1. Introduction

Understanding of carbon dynamics in forest ecosystems has advanced significantly in recent decades, and forests are now widely recognized for their role in climate change adaptation and mitigation (Gibbon et al., 2010; IPCC, 2007; van der Werf et al., 2009). Deforestation currently generates ~8–20% of anthropogenic carbon emissions globally (van der Werf et al., 2009). To reduce this impact, economic mechanisms are emerging to incentivize the conservation of forests at local to national scales—especially in developing countries (e.g., REDD+; Tvinneimeir and Reine, 2010; van der Werf et al., 2009). These carbon valuation programs can provide a practical tool supporting sustainable forest management, with additional co-benefits such as improved rural income and biodiversity conservation (Gibbon et al., 2010; Kanninen et al., 2009).

Climate change and associated policies are expected to strongly impact tropical island communities and ecosystems (IPCC, 2007). Island regions are especially vulnerable to projected changes in eustatic sea level, storm impacts, and habitat suitability due to low-lying land and limited migration potential. National and local governments in many island regions aim to respond proactively to climate change while meeting broad conservation objectives (HOAFS, 2010). Across much of Oceania—a 30 million km² area of the tropical Pacific Ocean comprising 22 countries (Haberkorn 2008)—there is particular interest in obtaining the local benefits...
of carbon valuation for forest conservation and social values (HOAFS, 2010). However, these efforts are currently hindered by a lack of information on carbon (C) storage in island ecosystems. This study addresses this information need (Baker et al., 2010; Gibbs et al., 2007) by quantifying and comparing C storage in major vegetation types of two Pacific Island landscapes in western Micronesia (Yap state, Federated States of Micronesia; and the Republic of Palau).

Forest management issues of the Pacific Islands reflect a long history of human resource utilization and increasing population pressure (Rolett and Diamond, 2004). In Micronesia, much of the local economy is associated with subsistence agriculture and agroforestry, and most upland vegetation has been modified by human activities (Devoe and Cole, 1998; Ewel, 2010; Falanruw et al., 1987). The island landscapes of Yap and Palau are a patchwork of upland forest and open savanna, fringed by mangroves (Fig. 1). Upland forests comprise a mix of native and secondary or introduced vegetation. Savannas typically occupy degraded soils and are a legacy of past intensive land-use practices, including attempted agriculture and repeated burning, especially during foreign occupations prior to World War II (Falanruw et al., 1987; Mueller-Dombois and Fosberg, 1997). Mangroves are the most intact systems but are also accessible and utilized in Micronesia for building materials, fuelwood, thatch, medicine, and food; this pressure is increasing with rising human populations (Cole et al., 1999; Ewel, 2010).

Mangroves commonly occupy tropical island coasts and are among the most ecologically and socially important forests of Oceania (Mueller-Dombois and Fosberg, 1997). These forests provide a broad array of ecosystem services such as storm protection and fishery production (Duke et al., 2007), are centers of rapid C cycling (Bouillon et al., 2008; Kristensen et al., 2008; Twilley et al., 1992), and have recently been found to rank among the most carbon-dense forests in the tropics due in part to deep organic-rich soils (Donato et al., 2011; Fujimoto et al., 1999; Kauffman et al., 2011). Mangroves are being deforested at rapid rates globally (~1–2% yr⁻¹; Duke et al., 2007; FAO, 2007), and because land-use activities may affect organic soils to deep layers (De la Cruz, 1986; Eong, 1993; Hooijer et al., 2006), the large C stores of mangroves may generate large greenhouse gas emissions when disturbed (Donato et al., 2011). In addition, population pressure on islands can lead to especially high mangrove loss rates in localized settings (e.g., 8% yr⁻¹ in Borneo from 2002 to 2005; Langner et al., 2007).

Improved estimates of mangrove C storage have recently been obtained at global/regional (Donato et al., 2011) and local (Fujimoto et al., 1999; Kauffman et al., 2011) scales, but to date these have not been placed within the context of management of larger coastal or island landscapes. There are several key reasons to study oceanic islands. Twelve percent of the world’s mangroves occur in Oceania (Giri et al., 2010), and a significant portion of mangroves around the world occur on islands. Understanding their landscape context within island settings is thus relevant throughout the tropics. Islands are also frequently used as discrete ‘model’ systems that yield insights relevant to other coastal areas (Ewel, 2010); e.g., the adjacent Southeast Asia and Indo-Pacific regions which are biogeographically connected to the western Pacific (Duke et al., 1998;
anoxic conditions. Tidal ranges are generally 1 m with saltwater for much of the tidal cycle, resulting in sub- to suprimum and in situ organic matter accumulation, and are saturated sand or rock (Smith, 1983); these soils are a combination of allu-

