Journal of Applied Ecology
British Ecological Society

Journal of Applied Ecology 2011, **48**, 310–316 doi: 10.1111/j.1365-2664.2010.01955.x

Effect of biodiversity on economic benefits from communal lands in Namibia

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Summary

1. The conservation of biodiversity is increasingly justified by claims that human livelihoods are improved through its protection. Nature's ecosystem services do indeed benefit people, but how necessary is a diversity of living things to provide these services? Most studies cited as addressing this question in natural systems do not actually quantify relevant metrics (e.g. species richness) and assess their relationship with services and/or economic benefits. On the other hand, numerous small-scale experimental studies have demonstrated that more diverse systems do indeed tend to function better, but the relevance of these results to much larger, more complex socio-ecological systems is unclear.

2. Here, we investigate how biodiversity affects the gains from two ecosystem services, trophy hunting and ecotourism, in communal conservancies of Namibia, an arid country in southern Africa. We used statistical methods to explicitly control for confounding variables so that the effect of biodiversity *per se* on financial benefits to local communities was isolated.

3. Our results show that biodiversity exerts a positive effect on the economic benefits generated from these two ecosystem services produced on communal lands in Namibia. The richness of large wildlife species is positively related to income derived from ecotourism and trophy hunting after statistically controlling for potentially confounding variables such as a conservancy's geographic characteristics and human population size.

4. *Synthesis and applications*. Our results demonstrate that the conservation of biodiversity can indeed generate increased services from real-world ecosystems, in this case for the benefit of impoverished rural communities in sub-Saharan Africa. More such studies are needed from various ecological and socioeconomic contexts in order to boost the evidence base for positive effects of biodiversity on ecosystem services.

Key-words: Africa, biodiversity, biodiversity-ecosystem function, community-based conservation, conservancies, economic benefits, ecosystem services, valuation, wildlife

Introduction

Arguments for the conservation of biodiversity increasingly cite its positive contribution to human welfare (Goldman *et al.* 2008; Redford & Adams 2009; Sukhdev 2009). By making explicit the link between conservation of the natural world and the benefits that people derive from nature, it is hoped that support for conservation from constituents not typically concerned with nature's intrinsic values will increase. A fundamental assumption of this line of reasoning is that higher levels of biodiversity *per se* result in a greater delivery of ecosystem services. How well supported is this assumption?

Two lines of evidence are typically presented in support of the assertion that humans depend on biodiversity. On the one hand, many studies have quantified ecosystem service values from natural systems and demonstrated that these provide significant, though often overlooked, benefits to people (Costanza *et al.* 1997; Balmford *et al.* 2002; Elmqvist *et al.* 2009). Ecosystem service values have been quantified for crop pollination (Ricketts *et al.* 2004), rainforest products (Godoy *et al.* 2000), ecotourism (Chase *et al.* 1998), cultural artifacts (Boxall, Englin & Adamowicz 2003), and for particular species or sets of species (Loomis & White 1996; Naidoo & Adamowicz 2005a), to cite just a few of the many examples that exist. Crucially, however, save for one case from marine fisheries (Worm *et al.* 2006), none of these studies have

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examined the provision of ecosystem services at varying levels of biodiversity in a natural system.

On the other hand, a multitude of experimental studies, at scales ranging from test tubes to field plots of tens of metres, have investigated the effect of biodiversity on ecosystem functioning and performance (see reviews by Balvanera *et al.* 2006; Cardinale *et al.* 2006). These studies provide strong evidence that biodiversity does indeed directly affect ecosystem functioning and the provisioning of the types of goods and services that could be important to people (Naeem *et al.* 1994; Tilman & Downing 1994; Loreau *et al.* 2001; Hooper *et al.* 2005; Tilman, Reich & Knops 2006). However, whether the evidence derived from these experiments applies to real, non-experimental systems remains an open question (Srivastava & Vellend 2005; Duffy 2009). Unifying these two strands of research, by explicitly examining how varying levels of biodiversity affect ecosystem services in the real world, would provide critical evidence of the importance to society of conserving the greatest variety of life on earth.

We pursued this idea by testing how biodiversity in communal areas of Namibia, an arid country in southern Africa, is related to financial benefits that local communities derive from two ecosystem services, trophy hunting and ecotourism.

