Di Minin et al. 2013). The biological diversity supply map was then overlaid with a layer on accessibility from major transportation infrastructure and airports to account for distance and travel time to the tourism sites (Adamowicz et al. 2011). Finally, we used tourists' visitation data and the average price paid by each tourist to calculate the gross revenue per unit area. We used ArcInfo 10.0 (ESRI, Redlands, California) for all analyses. For all models, we used the exchange rate of the International Monetary Fund to convert prices and cost data from South African Rands to 2011 U.S. dollars. Details on how the NPV was calculated for each individual land use, including investment periods, commodity prices, production and management costs, are in Supporting Information.

We converted NPV to equal annual equivalent terms,

$$\mathrm{EAE}^i_j = \mathrm{NPV}^i_j \frac{\delta(1+\delta)^t}{(1+\delta)^t - 1}. \qquad (2)$$

## Threats

Potential threat factors identified for KwaZulu-Natal were invasive non-native plants, urbanization, road development, and unsustainable resource use (CEPF 2010). We used a rule-based approach that relied on expert knowledge to estimate spatially each threat and assign a threat index (Lombard et al. 2002; Rouget et al. 2003). For urbanization we increased by a factor of 1.49 and 2.07 the current population to estimate the 2016 census in each urban polygon with and without factoring in HIV/AIDS, respectively (Lombard et al. 2002). We used a set of rules to create a buffer (a zone around a map feature measured in units of distance or time) around urban polygons. We based these rules on population in the polygons, polygon proximity to an urban core, and polygon distance from national and main roads (Rouget et al. 2003). We converted the buffered polygons to a raster categorized as no urban spread, existing urban areas, urban spread with HIV/AIDS, or urban spread without HIV/AIDS. Finally, urban threat was not allowed to spread into existing protected areas.

For road development, the existing roads were divided according to socioeconomic zones (e.g., economic core area to underdeveloped rural area [areas where people depend on migratory labor and remittances and government social grants for their survival]). On the basis of type of road (e.g., national) and socioeconomic zone, buffer polygons were created to a specified distance around the roads, and distance decreased from national highways in economic-core areas to rural roads in underdeveloped areas (Lombard et al. 2002). The buffered roads were then converted to a raster categorized as no risk (outside the buffer) and high risk (inside the buffer). For unsustainable resource use, data on human population density in community-owned areas were categorized into low harvesting threat for areas with <1 individual/ha, medium harvesting threat for areas with 1–5 individuals/ha, and high threat for areas with >5 individuals/ha (Lombard et al. 2002).

For invasive non-native plants, we considered 3 species, triffid weed (*Chromolaena odorata*), Spanish flag (*Lantana camara*), and bug weed (*Solanum maritianum*), for which potential distribution models were available (Goodman 2006). Areas with <0.01, 0.01–0.330.34–0.66, and 0.67–1.0 probability of infestation were categorized as no potential, low potential, medium potential, and high potential for invasion respectively. We then calculated the sum for each input grid and reclassified the output grid into no invasion potential (no input grid cell had high potential for invasion), low invasion potential (only one input grid had high potential of invasion), medium invasion potential (2 input grids had high potential of invasion); and high invasion potential (3 input grids had high potential of invasion) (Lombard et al. 2002).

## Zonation as Analysis Framework

We used Zonation (version 3.1) software and a new feature for balancing priority areas for conservation and alternative land uses (Moilanen et al. 2011*a*). Zonation produces a complementarity-based and balanced ranking of areas of conservation priority over an entire landscape, rather than satisfying targets with minimum cost (Moilanen et al. 2005; Di Minin & Moilanen 2012). Zonation produces the priority ranking via iterative loss minimization, and removes the landscape element that leads to the smallest loss of conservation value while accounting for, for example, total and remaining distributions of features, weights given to features, and feature-specific connectivity. When implementing single-objective spatial prioritization, value can be aggregated for competing land uses and for conservation. When implementing multiobjective spatial conservation prioritization, the priority ranking can be used to allocate the top fraction of the landscape to biological diversity conservation, while the low-priority areas are allocated to alternative land uses. In the latter case this is done by applying positive weights to conservation features (species, ecosystems, carbon maps) and negative weights to alternative land uses, opportunity costs, or threats.

The analysis produced a set of performance curves that described the extent to which each feature was retained at each fraction of the landscape (Moilanen et al. 2012). For multiobjective spatial conservation prioritization, these curves are used to assess whether a successful spatial separation between conservation and alternative land uses was obtained (Moilanen et al. 2011*a*). Although it is not a target-based approach primarily, Zonation can be used to prioritize areas through the irreplaceability–vulnerability approach (e.g., Moilanen et al. 2011*b*). We chose Zonation among other planning tools because it can run analyses with very large data sets (Kremen et al. 2008) and can, given fine-resolution data, evaluate species-specific connectivity considerations at large extents (Moilanen et al. 2005; Arponen et al. 2012).

## Prioritization Scenarios

We analyzed 8 spatial-prioritization scenarios. First, we developed spatial prioritization solutions for each land-use category separately. We based spatial prioritization for biological diversity on spatial-distribution models for conservation features and threats only, whereas we based spatial prioritizations for conservation businesses, agriculture, commercial forestry, and mining on spatial economic-return models only. We then developed multicriteria spatial conservation prioritizations in which we prioritized areas where conservation businesses could provide the highest economic return compared with alternative land uses (on the basis of spatial economic-return models only); reduced policy conflict over priority areas for biological diversity conservation at risk of transformation (on the basis of spatial-distribution models, spatial economic-return models, and threats); and identified important areas for protected-area expansion on the basis of the current public protected-area network (which we built from the previous analysis).

