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Coastal Ecosystem–Based Management with Nonlinear Ecological Functions and Values

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A common assumption is that ecosystem services respond linearly to changes in habitat size. This assumption leads frequently to an “all or none” choice of either preserving coastal habitats or converting them to human use. However, our survey of wave attenuation data from field studies of mangroves, salt marshes, seagrass beds, nearshore coral reefs, and sand dunes reveals that these relationships are rarely linear. By incorporating nonlinear wave attenuation in estimating coastal protection values of mangroves in Thailand, we show that the optimal land use option may instead be the integration of development and conservation consistent with ecosystem-based management goals. This result suggests that reconciling competing demands on coastal habitats should not always result in stark preservation-versus-conversion choices.

More than one-third of the world's human population lives in coastal areas and small islands (1), which together make up just 4% of Earth's total land area. Coastal population densities are nearly three times that of inland areas (2) and they are increasing exponentially. The long-term sustainability of these populations is dependent on coastal ecosystems and the services they provide, such as storm buffering, fisheries production, and enhanced water quality. Despite the importance of these services, degradation and loss of coastal ecosystems over the past two to three decades—including marshes (50% either lost or degraded), mangroves (35%), and reefs (30%)—is intense and increasing worldwide (2–4).

To aid in conservation of these coastal communities, ecosystem-based management (EBM) has recently been proposed as a benefit op-

timization and decision-making strategy that incorporates often conflicting development and conservation uses (5–7). EBM strives to reconcile these pressures by valuing ecosystem ser-

vices and thus justifying the maintenance of many natural systems “in healthy, productive and resilient conditions so that they can provide the services humans want and need” (5). Yet the implementation of EBM cannot take place without addressing a fundamental challenge: assessing the true value of these ecosystems and the services they generate, so that practical compromises can be made (8–11).

The interrelationship of ecosystem structure, function, and economic value is critical to coastal management decisions, which are often concerned with how much natural habitat to “preserve” and how much to allocate to human development activities (2, 3). In assessing such trade-offs, it is frequently assumed that ecosystem services change linearly with critical habitat variables such as size (e.g., area). This assumption can lead to the misrepresentation of economic values inherent in services, particularly at their endpoints. The endpoint values often either overestimate or underestimate the service value, resulting in an “all or none” habitat scenario as the only decision choice (9–11). A common reason for invoking such an assumption is that few data exist for examining the marginal losses associated with changes in nonlinear ecological functions, making