covian and introduced species; common species include Calophyllum inophyllum, Semecarpus venenosus, and Hibiscus tiliaeus. Upland forests are split into multiple subclasses in some vegetation inventories (Donnegan et al., 2003), but for purposes of this study are considered as one major physiognomic class. Savannas are typically dominated by Dicranopteris linearis fern, bare/grassy areas, and scattered Pandanus tectorius palms. Micronesian mangroves are composed primarily of Rhizophora spp. (most commonly R. apiculata), Sonneratia alba, and Bruguiera gymnorrhiza, and are intermediate in height and diversity relative to mangroves globally (Devoie and Cole, 1998; Saenger and Snedaker, 1993).

2. Methods

2.1. Study area

Yap state (9°33’N, 138°09’E), of the Federated States of Micronesia, and the Republic of Palau (7°35’N, 134°28’E) comprise two major island groups of the western Caroline Islands (Fig. 2). Both contain volcanic-metamorphic high islands fringed by coral reefs and numerous low coral islands. Maximum elevations are 174 and 240 m in Yap and Palau, respectively. Mean annual temperatures are 27–28 °C, with only 2° difference between the warmest and coolest months (Falanruw et al., 1987). Mean relative humidity ranges from 75 to 85%. Rainfall averages 3100 mm yr⁻¹ in Yap and ~3700 mm yr⁻¹ in Palau, with a relatively dry season from February to April (Cole et al., 1999). Upland soils are generally well-weathered, well-drained volcanic residuum on flat to >30° slope terrain, with loamy to clayey textures (Smith, 1983). Mangrove soils typically consist of a thick peat-muck layer overlying hard coral sand or rock (Smith, 1983); these soils are a combination of allu- 
vium and in situ organic matter accumulation, and are saturated with saltwater for much of the tidal cycle, resulting in sub- to anoxic conditions. Tidal ranges are generally 1–2 m.

Upland forest (65–72%), savanna (15–23%), and mangroves (12–13%) account for over 93% of the land area of each island group (Pacific Islands Committee spatial data). In this study we exclude urban or barren areas and other minor vegetation types accounting for <3% of area each. Our scope is the main land area of each island group: the four main islands that make up Yap Proper (Wa‘ab, referred to here as Yap), and the island of Babeldaob in Palau, which accounts for >85% of that country’s land area. Most upland forest is a mixture of native species, agroforest, secondary vegetation, and introduced species; common species include Calophyllum inophyllum, Semecarpus venenosus, and Hibiscus tiliaeus. Upland forests are split into multiple subclasses in some vegetation inventories (Donnegan et al., 2003), but for purposes of this study are considered as one major physiognomic class. Savannas are typically dominated by Dicranopteris linearis fern, bare/grassy areas, and scattered Pandanus tectorius palms. Micronesian mangroves are composed primarily of Rhizophora spp. (most commonly R. apiculata), Sonneratia alba, and Bruguiera gymnorrhiza, and are intermediate in height and diversity relative to mangroves globally (Devoie and Cole, 1998; Saenger and Snedaker, 1993).

2.2. Field sampling

We sampled eight stands in each of the three vegetation types (n = 24 stands total)—five of each in Yap and three of each in Palau. Study stands were selected randomly a priori from aerial imagery, subject to constraints of land ownership and access, as nearly all land is privately owned. Mangroves were sampled on both the windward (east) and leeward (west) sides of the islands. Upland forest sample stands spanned a range of primary, secondary, and agroforest vegetation. Savannas ranged from open grass/fern to dense Pandanus palm cover. Mangrove stands included all three common tree genera, and ranged from old undisturbed stands to those affected by typhoons or low-level human disturbances within the past two decades.