**Table 2. Minimum and maximum annual profit for a range of land uses in KwaZulu-Natal.**

| *Category and land use* | *Minimum (US$ · ha$^{-1}$ · yr$^{-1}$)* | *Maximum (US$ · ha$^{-1}$ · yr$^{-1}$)* |
|---|---|---|
| Agriculture | | |
| banana dry | 398 | 416 |
| banana irrigated | 383 | 800 |
| cotton dry | 69 | 176 |
| cotton irrigated | 134 | 242 |
| groundnut dry | 129 | 387 |
| groundnut irrigated | 339 | 659 |
| lucerne | 509 | 1298 |
| maize dry | 7 | 43 |
| maize irrigated | 134 | 237 |
| potato | 797 | 1075 |
| sorghum dry | 43 | 131 |
| sorghum irrigated | −29 | −19 |
| sunflower | 50 | 182 |
| sugarcane dry | −379 | −173 |
| sugarcane irrigated | 78 | 172 |
| wheat irrigated | 306 | 641 |
| Commercial forestry | | |
| *Eucalyptus grandiis* | 763 | 1386 |
| *Pinus patula* short | 293 | 474 |
| *Pinus patula* long | 267 | 431 |
| *Pinus taeda* short | 411 | 663 |
| *Pinus taeda* long | 306 | 494 |
| *Pinus elliottii* short | 301 | 464 |
| *Pinus elliottii* long | 274 | 423 |
| Wattle | 109 | 142 |
| Mining | | |
| titanium and coal | 90,000 | 140,000 |
| Conservation businesses | | |
| hunting and live sales | 17 | 94 |
| ecotourism | 82 | 611 |

*Negative values imply a net loss over the investment period for that land use. Not all 200 × 200 m grid cells used for the prioritization scenarios in our study were suitable for each land use.*

**Table 3. Percentage of overlapping grid cells for the top 10% (above and right of dashes) and 30% (below and left of dashes) of the landscape retained for conservation according to the respective Zonation priority-rank solutions.**

| | *AGR* | *FOR* | *MIN* | *CON* | *BIO* | *NOB* | *ALL* | *ALP* |
|---|---|---|---|---|---|---|---|---|
| AGR | – | 32.51 | 24.80 | 6.06 | 10.40 | 1.06 | 9.26 | 10.85 |
| FOR | 36.15 | – | 10.77 | 5.81 | 14.67 | 0.00 | 12.95 | 16.25 |
| MIN | 42.21 | 21.54 | – | 5.61 | 4.82 | 4.37 | 4.51 | 3.91 |
| CON | 27.27 | 15.57 | 33.56 | – | 19.59 | 83.84 | 25.22 | 29.81 |
| BIO | 27.84 | 33.90 | 24.67 | 43.66 | – | 17.49 | 93.62 | 49.13 |
| NOB | 19.60 | 0.00 | 36.40 | 70.22 | 42.55 | – | 22.76 | 23.50 |
| ALL | 25.91 | 30.88 | 21.50 | 47.43 | 93.53 | 40.45 | – | 50.62 |
| ALP | 24.56 | 37.35 | 21.48 | 44.03 | 82.16 | 34.53 | 85.85 | – |

*Abbreviations: AGR, agriculture; FOR, commercial forestry; MIN, mining; CON, conservation businesses; BIO, biological diversity only; NOB, agriculture, commercial forestry, mining, and conservation businesses, but no biological diversity; ALL, all land uses jointly; ALP, all land uses jointly with protected areas masked.*

In the latter case, we implemented a hierarchical analysis in which top priorities for conservation were forced into existing protected areas and areas of lower priority were fit into the rest of the landscape (Moilanen et al. 2012).

The additive-benefit function-cell-removal rule (Moilanen 2007) was used with features-specific weights and connectivity values (Supporting Information). The use of the additive-benefit function was appropriate because money is additive, and this work is about identifying compromises among land uses, implying that overall efficiency is desirable and that a degree of substitution among alternative land uses must be allowed. In addition, the use of a convex power function for ecotourism was appropriate to account for potentially diminishing returns should conservation businesses increase in the area. In addition, measured in terms of return on investment in species distribution coverage, the additive-benefit function performs better in this area compared with traditional target-based planning (Di Minin & Moilanen 2012). The exponent of the species-specific additive-benefit power function was set to 0.25 for all conservation features (corresponding to the species-area relation) and to 1.0 for all economic land uses (Moilanen 2007). All data were processed and analyses carried out at a 200 × 200 m resolution in a landscape of 2,369,400 effective grid cells of information.

All taxa and land-use categories were weighted equally, implying all conservation features of a certain biotic group, community, or ecosystem type were jointly considered equal to agriculture, commercial forestry, mining, and conservation businesses (Supporting Information). However, conservation features within each taxon were weighted differently according to their endemicity, conservation importance, and economic value (Goodman 2006) (Supporting Information). We used metapopulation-type declining-by-distance connectivity responses (distribution smoothing) to induce aggregation in Zonation (Moilanen et al. 2005). Distribution smoothing is a species-specific aggregation method that emphasizes areas that are well connected to others and thus results in a prioritization with more compact priority areas. The widths of the connectivity kernels were species specific and expressed the dispersal capability or scale of landscape use of the species (Supporting Information). We did not use distribution smoothing for economic features and threats.

We used automated postprocessing analyses in Zonation to compare the spatial overlaps and conflicts of the top 10% and 30% priority areas for each prioritization scenario. This was done by comparing the percentage of overlapping grid squares for the top 10% and 30% of the landscape according to the respective Zonation priority-rank maps (Moilanen et al. 2012). We used postprocessing analyses in ArcInfo 10.0 (ESRI) to calculate the total economic return generated by conservation businesses.