Materials and methods

Our study area was the set of customary landholdings that have been registered as communal conservancies in Namibia, an arid country in southern Africa (Fig. 1). Progressive legislation during the 1990s devolved conditional rights to benefits from natural resources to local communities; prior to this, they had been the property of the national government. In exchange for these rights, communities are required to register their customary landholdings as conservancies, i.e. locally-managed units that have defined boundaries, management goals, and verified plans for the sustainable harvest of wildlife and other natural resources. In terms of financial value, the dominant benefits generated by these conservancies are trophy hunting and ecotourism, which together typically account for one-half to two-thirds of annual income from all Namibian conservancies (NACSO 2008). The 'buyers' of these ecosystem services are foreign nationals, mainly from developed countries in Europe and North America, who visit communal lands for either consumptive (the harvesting and removal of trophy animals) or non-consumptive (visual and photographic safaris) purposes.

Fig. 1. Namibia, with location of communal conservancies indicated by shaded polygons.

We compiled data on income derived from trophy hunting and ecotourism, and on the diversity of wildlife species greater than 5 kg, for the 50 Namibian communal conservancies (covering $\sim$ 120 000 km^2) registered with the national government in 2006, which, at the time our study was initiated, was the latest year for which comprehensive data on income were available. Community-led monitoring of wildlife (via driving or walking transects) occurs annually on communal lands, and data from these counts have been used to generate profiles of the large wildlife species that occur on communal lands for all conservancies in Namibia (NACSO 2008). At the same time, robust accounting systems record, on an annual basis, the financial benefits generated from a wide range of activities on communal lands. We extracted the values for income based on hunting and on tourism from centralized databases maintained by the association of government and non-governmental organizations that support the national conservancy programme.

In addition, we compiled information on other variables beyond biodiversity that might be expected to influence the economic benefits generated by communal lands (NACSO 2008; Naidoo *et al.* 2011). We developed this set of variables (Table 1) based on many years of experience working on community-based conservation in Namibia, along with discussions involving other experts and reviews of literature on the relationship between biodiversity and ecosystem service production. Our primary motivation was to assess the relationship between large wildlife diversity and income from hunting and ecotourism, but in order to statistically isolate this effect we had to control for other potentially confounding effects. Due to the modest size of the data set and the plethora of variables with at least the possibility of affecting conservancy income, it was not feasible to include every potentially relevant variable in our analyses. Below we provide a brief rationale for each of the independent variables that we did include in the analysis (Table 1).

Number of large wildlife species: Our key hypothesis was that, as in the experimental literature referenced above, this variable would be positively related to both hunting and tourism income after controlling for other variables.

Number of Big 5 species: The 'Big 5' was originally coined by hunters to refer to the five most dangerous animals to hunt on foot in Africa, but is now also widely used by tourist operators when marketing photographic safaris. The species are black rhino *Diceros bicornis*, lion *Panthera leo*, leopard *Panthera pardus*, buffalo *Syncerus caffer* and elephant *Loxodonta africana*. We expected this variable to be positively related to both hunting and tourism income.

Presence of black rhino: Black rhino is a rare and charismatic species that is a major tourist draw, therefore we expected it to be positively related to tourism income (rhinos have not been hunted in conservancies and therefore were not included in the hunting analysis).

Elevation (mean and standard deviation): We include these variables to proxy for topographical diversity; all else being equal, we expected conservancies with higher mean altitudes and higher variation in altitude to have the greatest incomes from tourism, due to enhanced scenery. We expected a weak or non-significant effect on hunting income.

Soil fertility and livestock density: We consider both of these variables to be proxies for alternate economic opportunities to wildlife management, and therefore expected them to be negatively related to both hunting and tourism income.

