LETTERS

Resource-use efficiency and plant invasion in low-resource systems

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No species can maximize growth, reproduction and competitive ability across all environments, so the success of invasive species is habitat-dependent. Nutrient-rich habitats often experience more invasion than resource-poor habitats[1–4], a pattern consistent with traits generally associated with successful invaders (high growth rates, early reproduction and many offspring[5–8]). However, invaders do colonize resource-poor environments, and the mechanisms that allow their success in these systems are poorly understood. Traits associated with resource conservation are widespread among species adapted to resource-poor environments[9–11], and invasive species may succeed in low-resource environments by employing resource conservation traits such as high resource-use efficiency (RUE; carbon assimilation per unit of resource). We investigated RUE in invasive and native species from three habitats in Hawaii where light, water or nutrient availability was limiting to plant growth. Here we show that across multiple growth forms and broad taxonomic diversity invasive species were generally more efficient than native species at using limiting resources on short timescales and were similarly efficient when RUE measures were integrated over leaf lifespans. Our data challenge the idea that native species generally outperform invasive species under conditions of low resource availability[3], and suggest that managing resource levels is not always an effective strategy for invasive species control.

Invasive species represent one of the most serious threats to biodiversity and ecosystem function worldwide[12], and understanding the mechanisms by which invasive species outperform native species is crucial to controlling their spread. One mechanism that has received considerable recent attention is the fluctuating resource hypothesis[13,14], which proposes that invasion is facilitated by high resource availability resulting from disturbance or low resource uptake by the native plant community. This hypothesis suggests that resource-demanding invasive species are likely to enter low-resource habitats following a disturbance that increases resource availability, such as clear cutting, soil disturbance or fire. However, in the absence of continued disturbance, it is unclear whether invasive species will persist[15], particularly if introduced species experience strong competition from native species that are adapted to low-resource conditions[16]. The idea that the performance of invasive species will be suppressed under low-resource conditions is a crucial component of invasive species control programmes and native ecosystem restoration strategies that manipulate resource availability to promote the growth of native species[3,17,18]. Nevertheless, invasions into resource-poor habitats occur and we know relatively little about the mechanisms involved.

To outperform native species and persevere in a low-resource environment, invasive species must actively increase resource availability (for example, N_2-fixation or positive feedbacks through rapid litter turnover and decomposition[19]), promote continued disturbance that increases resource availability (for example, fire), be better

at acquiring limiting resources or be more efficient at using limiting resources. Relatively few invaders introduce 'novel' traits to a native community (for example, N_2-fixation or high flammability). More commonly, invasive species differ quantitatively in traits already present in existing native species[19,20]. Plants adapted to low-resource environments generally possess traits associated with resource conservation (a long leaf lifespan, high concentrations of defence compounds, low tissue-nutrient content or thicker leaves), which results in reduced rates of growth but maximizes RUE[9–11]. The few ecologically and taxonomically appropriate comparisons of RUE in invasive and native species in resource-poor systems show mixed patterns of RUE in invaders relative to co-occurring natives[21,22]. The paucity of data on RUE in invasive and native species, and the potential impact of RUE on invasive species control strategies warrant a thorough examination of RUE as a potential mechanism to explain the success of invasive species in low-resource systems.

We compared leaf-level physiological traits associated with RUE in 19 pairs of phylogenetically related invasive and native species from three habitats in Hawaii where light, water or nutrient availability was limiting to plant growth. Trait variation among species often reflects phylogenetic relationships in that more closely related taxa share similar trait values. Thus, we employed a phylogenetic comparative design to minimize trait differences associated with comparing unrelated species and disparate life forms[23,24]. To identify generalizations in patterns of RUE, we surveyed a broad array of plant groups, including ferns, C_3 and C_4 grasses, herbs, shrubs and trees (Supplementary Table 1).

Across all habitats, invasive species showed higher rates of carbon assimilation relative to native species (Fig. 1a). Higher assimilation rates for invaders corresponded with higher light-use efficiency (Fig. 1b), instantaneous nitrogen-use efficiency (PNUE) and instantaneous energy-use efficiency (PEUE) in light- and nutrient-limited systems (Fig. 2a, b). Instantaneous water-use efficiency (WUE) was not significantly different among invasive and native species in any habitat (Fig. 2c). Collectively, these instantaneous measures of RUE support the idea that invasive species can outperform native species in low-resource environments.