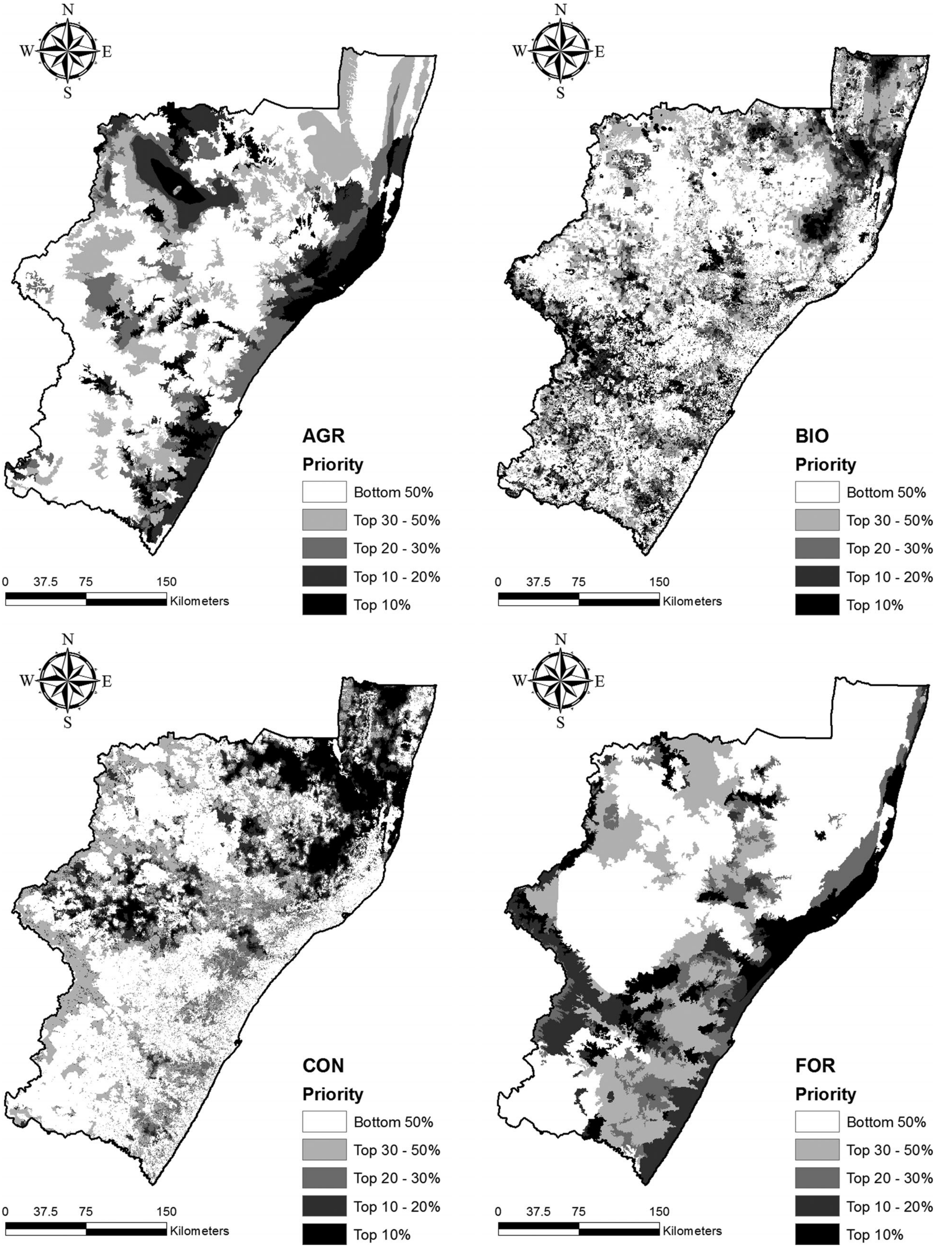


*Figure 2. Maps of priority ranking for each major land use and for conservation of biological diversity (BIO) in KwaZulu-Natal (AGR, agriculture; CON, conservation businesses; FOR, commercial forestry; MIN, mining).*

