

Promotion of ecosystem carbon sequestration by invasive predators

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Despite recent interest in understanding the effects of human-induced global change on carbon (C) storage in terrestrial ecosystems, most studies have overlooked the influence of a major element of global change, namely biological invasions. We quantified ecosystem C storage, both above- and below-ground, on each of 18 islands off the coast of New Zealand. Some islands support high densities of nesting seabirds, while others have been invaded by predatory rats and host few seabirds. Our results show that, by preying upon seabirds, rats have indirectly enhanced C sequestration in live plant biomass by 104%, reduced C sequestration in non-living pools by 26% and increased total ecosystem C storage by 37%. Given the current worldwide distribution of rats and other invasive predatory mammals, and the consequent disappearance of seabird colonies, these predators may be important determinants of ecosystem C sequestration.

Keywords: carbon; island ecology; rats; seabirds

1. INTRODUCTION

There has been considerable interest in determining the effects of global change on the storage of carbon (C) in terrestrial ecosystems (Schimel *et al.* 2001). Much of the effort directed to understanding these effects has focused on global climate change, CO₂ enrichment and nitrogen deposition (Körner 2000; De Vries *et al.* 2006). Although human-induced alterations of biological communities through invasions by exotic species are also major components of global change (Vitousek *et al.* 1997), we know little about the effects of biological invasions on ecosystem C storage. The handful of recent studies that have recognized this issue provide some evidence of alterations of ecosystem C stocks by locally abundant invasive plants (Jackson *et al.* 2002; Bradley *et al.* 2006; Litton *et al.* 2006), earthworms (Frelich *et al.* 2006) and deer (Wardle *et al.* 2001). However, most of these studies have focused only on above- or below-ground C storage, rather than on whole-ecosystem

storage, or on how storage is partitioned between above- and below-ground compartments.

Rat species (e.g. *Rattus rattus*, *Rattus norvegicus* and *Rattus exulans*) have been accidentally introduced by humans to many regions worldwide and are among the most widely distributed of all invasive mammals. In coastal and island communities, they frequently serve as top predators by consuming seabird eggs and chicks, thereby severely reducing their populations (Courchamp *et al.* 2003). In the absence of introduced predators, seabirds function as major ecosystem drivers in many coastal communities worldwide, in part because they transport labile forms of C and nutrients from the ocean to the land (Polis & Hurd 1996; Mulder & Keall 2001). Introduction of predators of seabirds to these communities therefore interrupts this sea-to-land transfer of resources (Croll *et al.* 2005; Fukami *et al.* 2006).

In this study, we considered a group of 18 forested islands off the coast of northern New Zealand, to determine how invasion by rats affects ecosystem C sequestration. These include nine islands that have never had rats and that support high densities of seabirds nesting in burrows, and nine that have been invaded by rats and have severely reduced densities of seabirds. We used this system to investigate whether and how invasion by predatory rats influenced ecosystem C storage both above- and belowground, as well as overall ecosystem C sequestration.

2. MATERIAL AND METHODS

For each of two plots on each of the 18 islands, we measured total ecosystem C storage both above- and below-ground. This included total C storage in live plant biomass and in each of three non-living pools. These non-living pools were coarse woody debris (CWD), surface litter (dead twigs and leaves) and soil at each of three depths (0–10, 10–20 and 20–30 cm). Individual islands served as the units of replication and all response variables were analysed by analysis of variance (ANOVA) or analysis of covariance (ANCOVA) to test for significance of differences between rat-invaded and rat-free islands.

Methodology is outlined in detail in the electronic supplementary material, appendix §A.

3. RESULTS

We found large differences between rat-free and rat-invaded islands in the total amounts of C stored (table 1; figure 1). The amount of C stored in live plant biomass on plots on rat-invaded islands was on an average 204% that on plots with dense seabird burrows on rat-free islands (figure 1). Conversely, the amount of C stored in non-living pools on rat-free islands was 138% that on rat-free than on rat-invaded islands. This is because rat-free islands had greater amounts of C stored in the soil than rat-invaded islands, particularly at lower soil depths (table 1; figure 1). Rat invasion did not have a significant effect on C storage in above-ground non-living pools such as CWD and plant litter; these pools collectively represented less than 3% of C stocks. Our results show that rat invasion causes a large increase in the proportion of ecosystem C stored in live plant biomass (figure 1). Since the positive effects of rats on C storage in live plants exceed their negative effects on C storage in non-living pools, invasion by rats promotes total ecosystem C sequestration on average by 36.7%.