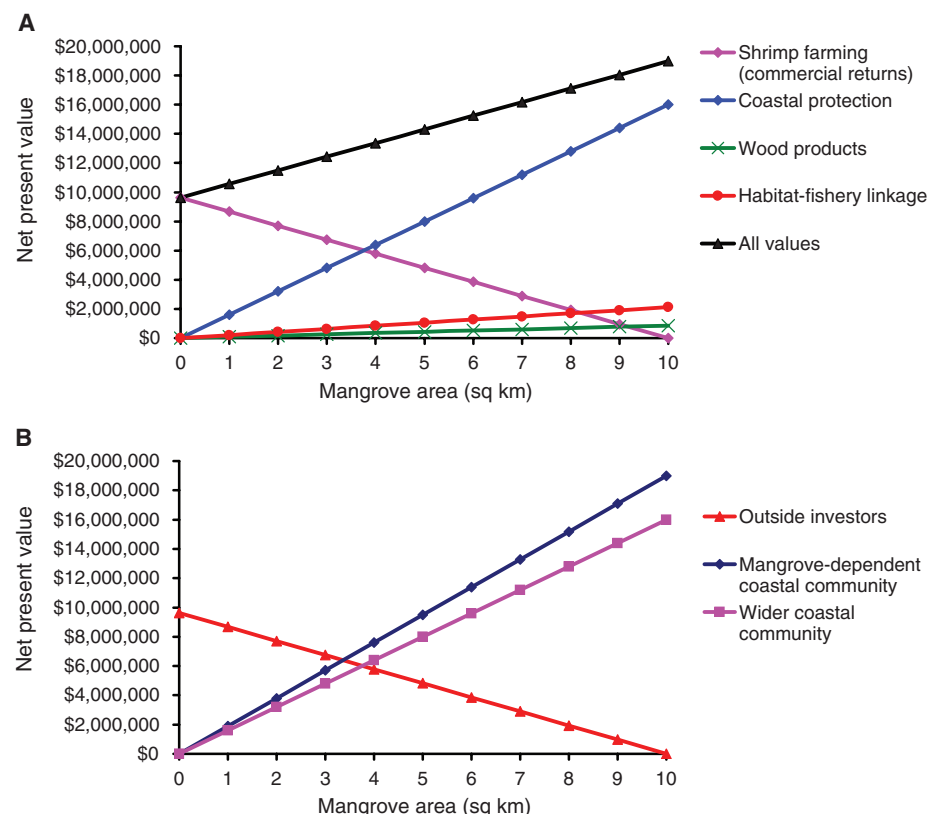


Fig. 1. Conventional comparison of shrimp farming to various mangrove services at coastal landscape level (10 km²), Thailand (net present value, 10% discount rate, 1996 dollars) on the basis of (A) total economic returns as a function of mangrove area (km²) for the commercial returns from shrimp farming plus three mangrove ecosystem service values: coastal protection, wood product collection, and habitat support for offshore fisheries; and (B) the distribution of benefits as a function of mangrove area (km²) among three stakeholders: outside investors in shrimp farms, the mangrove-dependent coastal community, and the wider coastal community (up to 5 km away). [Based on data from (11, 16, 17)]

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it difficult to value accurately the changes in ecosystem services in response to incremental changes in habitat characteristics (e.g., area). If, however, relationships between the structure and function of coastal habitats are nonlinear, as ecological theory suggests (12–14), then assuming that the value of the resulting service is linear (with respect to changes in habitat characteristics) will mislead management decisions.

To test the key assumption that ecosystem services and their economic value are linearly related to habitat area, we used data collected in the field from key coastal interface systems around the globe, including mangroves, salt marshes, seagrass beds, nearshore coral reefs, and sand dunes (15). We focused on arguably the most undervalued ecosystem service until recently: protection against wave damage caused by storms, hurricanes, and tsunamis. These field data reveal that for all these coastal habitats, nonlinear relationships exist between habitat area and measurements of the ecosystem function of wave attenuation (fig. S1). For mangroves and salt marshes, there are quadratic and exponential decreases, respectively, in wave height with increasing habitat distance inland from the shoreline (fig. S1, A and B). In the case of seagrasses and near-

shore coral reefs, wave attenuation is a function of the water depth above the grass bed or reef, and these relationships are also nonlinear (fig. S1, C and D). Additionally, there is an exponential relationship between the percent cover of dune grasses and the size of oceanic waves blocked by sand dunes produced by the grass (fig. S1E). These data suggest that the assumption of linearity is likely to be inaccurate for many ecosystem services that depend on habitat size—a result that could have important implications for conservation, especially as it relates to EBM.

To explore this possibility, we applied these nonlinear wave attenuation relationships for coastal systems to a case study from Thailand (11, 16, 17) where choices have been made between conversion of mangroves to shrimp aquaculture versus their preservation for key ecosystem services (such as coastal protection and fish habitat). Our case study assumes a mangrove habitat that extends 1000 m inland from the seaward edge along 10 km of coast. Nearby communities depend on the mangrove for forest and fishery products in coastal waters that are populated by mangrove-dependent fish. Coastal communities up to 5 km inland are protected from tropical storms by mangroves. The alternative to preserving mangroves is converting

them to intensive shrimp ponds, which overwhelmingly benefits outside investors (11, 16, 17).

Figure 1A depicts the economic returns from converting the 10-km² mangrove habitat to commercial shrimp farms as well as the values generated by three ecosystem services: coastal protection, wood collection, and habitat-fishery linkage. The figure also aggregates all four values to test whether an “integrated” land use option involving some conversion and some preservation yields the highest total value. When all values are linear, the outcome is a typical “all or none” scenario; either the aggregate values will favor complete conversion, or they will favor preserving the entire habitat (Fig. 1A). Because the ecosystem service values are large and increase linearly with mangrove area, the preservation option is preferred (Fig. 1A). The aggregate value of the mangrove system is at its highest (\$18.98 million) when it is completely preserved, and any conversion to shrimp farming would lead to less aggregate value compared to full preservation. Thus, an EBM strategy that considers all the values of the ecosystem would favor mangrove preservation and no shrimp farm conversion.