Species adapted to resource-limited environments often have slower leaf turnover and create thicker leaves to minimize nutrient and leaf loss[11]. Retaining leaves for a longer time period maximizes carbon assimilation per unit resource invested in leaf construction over the lifespan of the leaf[9,10]. Thus, RUE integrated over leaf lifespan more accurately depicts species differences in resource use over longer timescales[25]. Higher leaf lifespan in native relative to invasive species (see Supplementary Table 2) compensated for higher instantaneous RUE in invasive species and resulted in similar integrated PNUE and PEUE (Fig. 2d, e). In one habitat (PNUE in N-limited habitat; Fig. 2d), a measure of integrated RUE was significantly higher for natives relative to invaders. Leaf $\delta^{13}C$, which is often used

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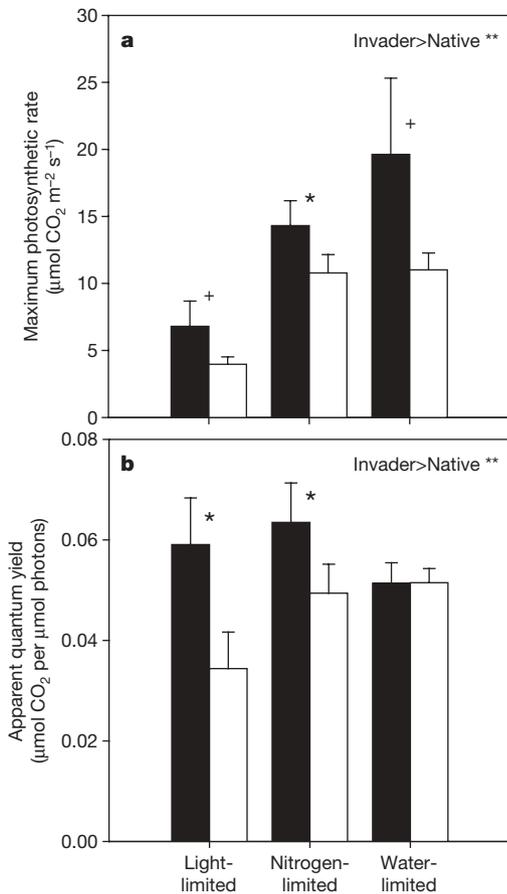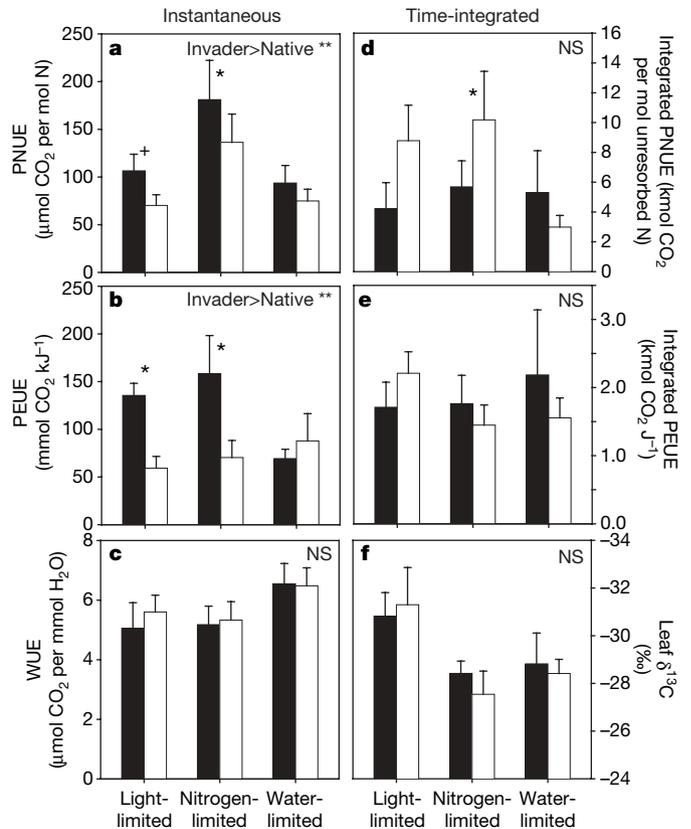
Figure 1 | Photosynthetic rates and light-use efficiency (apparent quantum yield) for 19 phylogenetically related pairs of invasive and native plant species from three habitats in Hawaii. Data are means and standard error for invasive (black bars) and native (open bars) species. Data for each trait were analysed using paired t-tests across all 19 pairs and also within each habitat (+ denotes $P < 0.1$, * denotes $P < 0.05$ and ** denotes $P < 0.01$). The number of paired comparisons was 4, 10 and 5 for light-, nitrogen- and water-limited habitats, respectively.

Figure 2 | Instantaneous and time-integrated measures of nitrogen-, energy- and water-use efficiency for phylogenetically related pairs of invasive and native plant species from three habitats in Hawaii. **a, d**, Photosynthetic nitrogen-use efficiency; **b, e**, photosynthetic energy-use efficiency; and **c, f**, water-use efficiency. Data and symbols as in Fig. 1 (NS, no significant differences across habitats). Instantaneous PNUE, PEUE and WUE measures include data from 19, 13 and 19 pairs, respectively. Integrated PNUE, PEUE and WUE include data from 12, 13 and 17 pairs, respectively.

to integrate WUE over leaf lifespan (see Supplementary Methods), was similar among native and invasive species (Fig. 2f). Overall, the time-integrated RUE data suggest that invaders have no long-term advantage or disadvantage under conditions of continued low resources.