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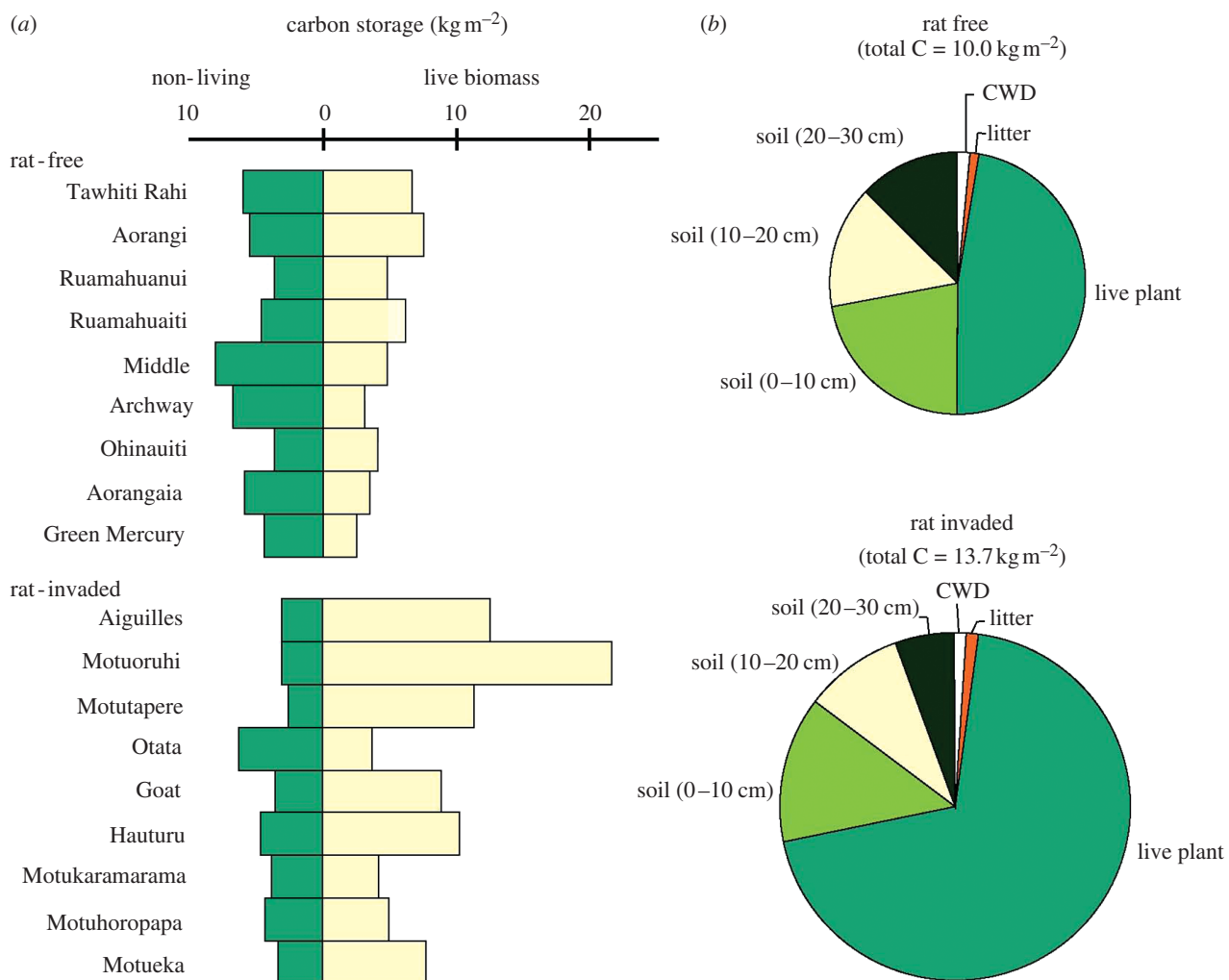


Figure 1. (a) Carbon storage in live plant biomass and in non-living pools (soil, litter and CWD) on nine rat-free (seabird-dominated) and nine rat-invaded islands. For both categories, islands are arranged in decreasing order of size. (b) Proportions of total ecosystem C stored in different pools for rat-free and rat-invaded islands. Data analyses and significance tests are presented in table 1.