Figure 1B shows that mangrove-dependent communities and the wider coastal community would benefit from the EBM decision, whereas outside investors would prefer conversion of the mangrove to shrimp ponds. Overall, our analysis shows that the EBM strategy of full preservation of the mangroves would face opposition from outside investors, who would obtain no commercial gains from this scenario but would make profits of more than \$9.6 million from complete conversion (Fig. 1B). It is also clear that the “all or none” decision to preserve mangroves hinges on the coastal protection value service of the mangroves, which is assumed to increase linearly with mangrove area.

However, if we consider that coastal protection afforded by mangroves depends on their functional ability to attenuate storm waves (18–21) and that this relationship is nonlinear (fig. S1A), a different EBM strategy is supported (Fig. 2). In fig. S1A, we show that a wave height of 1.1 m at the offshore edge of the mangrove forest would be reduced to 0.91 m if the forest extended 100 m inland; if the forest extended 200 m inland, the wave would drop to roughly 0.75 m. The wave would continue to fall, albeit at a declining rate, for every additional 100 m of mangroves inland from the sea. For a forest extending 1000 m inland, the wave would be reduced to a negligible 0.12 m.

Using the nonlinear wave attenuation function for mangroves (fig. S1A), it is possible to revise the estimate of storm protection service value for the Thailand case study (22) (Fig. 2). The storm protection service of mangroves still dominates all values, but small losses in mangroves will not cause the economic benefits of storm buffering by mangroves to fall precipitously (Fig. 2A). The consequence is that the aggregate value across all uses of the mangroves (i.e., shrimp farming and ecosystem values) is at