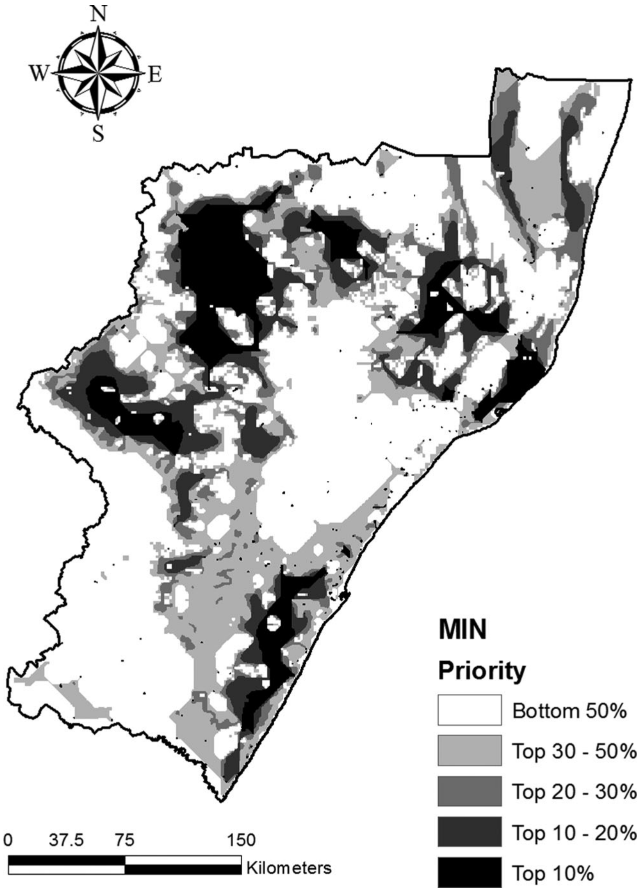


*Figure 2. Continued.*

## Results

Mining was the most profitable land-use in the planning region, and nonirrigated sugarcane farming was the least profitable (Table 2). Prioritizing for each land use separately revealed that commercial forestry posed the largest threat to biological diversity; there was a 14.7% and 33.9% spatial overlap of the 10% and 30% of priority areas, respectively (Table 3 & Fig. 2). The second-largest threat to biological diversity was agriculture; there was a 10.4% and 26.8% spatial overlap of the 10% and 30% of priority areas. In addition, there was considerable conflict (24.7%) between mining and biological diversity at the 30% of priority areas (Table 3). The top 30% priority areas for conservation businesses could potentially protect up to 43.7% of the distributions of all biological diversity features in the planning region (Table 3). Only 4.4% of the features would have a representation of <10% of their distributions in the top 30% priority areas for conservation businesses.

When all land uses were considered together in the same analysis, the spatial conflict between biological diversity and alternative land uses decreased (Table 3). In addition, the spatial overlap between the solution based on conservation features and threats only and the one where all land uses and threats were considered jointly was very high (>93% for both the 10% and 30% of priority areas) (Table 3). In the hierarchical analysis for expansion of protected area, where top priorities for conservation were forced into existing protected areas, there remained considerable conflict with commercial forestry because current protected areas were in areas where economic return from such land use was high (Figs. 2 & 3). The current protected-area network (top 10% of the landscape) provided a mean coverage of all distributions of 49.1%, whereas protecting the top 30% of the landscape increased the mean coverage to 82.2%. When only spatial economic-return models for all land uses were considered, conservation businesses were the most profitable land use in the central and northern parts of the province (Fig. 3). The 30% top priority areas for conservation businesses could potentially generate up to $62 million ($50 million from ecotourism and $12 million from hunting and live sales) per year and provide a 42.5% mean coverage of all conservation features' distributions (Table 3).

Trade-offs and conflicts between biological diversity and other land uses were also apparent in the performance curves for the priority maps (Fig. 4). Prioritizing for biological diversity only, for instance, increased conflict with agriculture and commercial forestry. Including all land uses, instead, produced a solution with less conflict between biological diversity and alternative land uses. The general shapes of performance curves for positively weighted features (biological diversity and conservation businesses) curved away from the origin, whereas those for agriculture, forestry, and mining curved toward the origin, meaning a successful separation between these features was possible (Fig. 4).

## Discussion

We found that conservation businesses could help meet conservation goals for almost half the conservation features in the planning region and deliver considerable financial benefits to local stakeholders. Such results are important because they reveal opportunities for strategies that combine successfully conservation and human and economic development (Adams et al. 2004), which represents a massive financial incentive for conservation in a biological diversity hotspot. In addition, the financial benefits provided by conservation businesses can generate tangible benefits for human well-being (Sukhdev 2009).

The economic value of biological diversity and ecosystem services is often undervalued by policy makers because most goods and services in relatively undeveloped ecosystems are not traded in conventional markets (MacMillan et al. 2004) or because conservation