Table 1. Results of ANOVA or ANCOVA (F and p values) testing for significance of differences in C storage between rat-free and rat-invaded islands. Absolute values relate to total C storage values (mass per unit area) in each pool, and proportional values relate to C storage values in each pool as a proportion of total C storage. The covariates that had a significant effect are listed for each response variable. (Degrees of freedom for the main treatment effect are 1,15 when a covariate is included and 1,16 when it was not.)

carbon pool	absolute values for C storage			proportional values for C storage		
	F	p	covariates	F	p	covariates
live plant ^a	22.64	<0.001	island area ($p < 0.001$)	22.04	<0.001	island area ($p = 0.003$)
soil (0–10 cm)	2.73	0.118	none	7.85	0.013	island area ($p = 0.008$)
soil (10–20 cm)	3.45	0.082	none	16.34	<0.001	island area ($p = 0.043$)
soil (20–30 cm)	8.39	0.010	none	21.83	<0.001	island area ($p = 0.037$)
soil (total)	5.54	0.031	none	20.89	<0.001	island area ($p = 0.005$)
coarse woody debris	0.39	0.542	none	1.51	0.237	none
litter	4.09	0.061	none	0.42	0.528	none
total non-living pools ^b	5.29	0.035	none	22.01	<0.001	island area ($p = 0.003$)
total of all pools ^a	7.87	0.010	island area ($p = 0.002$)	—	—	—

^a Analyses performed on log-transformed values for absolute C storage data.

^b Includes soil, litter and CWD.

4. DISCUSSION

Few studies have considered effects of invasive organisms on ecosystem C sequestration either above-ground (e.g. Bradley *et al.* 2006; Litton *et al.* 2006) or

below-ground (e.g. Wardle *et al.* 2001; Frelich *et al.* 2006). Further, the issue of how invasive species affect partitioning of stored C between the above- and below-ground subsystems has been seldom explored

(but see Jackson *et al.* 2002). Our study provides clear evidence that invasion by introduced rats has significant effects on both above- and below-ground C storage, but that these effects work in different directions.

Seabirds have two main effects on C storage which are impaired when they are subjected to predation by rats. First, seabird damage to tree roots through burrowing during nesting undermines tree stability (Maesako 1999), and this may reduce tree biomass and C storage in live tissue, which is consistent with our data. These effects override any positive effects that seabirds might exert on plant growth through fertilization due to transport of nutrients from the ocean to the land (Fukami *et al.* 2006). Second, seabirds transfer significant quantities of resources containing C from the ocean to the land (Polis & Hurd 1996; Croll *et al.* 2005; Fukami *et al.* 2006), which increases the amount of C stored in the soil. In this light, earlier work has shown that seabirds on offshore islands in central New Zealand can add 4–50 g m⁻² of guano to the ground surface each week (Mulder & Keall 2001). Our data also show that burrowing by seabirds results in greater amounts of C being sequestered deeper in the soil profile (i.e. at 20–30 cm depth).

These effects are all reversed by predation of seabirds by rats. Rats are omnivores that consume vegetative biomass and reduce tree seedling establishment (Atkinson 1985), but these negative effects are apparently overridden by their positive effects on seedling density and plant biomass through reducing seabird burrowing activity (Fukami *et al.* 2006). Thus, rat invasion causes the ecosystem to shift from a state where just over half the total C is stored in non-living pools to one in which most of the C is stored in live plants. Since the positive effects of rats on live plant C storage outweigh their negative effects on C storage in non-living pools, invasion by rats promotes the total amount of C sequestered in the ecosystem.

Our study focused on offshore islands and is most relevant to coastal forests. However, these types of effects are likely to be important in many other coastal systems, given the widespread influence of invasive predatory mammals on seabird populations throughout the world (Courchamp *et al.* 2003; Blackburn *et al.* 2004). In New Zealand, the disappearance of extensive nesting seabird communities over the past several centuries following the introduction of predators (notably rats; Worthy & Holdaway 2002) has probably exerted large effects on C storage in many coastal forests. Some of these effects probably occur further inland given that, in the absence of predators, several seabird species nest 50 or more kilometres inland from the coast (Worthy & Holdaway 2002). While our results are most relevant in the order of 50–150 years following predator invasion, the nature of these effects in the long-term perspective (i.e. multiple tree generations) is less clear. Factors that may determine these longer-term effects are the long-term nature of population dynamics of rats and seabirds and the rate at which C turns over in both the above- and below-ground pools.