Table 1. Summary statistics for variables included in models of trophy hunting and ecotourism income from 50 communal conservancies in Namibia

Variable	Abbreviation	Min	Median	Mean	Max	No. zeros
Ecotourism income (U.S. $)	–	0	0	25 405	325 946	31
Hunting income (U.S. $)	–	0	0	9616	110 230	27
Number of large wildlife species	major.wildlife	2	10	9·86	18	–
Number of 'Big 5' species	big5	0	2	2·04	4	–
Presence/absence of black rhino *Diceros bicornis*	rhino	0	0	0·16	1	–
Average elevation (m)	elev.avg	608·3	980·6	997·8	1486·5	–
Standard deviation of elevation (m)	elev.std	0·9281	49·95	81·92	300·6	–
Soil fertility (expert opinion; 0–low; 1–medium; 2–high)	soil.fert	0	0·17	0·29	1·04	–
Distance to the nearest tourist route (km)	dist.tour.route	0	174	249	829	–
Biome (types: Savanna, Nama, Nama–Namib, Mixed)	biome	–	–	–	–	–
Human population	pop	120	2000	4483	35 354	–
Rainfall (mm)	rain.mm	100	325	324	600	–
Livestock density (kg/ha)	livestock.dens	10	13·9	22·52	90	–
Area (km^2)	area.km^2	43·1	1599	2374	9151	–

Distance to nearest tourism route: We expected those conservancies nearest to western Namibia's well-defined tourist route to have higher incomes than those that are further away and therefore less accessible.

Biome: We included this variable to control for unknown but potentially important preferences, on the part of both tourists and hunters, for particular habitat types.

Human population and conservancy area: By including both these variables we control for population density on conservancies. We were unclear in which direction this variable might act to influence income, as conservancies with higher population densities may have greater human capital and infrastructure, but might also have a lower quality of natural resources due to higher levels of exploitation.

Rainfall: All else being equal, we expected rainfall to be positively associated with tourism income, since it is correlated with general biodiversity levels (i.e. beyond the large wildlife species considered explicitly). We did not expect any relationship with hunting income.

To evaluate the effects of wildlife diversity on economic benefits while statistically controlling for confounding variables, we used several multivariate regression approaches. All analyses were conducted using the statistical software package R, version 2·92 (R Development Core Team 2008; Naidoo et al. 2011). Hierarchical partitioning (Chevan & Sutherland 1991) assesses the independent contribution to the explanation of variance in a dependent variable for every variable in a set of predictors. We used package 'hier.part' in R for our analyses and assessed the most important variables using bar plots and a randomization test for the significance of a variable's contribution to explained variance.

To assess the magnitude and direction of the coefficients on predictor variables, we used a model-averaging, information-theoretic approach (Burnham & Anderson 2001). Rather than relying on a single 'best' model, model-averaging uses information from all candidate models to produce coefficient estimates that often result in more precise parameter estimates. In the absence of any compelling theory or method to group our variables into particular candidate models, we used all possible permutations and combinations of our 12 predictor variables, which resulted in a total of 4096 models being evaluated. Models were ranked according to the small sample size AIC_c criterion, and differences in AIC_c among models, along with the Akaike weights (Burnham & Anderson 2001), were calculated using package 'AICcmodavg' in R. Model-averaged parameters for each variable were generated by summing, over all models, the parameter estimate multiplied by the corresponding model weight. We calculated the importance of each variable by summing the Akaike weights over all models in which the variable was present.

All analyses described above were conducted separately for income generated by hunting, and for income generated by ecotourism. Furthermore, because there was a large number of zeros for each of these income types, we took a zero-inflated approach (Fletcher, MacKenzie & Villouta 2005) that combined logistic regression (using all 50 conservancies with income variable coded to 1 if any income was generated and 0 otherwise) and linear regression (using only the conservancies with incomes greater than zero, and log-transforming these data to improve normality).

For each of these combinations (linear/logistic regression and hunting/ecotourism income) we used partial residual plots (Fox 2002) to visualize the relationship between biodiversity and income after the effect of potentially confounding variables had been statistically controlled for. Partial residual plots show the relationship between the dependent variable and a predictor variable of interest after controlling for the effect of all other predictor variables in a regression model. Partial residuals are constructed by adding the model residuals to the product of the variable of interest and its associated regression coefficient. The partial residuals are then plotted against the variable of interest to show the shape of the relationship (note that the actual *y*-axis units are not informative). We used our model-averaged regression coefficients to produce partial residual plots, and view these as being analogous to those produced by the body of experimental work referenced above (e.g. Fig. 2a in Tilman, Wedin & Knops 1996). We also used the model-averaged regression coefficients to calculate, for a conservancy with an average amount of income, the effect of a one-species increase in our three biodiversity-related variables (number of major wildlife species, number of Big 5 species, and presence/absence of black rhino).