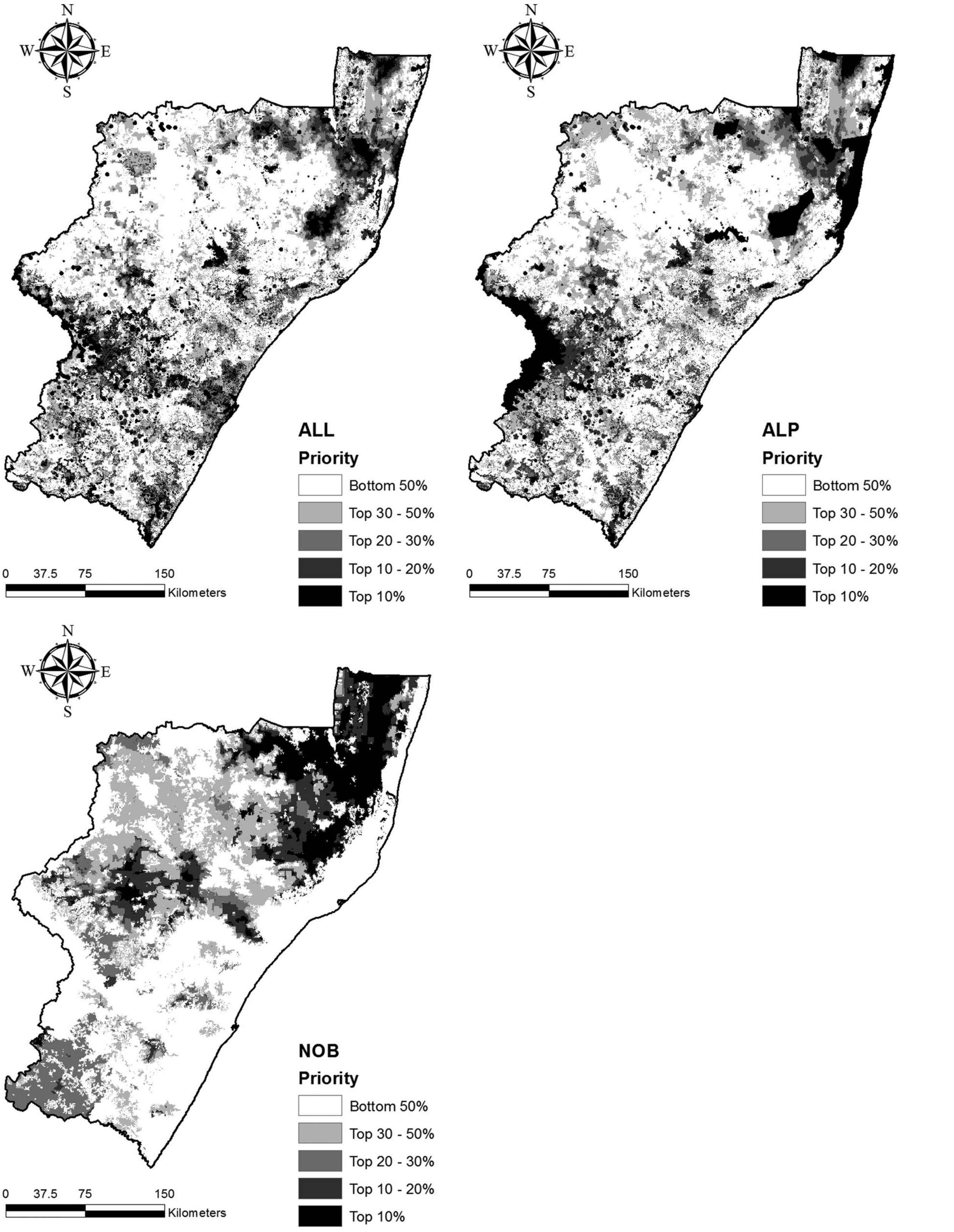


*Figure 3. Maps of priority ranking for multiple-objective planning areas in KwaZulu-Natal (ALL, all land uses and conservation of biological diversity; ALP, all land uses and conservation of biological diversity with protected areas masked; NOB, agriculture, commercial forestry, mining, and conservation businesses with no conservation of biological diversity).*

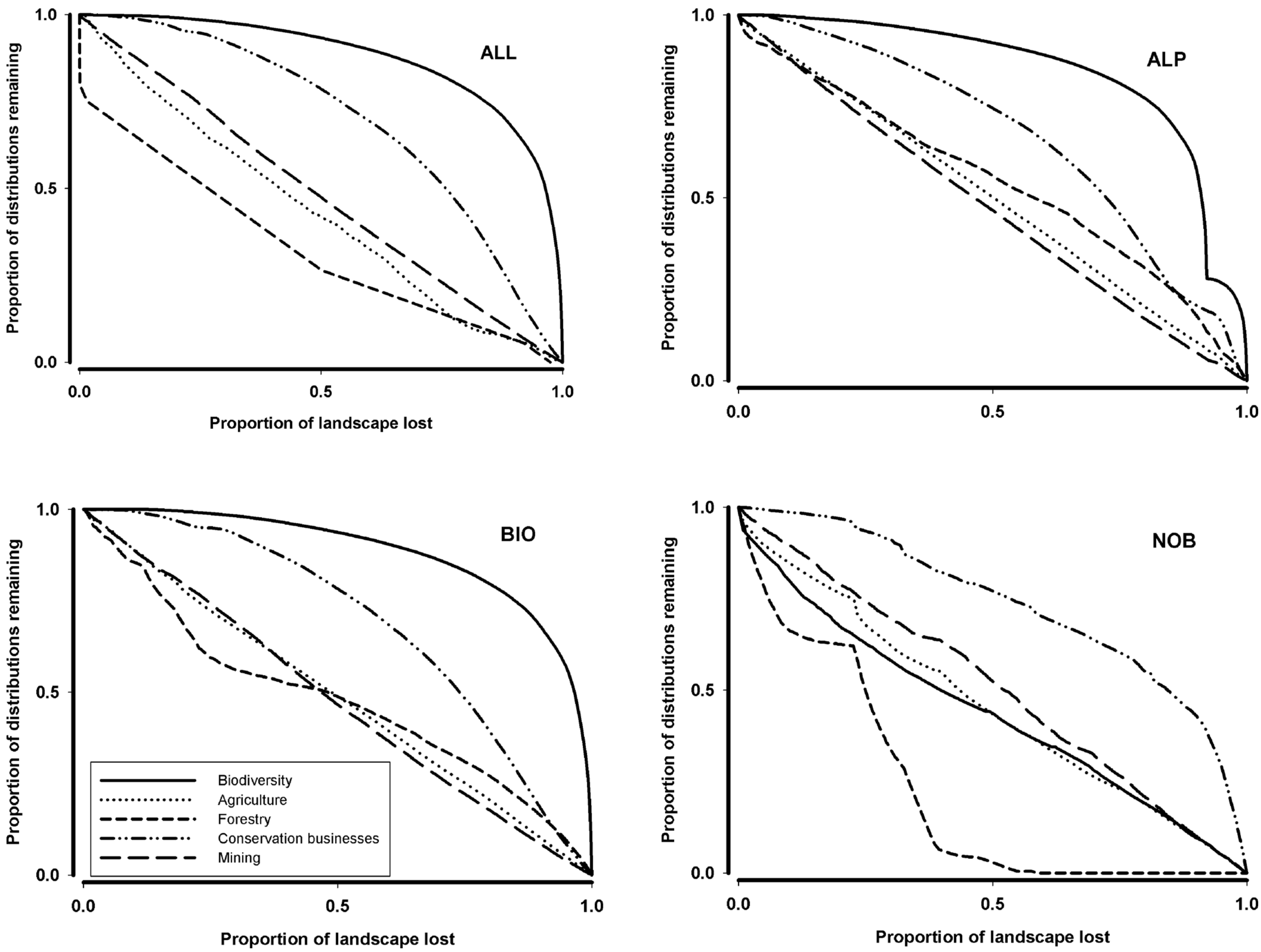


*Figure 4. Performance curves for different prioritization scenarios in KwaZulu-Natal describing the mean representation across features at the given level of cell removal. For biological diversity, the performance curve is an average across all conservation features, whereas for the land-use categories it is an average across all economic features (ALL, all land uses and conservation of biological diversity; ALP, all land uses and conservation of biological diversity with protected areas masked; BIO, biological diversity only; NOB, agriculture, commercial forestry, mining, and conservation businesses, but no conservation of biological diversity).*