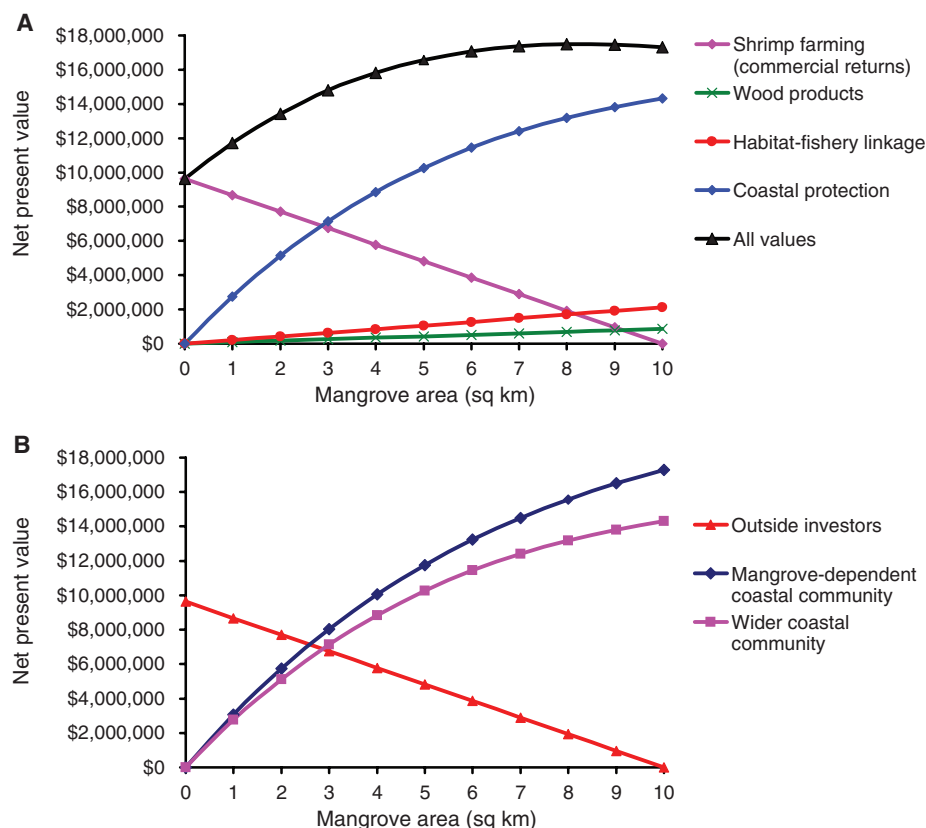


Fig. 2. Alternative comparison of shrimp farming to various mangrove services at coastal landscape level (10 km²), Thailand (calculated as in Fig. 1), incorporating the nonlinear wave attenuation function from fig. S1A, on the basis of (A) total economic returns as a function of mangrove area (km²) for the commercial returns from shrimp farming plus three mangrove ecosystem service values: coastal protection, wood product collection, and habitat support for offshore fisheries; and (B) the distribution of benefits as a function of mangrove area (km²) among three stakeholders: outside investors in shrimp farms, the mangrove-dependent coastal community, and the wider coastal community (up to 5 km away).

its highest (\$17.5 million) when up to 2 km² of mangroves are allowed to be converted to shrimp aquaculture and the remainder of the ecosystem is preserved. This outcome also yields a more equitable distribution across stakeholders (Fig. 2B), which may be an important objective in any EBM strategy for coastal management. Local mangrove-dependent coastal communities and other coastal communities living within 5 km inland would obtain approximately the same share of economic benefits from the mangrove system (\$15.6 and \$13.2 million, respectively), but now outside investors would earn some commercial profits from shrimp farming (\$1.9 million). Finally, we note that the outcome from our Thailand mangrove valuation example corresponds to “best practice” guidelines for mangrove management in Asia, which recommend that ideal mangrove/pond ratios should not exceed 20% of the habitat area converted to ponds (23, 24).

By including nonlinear relationships in an economic valuation of ecosystem services, our results challenge the assumption that the competing demands of coastal interface systems must always result in either conservation or habitat destruction. As the case study of Thailand mangroves illustrates, the way in which ecological and economic analysis is combined to estimate the values of various ecosystem services can have a large impact on coastal EBM outcome. If point estimates of these values are used to project linear relationships between the benefits of ecosystem services with respect to changes in key ecosystem physical attributes, such as area or distance from shore, then the result might be to force EBM decision-making into a simple “all or none” choice. This result is at odds with EBM

strategies, which emphasize reconciliation between economic development pressures and conservation of critical ecosystem resources and services (5–8). However, if the nonlinear ecological function underlying a service, such as coastal protection afforded by mangroves, is incorporated into economic valuation, then we more realistically represent how ecosystem services change with habitat conversion and how EBM may best be used.

References and Notes

1. Coastal areas are defined in (2, 3) as habitat from the low water mark (<50 m depth) to the coastline and inland from the coastline to a maximum of 100 km or 50-m elevation (whichever is closer to the sea).
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22. The wave attenuation relationship of fig. S1A was transformed into percent wave reduction as a function of 100-m inland mangrove distance, and this relationship was used to adjust the net present value per km² estimate for storm protection used in Fig. 1A, assuming that each km² of mangroves deforested involved the equivalent loss of 100 m of mangroves inland along the 10-km coastline. See (15) for details.
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25. This work was conducted as part of the “Measuring ecological, economic, and social values of coastal habitats to inform ecosystem-based management of land-sea interfaces” Working Group supported by the National Center for Ecological Analysis and Synthesis, funded by NSF grant DEB-0553768; the University of California, Santa Barbara; the State of California; and the David and Lucile Packard Foundation. We thank B. Halpern for his assistance with this project and work, and three anonymous reviewers for their constructive comments.