In each stand, we obtained vegetation measurements and soil cores in a series of circular subplots oriented along a central transect. Upland transects paralleled the primary axis of the vegetation patch, and in Yap contained six 7-m radius subplots spaced at 25-m intervals; Palau upland stands had a similar design but with one less subplot. Sampling design for mangroves was similar to that for uplands (transects of 5–8 subplots) and are described in detail by Kauffman et al. (2011) and Donato et al. (2011). In each subplot, we measured all stems >5 cm diameter (at 1.3 m height [dbh]) in the full subplot area. Stems <5 cm dbh were measured in a 2-m radius inner circle. Live trees were recorded for species and dbh; dead trees were additionally noted for broken top, height if broken, and decay status (sound or rotten). Down wood was measured along four 12-m long planar intercept transects (Brown, 1974; Kauffman et al., 2011) oriented at 45° angles from the main transect at each subplot center. Down wood particles ≤7.6 cm diameter were tallied by size class along subsections of the sampling plane: <0.62 cm, 2 m sampling plane; 0.62–2.54 cm, 5 m plane; 2.54–7.62 cm, 10 m plane. Particles >7.62 cm diameter were measured for actual diameter and decay status along all 12 m of the sampling plane. We destructively harvested understory vegetation (<1.3 m height) and forest floor litter (combined pool termed hereafter as ‘understory’) from a 50 × 50 cm quadrant within each subplot, and dried the samples at 60 °C to constant mass. Under- story/litter mass in mangroves is generally negligible (Kauffman et al., 2011; Snedaker and Lahmann, 1988) and was not collected.

We sampled soils as described by Kauffman et al. (2011) and Donato et al. (2011). Briefly, a soil core was extracted from a random point near each subplot center using a 4.8-cm gauge slide hammer (uplands) or 5.5-cm gauge open-face peat auger (mangroves). We collected samples for determination of soil bulk density and C concentration at regular depth intervals to 1 m depth, plus a deep interval in mangrove soils depending on depth to underlying coral sand/rock (Donato et al., 2011). We measured mangrove soil depth at three locations around each subplot center by inserting a graduated probe until refusal at the underlying coral layer. Probe length

Fig. 2. Location of Yap state, Federated States of Micronesia, and the Republic of Palau, in the western Caroline Islands.
(and thus scope of inference) was 300 cm; our C storage estimates are therefore conservative for sites with pockets of deeper soils. Soils were immediately dried at 60 °C to constant mass and weighed for bulk density determination. The samples were then ground, homogenized, treated with dilute acid to remove carbonates (Harris et al., 2001; Schumacher, 2002), and analyzed for carbon concentration via the induction furnace method at the University of Hawaii Agricultural Diagnostics Laboratory.

2.3. Biomass and carbon computations

We computed aboveground tree biomass using species-specific allometric equations based on dbh. Mangrove equations used for tree volume and mass were developed for Micronesian mangroves by Cole et al. (1999) and Kauffman et al. (2011). Stilt root biomass for Rhizophora spp. and leaf biomass for all species were obtained from equations of Clough and Scott (1989) and Kauffman et al. (2011). Belowground tree mass was calculated using a general allometric equation developed for mangroves by Komiyama et al. (2005). For upland sites, we used a well-tested general equation for biomass of tropical moist forest trees (Chave et al., 2005) and species-specific wood density (Hidayat and Simpson, 1994; Simpson, 1996). All computations were slope corrected. Root biomass for upland stands was calculated from plot-level aboveground biomass rather than at the individual tree level, using common procedure and equations for upland systems (Cairns et al., 1997; IPCC, 2003). Dead trees were corrected for foliage loss, reductions in stem volume if broken, and reduced wood density based on decay status (30% mass loss if rotten) (Murdijarso et al., 2009). We constructed a new biomass allometry for P. tectorius palm via destructive harvests (Appendix A). We computed down wood biomass via standard volumetric formulas (Brown, 1974) combined with site-specific data on particle diameters and wood densities by size class (Kauffman et al., 2011).

We converted dry biomass of trees, understory, and down wood to C mass using locally derived carbon:biomass ratios (Kauffman et al., 2011). Soil C storage was obtained as the product of soil carbon concentration, bulk density, and depth. To facilitate even comparisons among vegetation types while still accounting for the whole soil profile in mangroves (which was deeper than the 1-m depth to which upland soils were sampled), we used our empirical data and first principles to estimate deep soil C in upland soils. Nonlinear regression was used to fit a hyperbolic decay function to the well-defined negative trend of soil C content versus depth (adj. $R^2 = 0.93$) to estimate C content to the same mean soil depth measured in each island's mangroves (162 cm and 135 cm in Yap and Palau, respectively). We chose to include all mangrove soil C because deeper layers are considered vulnerable to land-use change in organic-dominated soils (De la Cruz, 1986; Eong, 1993; Hooijer et al., 2006). Overall this adjustment made little difference to total C estimates for both savannas (9.8%) and forests (4.1%), and all conclusions are highly similar with or without the adjustment.