professionals fail to conduct interdisciplinary research (Balmford & Cowling 2006; Reyers et al. 2010). The result is that conservation-planning efforts do not identify opportunities to finance conservation in innovative ways (Naidoo & Ricketts 2006). Conservation-planning assessments, such as the one we developed here, can be used to reveal the economic benefits private landowners and local communities can derive from ecosystem services such as sustainable resource use and ecotourism. The real strength of our approach, however, is that it is not based solely on a utilitarian view of conservation, in which benefits and costs are assessed in purely economic terms (Naidoo & Ricketts 2006). Rather, it takes into account priority conservation areas and landscape connectivity, which can enhance biological diversity persistence and ecosystem functioning. Thus, our results can be used to motivate both policy makers and private investors to support and finance activities that can simultaneously achieve conservation and development goals. In regions where acquiring land for conservation is not an option (Knight et al. 2011), but land owners are potentially interested in conservation initiatives (Knight et al. 2010), highlighting potential areas where conservation and development goals can both be met may help create further opportunities to protect biological diversity.

Biological diversity need to be better integrated into the policies and alternative plans for development (Theobald et al. 2000; Pierce et al. 2005). Yet, the failure to account for policy objectives of competing sectors (Faith & Walker 2002) and to include socioeconomic data (Polasky 2008) in conservation planning is making conservation plans less relevant to decision makers (often despite supportive legislation) (Reyers et al. 2010). Expensive sites (high opportunity costs) are usually in demand for competing activities, and targeting them for conservation may generate conflict with development interests. Thus, reducing potential policy conflicts over priority conservation areas is an important factor in reducing the socioeconomic costs of conservation (Knight et al. 2008). We found that including opportunity costs in conservation-planning assessments may help alleviate conflicts between alternative plans for human and economic development (Carwardine et al. 2008). Moreover, the reduction of such conflict can be achieved with substantial spatial overlap through a conservation plan that is based on biological data and threats only. However, in contrast to previous studies that incorporated opportunity costs into conservation planning (e.g., Naidoo & Adamowicz 2006; Bode et al. 2008; Carwardine et al. 2008), our approach included (and can be used to include) a wider range of land uses than agriculture and used the fine scale required to inform decision making.

Approaches to spatial conservation prioritization range from proactive to reactive conservation with regards to how they take into account threats and vulnerability (Brooks et al. 2006). Proactive approaches seek to protect areas that are not yet threatened (Laurance 2005), whereas reactive approaches prioritize areas that are under imminent threat (Visconti et al. 2010). Focusing investments on reactive approaches only may exacerbate the conflict between conservation and development interests (Faith & Walker 2002). In addition, information about threats is often incomplete (Visconti et al. 2010), and threats are difficult to eradicate even when protection is guaranteed (Laurance et al. 2012). An approach such as our may be more appropriate in complex socioecological systems where trade-offs between conserving priority areas (high conservation value and vulnerability) and embracing conservation opportunities (low opportunity costs and high economic benefits) may be required (Faith & Walker 2002; Knight & Cowling 2007). Doing so may facilitate linking a conservation-planning assessment to a broader implementation strategy (Knight et al. 2006).

Conservation businesses can provide an important opportunity to bring under protection threatened and endemic biological diversity while delivering financial benefits to private and communal landowners. Such information will be very important to support on-going initiatives on the integration of conservation practice into land-reform agreements to expand the protected-area network and sustain human and economic development in the Maputaland–Pondoland–Albany hotspot (CEPF 2010). More broadly, our approach can be used by conservation planners elsewhere to evaluate how well payment for ecosystem services (e.g., carbon sequestration [Crossman et al. 2011] and others [Nelson et al. 2009; Gallai et al. 2009]) and government subsidies and tax incentives can protect biological diversity. As governments shift their policies toward greener economies, future assessments should include the negative effects alternative land uses to conservation may have on ecosystem services (Sukhdev 2009). The inclusion of such effects may highlight more opportunities for protecting biological diversity.

## Acknowledgments

E.D.M. was supported by a Panthera Kaplan Graduate Award and a U.S. Fish & Wildlife Service Rhinoceros grant. Research was carried out with the permission of Ezemvelo KwaZulu-Natal Wildlife and the iSimangaliso Wetland Park Authority. Data on commercial forestry were provided by W. Meyer from the Forestry Economics Services, and data on agriculture was provided by G. Archer and O. Howison. Species-distribution models were provided by Ezemvelo KwaZulu-Natal Wildlife. A.M. was supported by the European Research Council -Starting Grant project 260393 (GEDA), and the Academy of Finland Centre of Excellence Programme 2006–2011.

## Supporting Information

Additional information on conservation and economic features' weights and connectivity values (Appendix S1) and spatial economic return models (Appendix S2) is available online. The authors are responsible for the content and functionality of these materials. Queries (other than missing material) should be directed to the corresponding author.

### Literature Cited

Adamowicz, W. L., R. Naidoo, E. Nelson, S. Polasky, and J. Zhang. 2011. Nature-based tourism and recreation. Pages 188–205 in P. Kareiva, H. Tallis, T.H. Rickets, G.C. Daily, and S. Polasky, editors. Natural capital. Theory and practice of mapping ecosystem services. Oxford University Press, Oxford, United Kingdom.

Adams, W. M., R. Aveling, D. Brockington, B. Dickson, J. Elliott, J. Hutton, D. Roe, B. Vira, and W. Wolmer. 2004. Biodiversity conservation and the eradication of poverty. Science **306:**1146–1149.