Results

Model-averaged results did not reveal any one dominant model in any of our four analyses, but rather a large number of models with moderate levels of support (Table 2; Supporting Information, Table S1). Overall, 12 – 32% of support over all models was found in the strongest 0·1 – 0·6% of models, with 'strong' models being considered those with a delta-AICc value of 2 or less (Burnham & Anderson 2001). Fewer strong models for hunting were observed than for tourism.

For hunting (Fig. 2a), variables characterizing the diversity of wildlife species were among the strongest independent predictors of variation in income. The most important predictors were the number of large wildlife species present on a conservancy and the number of 'Big 5' species. In addition, the relationships between species richness and presence of any level of income (Fig. 3a, partial $r = 0{\cdot}69$, $P < 0{\cdot}0001$) and amount of income (Fig. 3b, partial $r = 0{\cdot}65$, $P = 0{\cdot}0008$) were both positive and highly significant.

For ecotourism there was a positive and significant relationship between species richness and presence of income (partial $r = 0{\cdot}91$, $P < 0{\cdot}0001$, Fig. 3c), and a positive but non-significant relationship for amount of income (partial $r = 0{\cdot}15$, $P = 0{\cdot}53$, Fig. 3d). In addition, the same biodiversity variables, along with presence/absence of black rhino were also significant contributors to variation in income, although not so strongly as in hunting (Fig. 2b). Elevation was the most important explanatory factor; conservancies at lower elevations, but with higher topographical diversity, generated more income from tourism than those at higher but more uniform elevations. Distance to established tourism routes (positively related) and rainfall (negatively related) were also significant predictors of tourism income. Table 3 shows the standardized regression coefficients (Gelman 2008) and standard errors for all variables in our analyses.

Table 2. Best models for logistic and ordinary least-squares regression of hunting and ecotourism income on communal conservancies in Namibia (see Supporting Information, Table S1, for the variables in each of the individual models listed below)

Model no.	No. parms.	AICc	Delta AICc	Akaike weight	Log-like.	Cum.Wt
1) Tourism income, OLS regression						
31	4	69·28	0·000	0·066	−29·21	0·07
147	5	69·39	0·112	0·062	−27·39	0·13
30	4	69·62	0·345	0·056	−29·38	0·18
173	5	70·73	1·457	0·032	−28·06	0·22
148	5	70·91	1·631	0·029	−28·15	0·24
522	6	71·08	1·803	0·027	−26·04	0·27
85	5	71·18	1·905	0·025	−28·28	0·30
161	5	71·35	2·074	0·023	−28·37	0·32
2) Hunting income, OLS regression						
828	7	73·38	0·000	0·080	−25·96	0·08
118	5	74·93	1·556	0·037	−30·70	0·12
378	6	75·32	1·944	0·030	−29·04	0·15
807	7	75·43	2·048	0·029	−26·98	0·18
3) Tourism income, logistic regression						
272	4	49·71	0·000	0·019	−20·41	0·02
60	3	49·76	0·051	0·019	−21·62	0·04
639	5	50·13	0·417	0·016	−19·38	0·05
435	5	50·15	0·437	0·016	−19·39	0·07
270	4	50·26	0·550	0·015	−20·69	0·08
762	5	50·81	1·099	0·011	−19·72	0·10
196	4	50·88	1·166	0·011	−20·99	0·11
115	4	51·01	1·296	0·010	−21·06	0·12
1436	6	51·06	1·350	0·010	−18·55	0·13
557	5	51·22	1·512	0·009	−19·93	0·14
437	5	51·23	1·519	0·009	−19·93	0·14
771	5	51·23	1·524	0·009	−19·94	0·15
641	5	51·25	1·544	0·009	−19·95	0·16
643	5	51·28	1·571	0·009	−19·96	0·17
160	4	51·29	1·581	0·009	−21·20	0·18
224	4	51·31	1·595	0·009	−21·21	0·19
697	5	51·41	1·702	0·008	−20·02	0·20
1302	6	51·51	1·804	0·008	−18·78	0·20
1090	6	51·54	1·827	0·008	−18·79	0·21
271	4	51·75	2·038	0·007	−21·43	0·22
773	5	51·75	2·039	0·007	−20·19	0·23
197	4	51·78	2·066	0·007	−21·44	0·23
1426	6	51·80	2·087	0·007	−18·92	0·24
4) Hunting income, logistic regression						
2	2	45·74	0·000	0·041	−20·74	0·04
22	3	46·65	0·904	0·026	−20·06	0·07
13	3	47·00	1·257	0·022	−20·24	0·09
76	4	47·79	2·049	0·015	−19·45	0·10
18	3	47·81	2·064	0·015	−20·64	0·12