Quantitative comparisons between vegetation types were evaluated via 95% confidence intervals (CI); intervals mutually excluding other groups’ means indicate strong differences. Confidence intervals for total ecosystem C were obtained by propagating errors of component pools (IPCC, 2003). We scaled per-hectare estimates up to the island level using aerial photo-derived spatial coverage of vegetation types (Pacific Islands Committee data).

3. Results

3.1. Carbon pools

Ecosystem C storage ranged from 156 to 203 Mg C ha$^{-1}$ in savannas to 830–1218 Mg C ha$^{-1}$ in mangroves (Fig. 3). Upland forests were intermediate, with C storage of 375–437 Mg C ha$^{-1}$. Mangroves contained 4–8 times the C contained in savannas and 2–3 times that in upland forests. This trend was driven primarily by belowground storage in mangroves, which far exceeded all pools combined in each of the other types (Fig. 3). Savannas and upland forests also differed from each other, principally due to lower aboveground C in savannas (Fig. 3). On average, upland forests contained 219–234 Mg C ha$^{-1}$ (2.2–2.4 $\times$) more total C than savannas (Fig. 3).

Separated by C pool (Table 1), Yap mangroves contained as much or more of every pool compared to other vegetation types (except understory). Palau mangroves showed a similar pattern, but generally smaller-stature, lower basal area mangroves (Fig. 4) resulted in lower tree C mass than in upland forests there (Table 1). Down wood C mass was highly variable and accounted for 3–12% of aboveground C in upland forests, and 5–23% in mangroves. Understory C mass was the primary aboveground component in savannas (Table 1). The much larger belowground C storage in mangroves relative to other types was due to both root C mass and, to a larger degree, soil C (Table 1). Soils alone accounted for 62–76% of ecosystem C storage in mangroves (Table 1).

3.2. Soil properties

Compared to upland soils (0.4–5.5%), mangrove soils were much higher in organic C concentration (13–15%), and this high concentration remained throughout the soil profile to depths well below 1 m (Fig. 5). Mean depth of the peat-muck layer was 162 cm (±17 S.E.) in Yap mangroves and 135 cm (±12 S.E.) in Palau mangroves. Upland soils, in contrast, showed a common pattern of rapidly (exponentially) decreasing organic C concentration with

![Fig. 3. Ecosystem C storage (mean, 95% CI in Mg C ha$^{-1}$) in the three major vegetation types of Yap and Palau. Evidence of statistical difference among groups arises when confidence intervals do not overlap means of other groups.](image-url)
3.3. Island-wide C stock estimates

Multiplying per-hectare carbon storage by the land area of each vegetation type yields an estimated island-wide C stock of 3.9 Tg C on Yap, and 15.2 Tg C on Palau (i.e., 14.3 and 55.8 Tg CO₂ equivalent (CO₂e), respectively). Mangroves account for a disproportionally large fraction of the total. On Yap, mangroves account for only 12% of land area, but 34% of the total C stock (Fig. 6). On Palau, mangroves occupy 13% of land area, but account for 24% of the total C stock (Fig. 6). Upland forests also account for a substantial portion of the total, but slightly less than their proportion of land area. Savannas store much less C than their proportion of land area (Fig. 6).

4. Discussion

4.1. Carbon pools

The C storage we quantified in Yap and Palau mangroves (830–1218 Mg C ha⁻¹) was at the moderate to high range reported for oceanic mangroves of the Indo-West Pacific (890–1188 Mg C ha⁻¹; Donato et al., 2011; Kauffman et al., 2011), and high compared to the limited available data from estuarine/deltaic mangroves of the region, such as the Sundarbans of Bangladesh and India (~500–600 Mg C ha⁻¹; Donato et al., 2011). Comparison with total C storage in other mangroves of the world is not possible because few relevant data exist. Comparing aboveground C stocks only, Yap and Palau (101–249 Mg ha⁻¹) are generally at the moderate to high range of values reported for Asian deltaic mangroves of the region, such as the Sundarbans of Bangladesh and India (~30–60 Mg C ha⁻¹; Komiyama et al., 2008), but those values generally included only tree biomass. We found that down wood accounted for as much as 23% of aboveground C (mean depth; concentrations exceeded 3% only in the uppermost layer in uplands (Fig. 5). Upland forest soils (4.5–6.5%) had significantly higher organic C concentration in the surface layer than savanna soils (3.3–4.2%) (Fig. 5).