Our results suggest that high RUE is a plausible mechanism for plant invasion and persistence in low-resource systems; however, the importance of RUE to invasive species success will vary across habitats and timescales of observation. Specifically, instantaneous and integrated measures of RUE portray two different scenarios for invasive species success. The instantaneous measures of RUE suggest that invasive species can outperform natives on short (for example, seasonal) timescales. In contrast, our time-integrated RUE measures indicate that invaders are not at a disadvantage on longer timescales (for example, multiple seasons) and may persist under conditions of continued low-resource availability. These results contradict the general paradigm that invasive species allocate resources to growth and reproduction at the expense of resource conservation[5–8]—an idea resulting from studies conducted in predominantly disturbed or resource-rich environments. However, the potentially different conclusions derived from instantaneous versus integrated measures of RUE highlight the need to resolve their potential to influence plant community dynamics for various timescales and phases of invasion (for example, establishment and persistence).

Our finding that native species did not have appreciably higher instantaneous or integrated RUE relative to invaders indicates that

lowering resource availability to prevent the spread of invaders[17,18] may not always be effective. Furthering our understanding of the mechanisms governing the interactions among invasive and native species across resource gradients is crucial to developing successful management and restoration strategies. For example, future research should examine how RUE may act synergistically with other plant traits to promote invasiveness (such as positive feedbacks to enhance resource availability, formation of monospecific stands through vegetative reproduction or seed bank saturation). In addition, more data are needed on how patterns of resource acquisition and use vary spatially and temporally (for example, in response to resource pulses) and how they interact with processes occurring on larger spatial scales (such as propagule dispersal and herbivory[26]) to influence patterns of invasive species establishment, spread and persistence.

METHODS

Species and site description. Species comparisons were selected on the basis of co-occurring of phylogenetically related invasive and native species of a similar growth form and at a given site (similar light, precipitation, elevation and soil substrate age within a one-mile radius). In total, there were three congeneric, fourteen confamilial and two within-order comparisons (Supplementary Table 1). Sites were grouped based on light and water availability into three habitat types. 'Nitrogen-limited' sites occurred throughout Hawaii Volcanoes National Park on the windward side of the island of Hawaii and were characterized by high light-levels ($>600\,\mu mol\,photon\,m^{-2}\,s^{-1}$) and high precipitation ($>1,000\,mm\,yr^{-1}$). 'Light-limited' sites occurred in closed-canopy forests within the national park and were characterized by low light-levels ($<600\,\mu mol\,photon\,m^{-2}\,s^{-1}$) and high precipitation ($>1,000\,mm\,yr^{-1}$). 'Water-limited' sites occurred on the leeward side of Hawaii in the Puu Waa Waa ranch and

the Palamanui Preserve. These sites were characterized by high light-levels (>600 µmol photon m^{-2} s^{-1}) and low precipitation (<500 mm yr^{-1}). All sites were characterized by young, nitrogen-poor volcanic soils ranging in age from 100 to 10,000 years (ref. 27).

Measurements. In June and July of 2004, two recently initiated leaves on five plants per species were tagged and monitored every two to four weeks for eighteen months to determine leaf longevity. Leaf lifespan was estimated from leaf number, leaf birth rate and plastochron interval[28]. In September and October of 2004, gas exchange measurements were conducted on one recently mature leaf per plant (five plants per species). Photosynthetic rates were measured with an LI-6400 portable photosynthesis system (LI-COR). Ambient CO_2 concentration was maintained at 400 µl per litre and relative humidity was maintained between 40 and 80%. Light response curves were conducted by varying light level between 0 and 2,000 µmol photon m^{-2} s^{-1}, while leaf temperature was held constant.

After each gas exchange measurement, leaves were clipped and area was measured using a scanner and imaging program (Beta 4.0.2, Scion Image). Leaves were then dried at 65 °C and weighed to determine leaf mass per area. Leaf material was ground and analysed for leaf N content with a Costech ECS 4010 elemental analyser (Costech Analytical Technologies). δ^{13}C was measured with an elemental analyser (Costech ECS 4010) interfaced to an isotope ratio mass spectrometer (Finnigan Delta V Advantage, Finnigan MAT). Cost of leaf construction was calculated as previously described[29], substituting total N for organic N (ref. 30). Heat of combustion was determined from 150–200 mg pellets of dry, ground leaf tissue using a Parr 1425 Semimicro bomb calorimeter (Parr Instrument Company). Equations for RUE measures can be found in the Supplementary Methods.

A mixed-model nested ANOVA was conducted to evaluate RUE differences among native and invasive species, using 'pair' as a random effect and 'invasive nested within pair' as a fixed effect[24]. All analyses were highly significant ($P < 0.001$), but conveyed nothing about directional trends across native and invasive species. Paired t-tests controlled for relatedness and were used to assess directional differences in RUE traits (data presented in Figs 1 and 2). Data that violated the ANOVA assumptions of normality and homogeneity of variance were rank transformed. All analyses were performed in JMP 5.1.2 (SAS Institute).

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