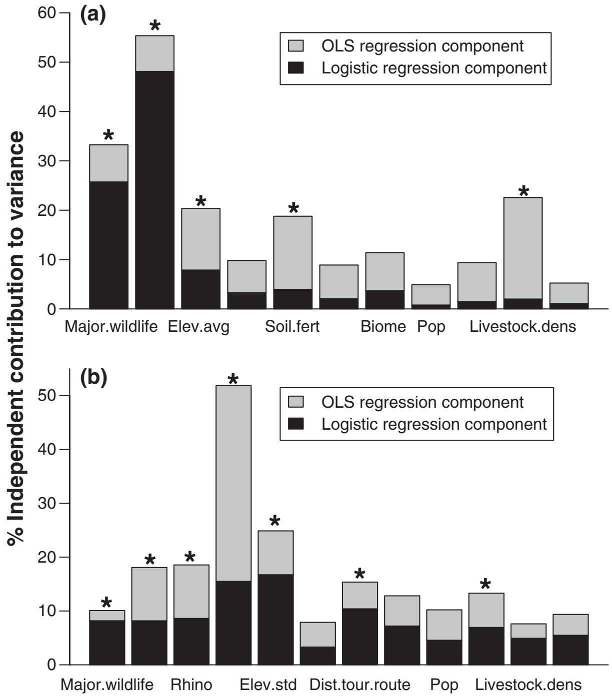

Fig. 2. Importance of variables to contribution of variance explained by regression models for hunting (a) and ecotourism (b) income. Asterisks indicate statistical significance of a variable for either the ordinary least-squares or the logistic component.

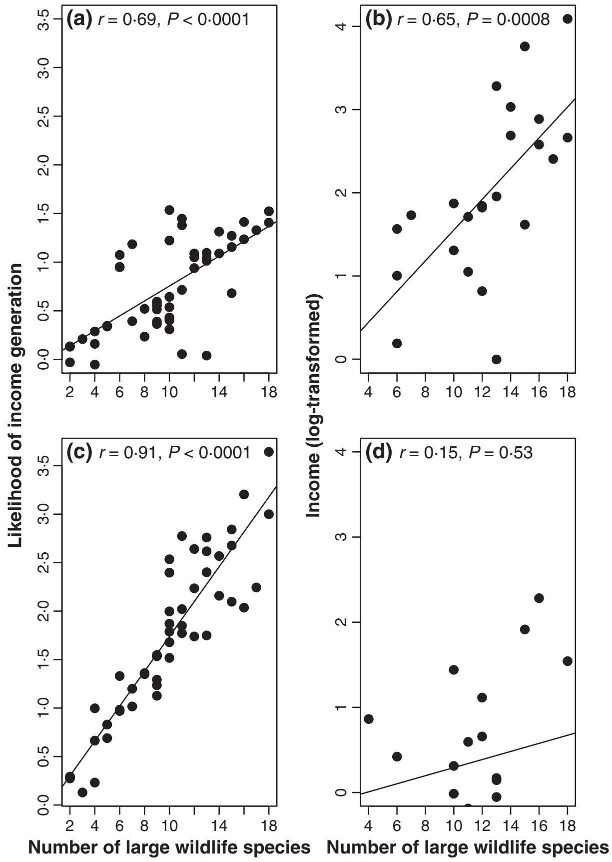

Fig. 3. Partial residual plots (indicating independent effects after controlling for other variables in the regression models) of the effect of number of large wildlife species on the likelihood that a conservancy earns income from (a) hunting and (c) ecotourism, and on the amount of income generated by (b) hunting and (d) ecotourism on conservancies.

We used our models to estimate the contribution of each additional species of wildlife to income generation. An increase of one species leads to an additional \$3362 (U.S.) in income for an average conservancy on which hunting occurs, while for the average conservancy on which ecotourism occurs, the equivalent figure is \$2134. This value increases to \$10 552 (hunting) or \$21 896 (ecotourism) if the species is a member of the 'Big 5', and to \$110 978 (ecotourism) if black rhino are present on a conservancy.