![Fig. 4. Forest structure metrics (mean, 95% CI) of the three major vegetation types of Yap and Palau. A) Tree basal area (cross-sectional stem area at 1.3 m height); B) Tree stem density. Evidence of statistical difference among groups arises when confidence intervals do not overlap means of other groups.](image)

![Fig. 5. Soil organic carbon concentration (% dry mass) versus depth in the three major vegetation types, combined across Yap and Palau. Trends were highly similar on both islands. Data are mean ± 95% CI. The single point representing deep soil C (>100 cm) in upland types is modeled based on hyperbolic decay function (see methods, Section 2.3). Evidence of statistical difference among groups arises when confidence intervals do not overlap means of other groups.](image)
14%). As is becoming increasingly recognized (Donato et al., 2011; Fujimoto et al., 1999; Kauffman et al., 2011), we found soil to be the principal C pool in mangroves, even when tree biomass was large. Lower quantities of C in Palau mangroves compared to Yap were explained in part by shallower soils.

Upland forest C storage (375–437 Mg C ha$^{-1}$) in Yap and Palau was at the high end of ranges reported from adjacent Southeast Asia. As with mangroves but to a lesser extent, most other upland forest studies included aboveground biomass in trees only. The few studies of total ecosystem C in Southeast Asian upland forests report values of ~250–400 Mg C ha$^{-1}$ (e.g., Lü et al., 2010), which is similar to values reported for African and New World tropical forests (Djomo et al. 2011; Hughes et al., 2000; Jaramillo et al., 2003; Kauffman et al., 1995). Considering aboveground pools alone, our values for upland forests (145–216 Mg C ha$^{-1}$) were comparable to most data from Southeast Asia, which generally range from 50 to 250 Mg C ha$^{-1}$, assuming that most biomass has a C content of ~50% (Brown et al., 1993; Hertel et al., 2009; Iverson et al., 1993; Laumonier et al., 2010; Lü et al., 2010). Within Palau, prior data relevant to forest C storage (based on vegetation inventories and allometries not designed for ecosystem C assessments; Donnegan et al., 2003) suggest somewhat lower estimates for C residing in forests, but such estimates only included tree stems—excluding branches, foliage, roots, down wood, understory, and soil.

As expected, savannas contained by far the lowest C stores. Scattered Pandanus trees (Figs. 1 and 4) and a dense shrub/grass layer amounted to low levels of aboveground biomass per area (Table 1). Consistent with possible legacies of past land use—especially intensive agriculture, repeated burning, and erosion—surface soil C concentration was also significantly lower in savannas than upland forests on otherwise similar sites (Fig. 5).

**4.2. Island-wide estimates: key role of mangroves**

Even though mangroves only occur as a coastal fringe of the islands (12–13% of land area), they accounted for as much as ~1/3 of total island C stocks. From a carbon management perspective, this highlights the critical role that exceptionally C-dense forests can play when viewed over a landscape (Keith et al., 2009). This is especially the case for islands, where mangroves commonly occur. The combined total of 17.8 Tg CO$_2$e stored in these mangroves alone is roughly two orders of magnitude higher than the combined annual fossil fuel emissions of these countries (0.22 Tg CO$_2$e yr$^{-1}$; U.N. Statistics Division 2007). Thus, for many tropical islands, deforestation or degradation of mangroves can significantly influence the regional C balance, particularly in the land-use sector (although relatively minor in the global order). For example, a loss of 1% of mangrove C stocks from land-use change could approximately double the greenhouse gas emissions from these islands.

As in many coastal regions of the tropics, rising human populations are exerting increasing pressure on Pacific mangroves (Allen et al., 2001; Devoe and Cole, 1998; Haberkorn, 2008; Pinzón et al., 2003), which are declining at a mean annual rate of 0.4% (FAO, 2007). Much higher loss rates in populated regions of adjacent Southeast Asia (Langner et al., 2007) suggest this number may rise as Pacific Island populations increase. Although data on land-use effects are limited, evidence suggests that when mangroves and other tropical wetlands are cleared or degraded, a significant portion of soil organic matter is oxidized (Granek and Ruttenberg, 2008; Lovelock et al., 2011; Sjöling et al., 2005; Strangmann et al., 2008), likely affecting even deep layers and leading to relatively large C emissions (De la Cruz, 1986; Eong, 1993; Hooijer et al., 2006). Initial published estimates for the amount of C released from Indo-Pacific mangroves with land-use change range from