Arponen, A., J. Lehtomäki, J. Leppänen, E. Tomppo, and A. Moilanen. 2012. Effects of connectivity and spatial resolution of analyses on conservation prioritization across large extents. Conservation Biology **26:**294–304.

Aylward, B., and E. Lutz. 2003. Nature tourism, conservation and development in KwaZulu-Natal, South Africa. The World Bank, Washington, D.C.

Balmford, A., and R. M. Cowling. 2006. Fusion or failure? The future of conservation biology. Conservation Biology **20:**692–695.

Bezuidenhout, C. N. 2005. Development and evaluation of model-based operational yield forecasts in the South African sugar industry. PhD dissertation. University of KwaZulu-Natal, Pietermaritzburg, South Africa.

Blignaut, J., and C. Moolman. 2006. Quantifying the potential of restored natural capital to alleviate poverty and help conserve nature: a case study from South Africa. Journal for Nature Conservation **14:**237–248.

Bode, M., K. A. Wilson, T. M. Brooks, W. R. Turner, R. A. Mittermeier, M. F. McBride, E. C. Underwood, and H. P. Possingham. 2008. Cost-effective global conservation spending is robust to taxonomic group. Proceedings of the National Academy of Sciences USA **105:**6498–6501.

Brooks, T. M., R. A. Mittermeier, G. A. B. da Fonseca, J. Gerlach, M. Hoffmann, J. F. Lamoreux, C. G. Mittermeier, J. D. Pilgrim, and A. S. L. Rodrigues. 2006. Global biodiversity conservation priorities. Science **313:**58–61.

Butchart, S. H. M., et al. 2010. Global biodiversity: indicators of recent declines. Science **328:**1164–1168.

Camp, K. 1999. Guide to the use of the bioresource programme. KwaZulu-Natal Department of Agriculture, Pietermaritzburg, South Africa.

Carpenter, S. R., et al. 2006. Millennium ecosystem assessment: research needs. Science **314:**257–258.

Carwardine, J., K. A. Wilson, G. Ceballos, P. R. Ehrlich, R. Naidoo, T. Iwamura, S. A. Hajkowicz, and H. P. Possingham. 2008. Cost-effective priorities for global mammal conservation. Proceedings of the National Academy of Sciences USA **105:**11446–11450.

CEPF (Critical Ecosystem Partnership Fund). 2010. Ecosystem profile. Maputaland-Pondoland-Albany biodiversity hotspot. Conservation International Southern African Hotspots Programme, Cape Town.

Crossman, N. D., B. A. Bryan, and D. M. Summers. 2011. Carbon payments and low-cost conservation. Conservation Biology **25:**835–845.

Di Minin, E. 2012. Biodiversity conservation and sustainable development in the Maputaland-Pondoland-Albany hotspot: an interdisciplinary approach to conservation planning. PhD dissertation. Durrell Institute of Conservation and Ecology, University of Kent, Canterbury, United Kingdom.

Di Minin, E., and A. Moilanen. 2012. Empirical evidence for reduced protection levels across biodiversity features from target-based conservation planning. Biological Conservation **153:**187–191.

Di Minin, E., I. Fraser, R. Slotow, and D. C. MacMillan. 2013. Understanding heterogeneous preference of tourists for big game species: implications for conservation and management. Animal Conservation DOI: 10.1111/j.1469-1795.2012.00595.x.

Dye, P. J., S. Jacobs, and D. Drew. 2004. Verification of 3-PG growth and water-use predictions in twelve *Eucalyptus* plantation stands in Zululand, South Africa. Forest Ecology and Management **193:**197–218.

EKZNW (Ezemvelo KwaZulu-Natal Wildlife). 2011. KwaZulu-Natal land cover 2008. Version 1.1. GIS coverage. Biodiversity Conservation Planning Division, Ezemvelo KZN Wildlife, Pietermaritzburg, South Africa.

Faith, D. P., and P. A. Walker. 2002. The role of trade-offs in biodiversity conservation planning: linking local management, regional planning and global conservation efforts. Journal of Biosciences **27:**393–407.

Gallai, N., et al. 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecological Economics **68:**810–821.

Goodman, P. 2006. Non marine biodiversity conservation targets for KwaZulu-Natal. Ezemvelo KwaZulu-Natal Wildlife, Pietermaritzburg, South Africa.

Hajkowicz, S., and M. Young. 2005. Costing yield loss from acidity, sodicity and dryland salinity to Australian agriculture. Land Degradation & Development **16:**417–433.

Knight, A. T., and R. M. Cowling. 2007. Embracing opportunism in the selection of priority conservation areas. Conservation Biology **21:**1124–1126.

Knight, A. T., et al. 2006. Designing systematic conservation assessments that promote effective implementation: best practice from South Africa. Conservation Biology **20:**739–750.

Knight, A. T., R. M. Cowling, M. Rouget, A. Balmford, A. T. Lombard, and B. M. Campbell. 2008. Knowing but not doing: selecting priority conservation areas and the research-implementation gap. Conservation Biology **22:**610–617.

Knight, A. T., R. M. Cowling, M. Difford, and B. M. Campbell. 2010. Mapping human and social dimensions of conservation opportunity for the scheduling of conservation action on private land. Conservation Biology **24:**1348–1358.

Knight, A. T., H. S. Grantham, R. J. Smith, G. K. McGregor, H. P. Possingham, and R. M. Cowling. 2011. Land managers' willingness-to-sell defines conservation opportunity for protected area expansion. Biological Conservation **144:**2623–2630.

Kremen, C., et al. 2008. Aligning conservation priorities across taxa in Madagascar with high-resolution planning tools. Science **320:** 222–226.

KZNDAE (KwaZulu-Natal Department of Agriculture, Environmental Affairs and Rural Development). 2011. Annual performance plan. 2011–2012. KZNDAE, Pietermaritzburg, South Africa.