Discussion

Many studies have demonstrated that biodiversity exerts a positive effect on ecosystem function and performance, but

Table 3. Model-averaged standardized regression coefficients for all variables included in models of hunting and tourism income from communal conservancies in Namibia

	OLS hunting		OLS tourism		Logit hunting		Logit tourism	
Variable name	Parameter	Std. error	Parameter	Std. error	Parameter	Std. error	Parameter	Std. error
major.wildlife	1·18	0·49	0·21	0·80	0·64	1·60	1·48	1·28
big5	0·74	0·81	0·55	0·73	2·66	0·90	0·72	0·81
rhino	–	–	1·33	0·96			0·56	1·48
elev.avg	1·06	0·52	−2·63	0·73	−1·57	1·56	−0·96	1·06
elev.std	−0·24	1·01	−1·87	0·96	0·07	1·73	3·96	2·20
soil.fert	1·02	0·51	0·78	0·62	1·26	0·73	0·10	0·85
dist.tour.route	−0·93	0·94	−0·04	1·58	0·07	0·97	3·62	1·63
biome (Savanna)	0·33	1·01	0·95	1·57	−1·25	2·20	−1·94	2·95
biome(Nama)	–	–	2·89	1·34			−2·05	3·43
biome (Nama-Namib)	−0·50	1·10	2·10	1·08	−1·21	2·72	−0·26	3·62
pop	−0·42	0·55	−0·33	0·71	0·25	1·82	1·04	1·18
rain.mm	0·10	1·17	1·85	1·11	−0·25	0·91	−3·23	2·22
livestock.dens	1·55	0·60	0·25	0·94	−0·34	0·91	1·19	1·20
area.km^2	0·89	0·50	0·02	1·31	0·15	2·41	−2·48	1·20

this evidence has been limited to experimental contexts. Controlling confounding variables via statistical rather than experimental methods, we have shown that biodiversity in a large socio-ecological system in Namibia has a positive effect on the generation of benefits from two ecosystem services. Biodiversity, as represented by large wildlife species, appears to play a dominant role in the generation of benefits from trophy hunting, relative to other contributing factors. In addition, biodiversity plays an important role in the generation of benefits from ecotourism, though its impact is more nuanced than with hunting. This is not surprising given the wide range of factors, aside from biodiversity, that structure the behaviour of nature-based tourists (Naidoo & Adamowicz 2005b). Both tourism and hunting are major sources of revenue for governments, private companies, and local communities in much of Africa (Walpole & Leader-Williams 2001; Lindsey *et al*. 2005; Lindsey *et al*. 2006; Lindsey, Roulet & Romanach 2007; Balmford *et al*. 2009). If biodiversity is indeed a driving factor in regulating these benefit flows from natural systems across the region, as it is in Namibia, this demonstrates a massive financial incentive for conservation in an area of enormous importance for both biodiversity and human development.

Our results show that biodiversity *per se* can have significant, positive effects on the economic benefits people derive from natural ecosystems. As in experimental studies, both the total number of species and the presence of certain key species independently increase the value of ecosystem services. We note that as in all non-experimental studies, our results cannot be taken as conclusive proof of the phenomena under investigation, as the data did not come from an experiment designed to address the question, but were rather harnessed and analysed opportunistically. In addition to this caveat, the results should not be interpreted as support for introducing wildlife species outside their native ranges, or to artificially high diversity levels, for hunting or ecotourism purposes. Nevertheless, we have shown that the strong positive relationship between biodiversity and ecosystem performance is not constrained to plot experiments, but can be found, using statistical methods, in real-world ecosystems that generate services for people. The conservation of biodiversity in Namibia is not only of aesthetic or ethical significance, but yields tangible economic benefits that enhance the well-being of rural communities in one of the world's poorest regions.

Acknowledgements

T. Ricketts, B. Fisher, M. Vellend, N. Haddad, R. Moore, and two anonymous reviewers provided helpful comments on an earlier draft of the manuscript. We are grateful to the many community members in Namibia for their tireless work in promoting conservation on their customary lands.

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Received 29 September 2010; accepted 17 December 2010
Handling Editor: Julia Jones

Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1. Variables included in the best models from Table 1.

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