Fig. 6. Proportions of land area and total carbon stock by vegetation type in Yap and Palau.
~400–1400 Mg CO₂ per-hectare cleared, depending on severity of disturbance (Donato et al., 2011). At even conservative market prices (e.g., US$ 15 per Mg of CO₂e; Tvennereim and Raine, 2010), this suggests high economic potential for projects that avoid mangrove deforestation, adding a practical tool for sustainable management objectives. A prominent example is the ‘Micronesia Challenge,’ an intergovernmental program seeking to conserve 30% of near-shore marine resources and 20% of terrestrial resources in Micronesia by 2020 (micronesiachallenge.org). Although applying carbon market mechanisms to naturally dynamic ecosystems such as mangroves has a unique set of uncertainties (see Alongi, 2011 for a thorough discussion of these issues), initiatives such as the Micronesia Challenge could be catalyzed in part by effectively managing the large carbon stores of mangroves.

4.3. Restoration and climate change mitigation potential in uplands

Many Pacific Island landscapes contain savannas and other degraded areas that are a legacy of past land use, such as abandoned agriculture, bauxite mining, burning, etc. Most of these areas were likely covered in forest at one time (Donnegan et al., 2003; Mueller-Dombois and Fosberg, 1997), and restoration and climate change mitigation in these areas is becoming an objective for national land management agencies (Yap State Forestry and Palau Agriculture and Forestry, personal communication with the authors). Carbon payment programs such as Reduced Emissions from Deforestation and forest Degradation (REDD+, Kanninen et al., 2009) aim to assist and encourage these management objectives, but require knowledge of likely changes in carbon stores associated with given management actions.

Comparing carbon storage between savannas and upland forests suggests that actions that move savannas toward forest conditions could significantly increase per-hectare C storage. Current demonstration projects on the islands show this to be a feasible objective on some sites. Notably, our forest sample included agroforests, indicating that restoration to a broad range of forest-associated land uses could yield significant C gains. Again applying the conservative market price of US$ 15 per Mg of CO₂e, the difference between savannas and forests in terms of aboveground and root mass only (190 Mg C ha⁻¹, or 697 Mg CO₂e ha⁻¹) suggests potentially large revenues from climate change mitigation activities. Revenue estimates could be higher still if soil C is included. The potential restorable acreage on the islands (total savanna cover is over 7000 ha, a significant portion of which may be suitable) suggests that such projects could attract significant total funding for forest restoration activities. These data provide some of the first information which could be used to link carbon valuation with forest restoration in these ecosystems. Worth noting is that the economic valuations above are simplistic, and such projects would also need to consider input costs, the feasibility of restoring particular sites ecologically, and current land uses which may be incongruent with restoration. Input cost and effort would likely be non-trivial, since these soils often exhibit lasting legacies of prior land use, including reduced soil productivity and nitrogen availability (Motavalli and McConnell, 1998), suggesting a need for active restoration to successfully establish trees. Additionally, ancillary effects on other ecosystem functions would need to be monitored.

5. Conclusions

This evaluation of whole-island C stocks in Micronesia carries two primary implications. First, the exceptional C storage of mangroves—especially in soils—means they account for a disproportionately large fraction of total island C stocks, even though they generally only occupy the coastal fringe. These results suggest significant opportunities for carbon valuation programs (e.g., REDD+) to aid objectives for coastal conservation. Second, markedly higher carbon storage in forests compared to savannas suggests that reforesting degraded savanna sites could significantly enhance carbon stocks, and could attract significant carbon-based funding for land restoration where that is an objective. These data provide the first whole-ecosystem numbers that can be used to inform such efforts in tropical island environments.

Many of the land management issues facing island regions are also present in coastal zones throughout the tropics, including adjacent Southeast Asia where human populations are rapidly increasing, mangroves reach their greatest land area, and rates of deforestation are highest (FAO, 2007). Informed management of mangroves within the context of larger coastal landscapes will benefit by the emerging awareness of their key role in regional carbon storage, in addition to the long list of other ecosystem services for which mangroves are already known.

Acknowledgments

We thank the many members of the Yap Division of Agriculture, Palau Agriculture and Forestry, and the Palau International Coral Reef Center (PICRC) who helped us complete this work, and the people of Yap and Palau who allowed us to conduct field work on their lands. Margie Falanruw of the USDA Forest Service in Colonia, Yap, greatly assisted with field logistics. We thank M. Mitchell for invaluable assistance with the project, and four anonymous reviewers for constructive comments. This study was funded by the USDA Forest Service Pacific Southwest Research Station and the USDA Forest Service International Programs.

Appendix. Supplementary material


References