Laurance, W. F. 2005. When bigger is better: the need for Amazonian mega-reserves. Trends in Ecology & Evolution **20:** 645–648.

Laurance, W. F. et al. 2012. Averting biodiversity collapse in tropical forest protected areas. Nature **489:**290–294.

Lombard, M., D. Fairbanks, P.S. Goodman, and J. Mwicigi. 2002. Potential threats to the biodiversity of KwaZulu-Natal, South Africa. Report. KZN Nature Conservancy Service, Pietermaritzburg, South Africa.

MacMillan, D., N. Hanley, and M. Daw. 2004. Costs and benefits of wild goose conservation in Scotland. Biological Conservation **119:**475–485.

Moilanen, A. 2007. Landscape Zonation, benefit functions and target-based planning: unifying reserve selection strategies. Biological Conservation **4:**1–9.

Moilanen, A., A. M. A. Franco, R. I. Early, R. Fox, B. Wintle, and C. D. Thomas. 2005. Prioritizing multiple-use landscapes for conservation: methods for large multi-species planning problems. Proceedings of the Royal Society of London, Series B **272:**1885–1891.

Moilanen, A., et al. 2011*a*. Balancing alternative land uses in conservation prioritization. Ecological Applications **21:**1419–1426.

Moilanen, A., J. R. Leathwick, and J. M. Quinn. 2011*b*. Spatial prioritization of conservation management. Conservation Letters **4:**383–393.

Moilanen, A., L. Meller, J. Leppänen, F. Montesino Pouzols, A. Arponen, and H. Kujala. 2012. Zonation spatial conservation planning framework and software. Version 3.1. User manual. University of Helsinki, Helsinki.

Murdoch, W., S. Polasky, K. A. Wilson, H. P. Possingham, P. Kareiva, and R. Shaw. 2007. Maximizing return on investment in conservation. Biological Conservation **139:**375–388.

Naidoo, R., and W. L. Adamowicz. 2006. Modeling opportunity costs of conservation in transitional landscapes. Conservation Biology **20:**490–500.

Naidoo, R., and T. H. Ricketts. 2006. Mapping the economic costs and benefits of conservation. Public Library of Science Biology **4:**2153–2164.

Naidoo, R., A. Balmford, P. J. Ferraro, S. Polasky, T. H. Ricketts, and M. Rouget. 2006. Integrating economic costs into conservation planning. Trends in Ecology & Evolution **21:**681–687.

Nelson, E., et al. 2009. Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. Frontiers in Ecology and the Environment **7:**4–11.

OECD (Organization for Economic Cooperation and Development). 2011. Factbook 2011–2012. OECD, Paris. Available from http://new.sourceoecd.org (accessed July 2012).

Pierce, S. M., R. M. Cowling, A. T. Knight, A. T. Lombard, M. Rouget, and T. Wolf. 2005. Systematic conservation planning products for land-use planning: interpretation for implementation. Biological Conservation **125:**441–458.

Polasky, S. 2008. Why conservation planning needs socioeconomic data. Proceedings of the National Academy of Sciences USA **105:**6505–6506.

Polasky, S., J. D. Camm, and B. Garber-Yonts. 2001. Selecting biological reserves cost-effectively: an application to terrestrial vertebrate conservation in Oregon. Land Economics **77:**68–78.

Polasky, S. et al. 2008. Where to put things? Spatial land management to sustain biodiversity and economic returns. Biological Conservation **141:**1505–1524.

Reyers, B., D. J. Roux, R. M. Cowling, A. E. Ginsburg, J. L. Nel, and P. O' Farrell. 2010. Conservation planning as a transdisciplinary process. Conservation Biology **24:**957–965.

Richardson, E. A., M. J. Kaiser, G. Edwards-Jones, and H. P. Possingham. 2006. Sensitivity of marine-reserve design to the spatial resolution of socioeconomic data. Conservation Biology **20:**1191–1202.

Rouget, M., D. M. Richardson, R. M. Cowling, J. W. Lloyd, and A. T. Lombard. 2003. Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. Biological Conservation **112:**63–85.

Smith, J. M. B. 1996. Crop, pasture and timber yield estimate index. KwaZulu-Natal Department of Agriculture, Pietermaritzburg, South Africa.

Steenkamp, Y., B. Van Wyk, J. Victor. D. Hoare, G. Smith, A. Dold, and R. Cowling. 2004. Maputaland-Pondoland-Albany. Pages 219–228 in R.A. Mittermeier, P. Robles-Gil, M. Hoffmann, J.D. Pilgrim, T. Brooks, C.G. Mittermeier, and G.A.B. da Fonseca, editors. Hotspots revisited: earth's biologically richest and most endangered ecoregions. Cemex, Monterrey, Mexico.

Sukhdev, P. 2009. Costing the Earth. Nature **462:**277.

Theobald, D. M., N. T. Hobbs, T. Bearly, J. A. Zack, T. Shenk, and W. E. Riebsame. 2000. Incorporating biological information in local land-use decision making: designing a system for conservation planning. Landscape Ecology **15:**35–45.

Visconti, P., R. L. Pressey, M. Bode, and D. B. Segan. 2010. Habitat vulnerability in conservation planning-when it matters and how much. Conservation Letters **3:**404–414.

Wilson, K. A., R. L. Pressey, A. Newton, M. Burgman, H. Possingham, and C. Weston. 2005. Measuring and incorporating vulnerability into conservation planning. Environmental Management **35:** 527–543.

Wilson, K. A. et al. 2007. Conserving biodiversity efficiently: what to do, where and when. Public Library of Science Biology **5:** 1850–1861.

Wilson, K. A. et al. 2010. Conserving biodiversity in production landscapes. Ecological Applications **20:**1721–1732.