The effects of non-native organisms on ecosystem C sequestration have been largely overlooked, especially when compared with other drivers of human-induced global change. Our results in total point to large effects of a widely distributed invasive predator on ecosystem C storage and on the partitioning of C storage between above- and below-ground pools. As such, they highlight the need to explicitly consider the ecosystem-level consequences of invasive biota in order to better understand how the global C cycle responds to global environmental change.

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- Atkinson, I. A. E. 1985 The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifauna. In *Conservation of island birds* (ed. P. J. Moors), pp. 35–81. Cambridge, UK: ICBP.
- Blackburn, T. M., Cassey, P., Duncan, R. P., Evans, K. L. & Gaston, K. J. 2004 Avian extinction and mammalian introductions on oceanic islands. *Science* **305**, 1955–1958. (doi:10.1126/science.1101617)
- Bradley, B. A., Houghton, R. A., Mustard, J. F. & Hamburg, S. P. 2006 Invasive grass reduces aboveground carbon stocks in shrublands of the western U.S.. *Global Change Biol.* **12**, 1815–1822. (doi:10.1111/j.1365-2486.2006.01232.x)
- Courchamp, F., Chapuis, J. L. & Pascal, M. 2003 Mammal invaders on islands: impact, control and control impact. *Biol. Rev.* **78**, 347–383. (doi:10.1017/S1464793102006061)
- Croll, D. A., Maron, J. L., Estes, J. A., Danner, E. M. & Byrd, G. V. 2005 Introduced predators transform subarctic islands from grassland to tundra. *Science* **307**, 1959–1961. (doi:10.1126/science.1108485)
- De Vries, W., Reinds, G. J., Gundersen, P. & Sterba, H. 2006 The impact of nitrogen deposition on carbon sequestration in European forests and forest soils. *Global Change Biol.* **12**, 1151–1571. (doi:10.1111/j.1365-2486.2006.01151.x)
- Frelich, L. E., Hale, C. M., Scheu, S., Holdsworth, A. R., Heneghan, L., Bohlen, P. J. & Reich, P. B. 2006 Earthworm invasion into previously earthworm-free temperate and boreal forests. *Biol. Invas.* **8**, 1235–1245. (doi:10.1007/s10530-006-9019-3)
- Fukami, T. *et al.* 2006 Above- and belowground impacts of introduced predators in seabird-dominated island systems. *Ecol. Lett.* **9**, 1299–1307. (doi:10.1111/j.1461-0248.2006.00983.x)
- Jackson, R. B., Banner, J. L., Jobbagy, E. G., Pockman, W. T. & Wall, D. H. 2002 Ecosystem carbon loss with woody plant invasion of grasslands. *Nature* **418**, 623–626. (doi:10.1038/nature00910)
- Körner, C. 2000 Biosphere responses to CO₂ enrichment. *Ecol. Appl.* **10**, 1590–1619.
- Litton, A. F., Creighton, M., Sandquist, D. R. & Cordell, S. 2006 The effects of non-native grass invasion on aboveground carbon pools and tree population structure in a dry tropical forest of Hawaii. *Forest Ecol. Manage.* **231**, 105–113. (doi:10.1016/j.foreco.2006.05.008)

- Maesako, Y. 1999 Impacts of streaked shearwater (*Calonectris teucomelas*) on tree seedling establishment in a warm temperate evergreen forest on Kanmuriijima Island, Japan. *Plant Ecol.* **145**, 183–190. (doi:10.1023/A:1009882919122)
- Mulder, C. P. H. & Keall, S. N. 2001 Burrowing seabirds and reptiles: impacts on seeds, seedlings and soils in an island forest in New Zealand. *Oecologia* **127**, 350–360. (doi:10.1007/s004420000600)
- Polis, G. A. & Hurd, S. D. 1996 Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *Am. Nat.* **147**, 396–423. (doi:10.1086/285858)
- Schimel, D. S. *et al.* 2001 Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. *Nature* **414**, 169–172. (doi:10.1038/35102500)
- Vitousek, P. M., D'Antonio, C. M., Loope, L. L., Rejmanek, M. & Westbrooks, R. 1997 Introduced species: a significant component of human-caused global change. *New Zeal. J. Ecol.* **21**, 1–16.
- Wardle, D. A., Barker, G. M., Yeates, G. W., Bonner, K. I. & Ghani, A. 2001 Introduced browsing mammals in natural New Zealand forests: aboveground and belowground consequences. *Ecol. Monogr.* **71**, 587–614.
- Worthy, T. H. & Holdaway, R. N. 2002 *The lost world of the moa*. Christchurch, New Zealand: University of Canterbury Press.