Discussion

Deer and pigs can, but may not always, be important engineers of novel ecosystems. Seedling plot experiments on the islands of Guam and Rota revealed selective browsing on a sample of common forest species by deer. Deer abundance in native forest showed strong negative loglinear relationships with overall seedling abundance, including both native and exotic seedling abundance, and vine abundance. We also found that overall plant diversity is greatest at intermediate levels of deer abundance, consistent with the intermediate disturbance hypothesis (IDH) (Connell 1978). We did not detect these relationships with pig abundance, suggesting that deer may have a stronger role in determining species abundance and dispersal in these forests. However, pigs did appear to have a strong role in seed dispersal in Guam, selectively dispersing native seedlings.

Deer affect the community composition and size class in forest communities in Guam. The negative relationships we found between forest characteristics and deer abundance (Figure x) demonstrate that forests are heavily impacted, and about equally so, across all except extremely low deer abundances. This mirrors studies in other systems, such as in North America where population densities of native white-tailed deer (*Odocoileus viginianus*) only slightly higher than historic levels controlled forest regeneration of once common forest species (Alverson et al 1988). Therefore, only drastic reductions or elimination of deer are likely to lead to noticeable changes in forest communities.

Deer also had important effects on overall forest community diversity, with the greatest forest diversity at intermediate levels of deer abundance (Fig x). This pattern of plant diversity is consistent with the intermediate disturbance hypothesis (IDH) (Connell 1978). The IDH proposes that at low levels of disturbance, as is caused by ungulate herbivory, a few competitive dominants rule, while at high levels of disturbance, only disturbance-tolerant species survive. In contrast to our results, many studies about ungulate effects on biodiversity show a pattern of monotonic decline (Stockton *et al.* 2005, Spear and Chown 2009). In fact, a review by Milchunas *et al.* (1988) concluded that grazing as a disturbance often failed to support IDH because of concomitant changes in modes of competition among plant species with increasing disturbance. One of the few studies of herbivory that did support the IDH model involved deer, and was restricted to ground-cover in a temperate forest habitat. However, the pattern was only evident when other environmental factors were controlled (Suzuki *et al.* 2012). Our study, in contrast, showed an IDH pattern in forest community diversity as a response to deer herbivory, even with other environmental factors at play.

Just as deer in other systems selectively browse plant species, we found deer in Guam and Rota to be selective amongst tested species of seedlings (Figure x). With the high population densities of deer suspected in Guam (Knutson and Vogt 2002), this could have strong implications for species composition of forests with deer, especially combined with the loss of avian ecological functions in Guam. Very few studies have looked at species ingested by deer in the Marianas (Wheeler 1979), further stomach-content analyses could reveal which species are selectively browsed by deer and in what quantities. Stomach content analyses and long-term vegetation monitoring could shed light on whether ungulate-impacted forests with few to no birds dispersing seeds will begin shifting to a community composition favoring species that are resistant to deer herbivory and species not reliant on avian seed dispersal.

Feral pigs are notorious for having detrimental effects on plant communities in different ecosystems, so we were surprised that we could not detect relationships between forest characteristics and pig abundances. This may have to do with our indicator of abundance – scat counts may not be an accurate portrayal of relative pig abundances across sites (Andersen and Stone 1994). Pigs do, however, appear to play role in seed dispersal. Studies in Hawaii have implicated pigs not only of inhibiting forest regeneration (Katahira 1980, Nogueira-Filho et al 2009), but of indirectly affecting native plants by selectively dispersing invasive plants (Aplet et al 1991). In contrast, although some invasive species were found in scats collected in Guam, pigs selectively dispersed native species like *Morinda citrifolia* and *Ficus prolixa*. With the loss of avian and fruit bat seed dispersal in Guam due to the invasive brown treesnake and overhunting, dispersal by pigs may be the major remaining mode of dispersal for fruit trees in Guam.

Forests of the two adjacent islands had different responses to ungulate herbivory. Unlike in Guam, we did not observe any association between seedling abundance and deer abundance in Rota. The continued presence of avian seed dispersal in Rota may have obscured any associations between seedling abundance and deer abundance there. Other studies have observed complementary roles of herbivory and seed dispersal (Henry and Dubost 1999, Vellend et al. 2006), but focus on one species responsible for both herbivory and dispersal. We speculate that multiple species may be determining forest composition through a combination of herbivory and seed dispersal. Seedling mortality was higher in Rota for both fenced and unfenced treatments (Figure x), suggesting that an additional factor unimportant in Guam might be affecting seedling survival in Rota. The cause of this greater mortality is unclear, but we speculate that slug herbivory is responsible. We noticed a particularly high abundance of exotic slugs (Veronicellidae) at our sites in Rota. Slugs extensively damaged native plants in some areas of Hawaii (Joe and Daehler 2008).

Multiple ecological factors such as avian loss, invasive plants, and invertebrate herbivores make it difficult to predict the results of ungulate management, but this study provides a better understanding of their role and the likely impacts of various management options. Whether their roles are interpreted as positive or negative, ungulates are major parts of Guam and Rota’s ecosystems, and their removal or control is likely to have complicated results. Information from this study is important for formulating ecosystem management plans in the Marianas. For example, deer suppression would have to first reach a level low enough to elicit responses from plant communities, so low-level hunting pressure does not appear to be an effective tool for controlling deer herbivory. Enhanced suppression or eradication would be needed for recovery if deer control were deemed a priority for recovering native plant species. If deer suppression is achieved, invasive vines might become a problem when released from herbivory. Pig control or eradication could also have unwanted effects by disrupting what is likely the only vertebrate-facilitated seed dispersal in Guam. Ungulates and snakes might never be eradicated, but ecosystems can still be managed to maintain some native species and functions based on our developing knowledge of novel ecosystem interactions such as these.