Supporting Online Material

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Materials and Methods

Figs. S1 and S2

Tables S1 to S3

References

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β-Catenin Defines Head Versus Tail Identity During Planarian Regeneration and Homeostasis

Kyle A. Gurley, Jochen C. Rink, Alejandro Sánchez Alvarado*

After amputation, freshwater planarians properly regenerate a head or tail from the resulting anterior or posterior wound. The mechanisms that differentiate anterior from posterior and direct the replacement of the appropriate missing body parts are unknown. We found that in the planarian *Schmidtea mediterranea*, RNA interference (RNAi) of β-catenin or dishevelled causes the inappropriate regeneration of a head instead of a tail at posterior amputations. Conversely, RNAi of the β-catenin antagonist *adenomatous polyposis coli* results in the regeneration of a tail at anterior wounds. In addition, the silencing of β-catenin is sufficient to transform the tail of uncut adult animals into a head. We suggest that β-catenin functions as a molecular switch to specify and maintain anteroposterior identity during regeneration and homeostasis in planarians.

β-Catenin is a multifunctional protein that controls transcriptional output as well as cell adhesion. During embryonic development of both vertebrates and invertebrates, β-catenin regulates a variety of cellular processes, including organizer formation, cell fate speci-

cation, proliferation, and differentiation (1–9). In adult animals, the Wnt/β-catenin pathway participates in regeneration and tissue homeostasis; misregulation of this pathway can lead to degenerative diseases and cancer in humans (9–12). In response to upstream cues, such as Wnt ligands

binding to Frizzled receptors, β-catenin accumulates in nuclei (Fig. 1A) and invokes transcriptional responses that direct the specification and patterning of tissues (13, 14). Adenomatous polyposis coli (APC) is an essential member of a destruction complex that phosphorylates β-catenin, resulting in its constitutive degradation. Hence, loss of APC leads to a rise in β-catenin levels that is sufficient to drive transcriptional responses (15). The intracellular protein Dishevelled has multiple functions but plays an essential role as a positive regulator of β-catenin by inhibiting the destruction complex (16).

As part of a systematic effort to define the roles of signaling pathways in planaria, we analyzed the canonical Wnt signaling system in *Schmidtea mediterranea*. We cloned and determined the expression patterns of all identifiable homologs of core pathway components (Fig. 1A) and silenced them, individually or in combina-

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Supporting Online Material for

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This PDF file includes:

Materials and Methods

Figs. S1 and S2

Tables S1 to S3

References

The wave attenuation relationships based on field data for mangroves, salt marshes, seagrass beds, nearshore coral reefs, and sand dunes are displayed in Fig. S1 below. The materials and methods for describing each relationship depicted in the figure are as follows.

Fig. S1A Mangrove

Wave attenuation for mangroves is based on data from (S1) at the coast of Vietnam where *Kandelia candel* and *Sonneratia caseolaris* mangrove plantations have been created over a wide intertidal shoal as a coastal defense against typhoon waves. The *K. candel* plantation at the study site is 1.5 km wide (perpendicular to the coast) and 3 km long (parallel to the coast). Wave data was measured *in situ* at three locations: at the offshore edge of the forest (no attenuation by the vegetation), 100 m inside the forest, and approximately 1000m from the 1st sampling site.

RMD-type wave gauges (Rigosha et Co., Ltd) recorded water height at a 0.5 Hz frequency during one whole day (spring tide) with a 1.5 mm accuracy, during the passage of a typhoon offshore. The records were separated into two parts, the tidal elevation with a long period (12-24 hr) and the wind-induced random waves, i.e. the swells or long waves with short periods (ca 10 s period) by the running average method over 20 min. The significant wave height at the three sampling locations was calculated as the average of the highest one-third of the waves. Significant wave heights at other distances from the edge of the mangrove forest were then modeled based on wave theory using:

$$\frac{dH}{dx} = -rH$$

where H is the wave height ($H=H_0$ at $x=0$), x is the distance into the mangrove forest from the seaward edge, and r is the wave attenuation coefficient. The parameter r is a function of water depth and mangrove species (Table S1). Depth at the seaward edge of the mangrove forest was 1.5 m at high tide and 0.8 m at mid-tide. Depth at the landward side of the mangroves was 0.7 m less than that at the seaward edge. Depth was assumed to vary linearly with x and water level was assumed horizontal. Values of r per 100 m were between 17 and 60% (Table S1). The observed wave height of 1 m at the open sea was reduced to 0.05 m at the coast, enabling aquaculture ponds to exist behind a 2 m high coastal levee. Without the sheltering effect of

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