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Upper-montane plant invasions in the Hawaiian Islands: Patterns and opportunities

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Abstract

In the Hawaiian Islands, massive volcanoes have created extreme elevation gradients, resulting in environments ranging from nearly tropical to alpine, spread across a distance of only a few dozen kilometers. Although the Hawaiian Islands are widely recognized for opportunities to study lowland tropical forest invasions, less attention has been paid to invasions of Hawaii's upper-montane forest, sub-alpine and alpine environments. This study synthesizes current knowledge of plant naturalization in upper-montane environments of the Hawaiian Islands in order to (1) determine whether patterns of tropical versus temperate species invasion change with elevation, and (2) evaluate whether upper-montane invaders are having significant impacts on native plant communities. A total of 151 naturalized plant species have been recorded at 2000 m or higher. Most species (93%) are herbaceous, and over half (52%) are native to Europe/Eurasia. Twenty-one species (14%) are reported to be disruptive in native plant communities, mainly by forming dense stands that appear to inhibit recruitment of natives, but also by altering vegetation structure or causing changes in ecosystem processes. Fourteen species (9%) were first recorded within the past 30 years, indicating that new invasions of upper-montane habitats are ongoing. At 1200 m elevation, only 38% of naturalized species are temperate in origin, but the proportion of temperate species increases linearly with elevation up to 3000 m (alpine habitat), where all naturalized species are temperate in origin and over 80% are native to Europe/Eurasia. Declining temperature along the elevation gradient probably drives this pattern. The extreme elevation gradients in the Hawaiian Islands provide specific opportunities for comparative studies on the ecology and evolution of temperate invaders while also creating a unique field environment for understanding interactions between temperate and tropical species.

Keywords: Alpine; Elevation gradient; European weeds; Montane tropical forest; Sub-alpine; Tropical mountains

Introduction

Most tropical and sub-tropical montane habitats around the world have been greatly modified by a long history of human disturbance (Ellenberg, 1979; Kappelle and Juarez, 1995). On-going activities in upper tropical montane habitats include logging, cattle ranching, plantation cropping and agriculture. All these activities are likely to introduce alien plant propagules, and when combined with disturbance, invasions can be expected. Burke (2003) recognized upper-mountain regions as bioclimatic and biogeographic 'islands' and identified invasion by alien species as a serious threat to tropical mountains.

Future climate change has been predicted to increase invasions in tropical montane environments, even more

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so than in temperate montane environments (Bortenschlager, 1991). Nevertheless, few studies have examined plant invasions in high montane ecosystems of the tropics or subtropics. Ellenberg (1979) mentioned the occurrence of a "remarkably stable" community of introduced *Trifolium repens* and *Lolium perenne* in the Andean highlands of South America, while also noting, in general terms, the spread of thorny, poisonous, or less palatable plants. Some of these plants must have been aliens. A more detailed vegetation survey of disturbed grasslands in the Andes has recently identified some naturalized species there (Quiroga-Mendiola, 2004). In the central Andes of Columbia (2000 m), introduced *Pinus patula* and *Cupressus lusitanica* were observed reproducing in the immediate vicinity of plantations (Cavelier and Tobler, 1998), but broader-scale surveys were not undertaken. Taking a more systematic approach, Stadler et al. (2000) used information from a published flora to examine general relationships between the numbers of naturalized and native wildflowers in the high mountains of Kenya (>1500 m); they concluded that native species richness does not increase the resistance to invasions. Although several overviews of plant invasions in the Hawaiian Islands are available (Smith, 1985; Loope and Mueller-Dombois, 1989; Wester, 1992), little emphasis has been placed on patterns of invasion in montane habitats (but see Loope et al., 1992).

Climatic and vegetation characteristics of Hawaiian montane environments

The Hawaiian Islands have vertical elevation gradients spanning more than 4000 m, with climatic regimes that range from nearly tropical in the lowlands, to alpine environments with snow and freezing temperatures only a few dozen kilometers away. Montane forests, shrublands and wetlands occur on all the main islands (Hawaii, Maui, Oahu, Molokai, and Kauai) at elevations ranging from 1000 to 2260 m (Gagné and Cuddihy, 1990; Loope and Giambelluca, 1998). Sub-alpine and alpine habitats are restricted to the islands of Hawaii and Maui, which have volcanoes exceeding 1800 m in elevation (Fig. 1). The rainfall regime at any particular elevation varies greatly, depending on aspect. Rainfall is lowest on leeward aspects (300–1200 mm year^{-1}) where prolonged drought is typical in summer months (April–September). Windward aspects receive significantly more rain (2500–7000 mm year^{-1}) and seasonal soil water deficits are rare below the trade wind inversion layer (Gagné and Cuddihy, 1990).

General vegetation and climatic patterns across an elevation gradient from 1000 to 4200 m are illustrated for windward slopes on the Island of Hawaii (Fig. 2). The wet montane forest occurs from 1000 to almost 2000 m. The climate diagram for Camp Kulani is representative of conditions in the wet montane forest (Fig. 2). Most months are characterized by excessive rainfall and saturated soils, as indicated by the black shading on the climate diagram. The two most common trees in the montane wet forest are *Metrosideros polymorpha* (Myrtaceae) and *Acacia koa* (Fabaceae), both endemic to the Hawaiian Islands. Sub-alpine shrubland and forest occur primarily above the trade wind inversion layer (1800–3000 m); they are seasonally dry with rainfall primarily between October and March. The most common woody species are *Sophora chrysophylla* (Fabaceae, endemic), and *Styphelia tameiameiae* (Epicradaeceae, indigenous). The endemic grass, *Deschampsia nubigena* is also common in this zone. In the upper sub-alpine zone, the shrubland becomes sparse. Finally, the alpine zone is reached just above 3000 m on windward Mauna Kea (Fig. 2) or as low as 2600 m in some places (Medeiros et al., 1998). The alpine zone is characterized by high wind, frequent overnight frosts (with winter snow) and drought. Although the climate diagram for the alpine zone (Fig. 2) suggests extreme water deficits only in summer (where rainfall curve undercuts the temperature curve), the porous cinder substrate drains water very quickly, and high levels of solar radiation and persistent winds make the tropical alpine habitat effectively arid year round (Leuschner, 2000). The alpine vegetation is usually sparse, consisting of endemic grasses, such as *Agrostis sandwicensis*, and the endemic silversword, *Argyroxiphium sandwicense* (Asteraceae), a monocarpic perennial with a massive flowering stalk that can reach 3 m in height. Mueller-Dombois and Fosberg (1998) and Gagné and Cuddihy (1990) provide more detailed descriptions and finer-scale classification of Hawaiian vegetation zones.

Anthropogenic disturbance in Hawaiian upper-montane habitats

On both Maui and Hawaii, ungulates have had major impacts on the upper-montane vegetation. By the mid-1800s herds of feral cattle (*Bos taurus*) and goats (*Capra hircus*) were abundant on the slopes of Mauna Loa, Mauna Kea. In 1937, an estimated 40,000 feral sheep (*Ovis aries*), were roaming as high as 3960 m the alpine zone of Mauna Kea (Tomich, 1986). The sheep were eradicated in 1981, and feral goat and cattle populations are now greatly reduced; however, mouflon (*Ovis musimon*) were released on Mauna Kea in 1964, and they are now a source of disturbance up to 2800 m (Cuddihy and Stone, 1990). In the montane forest zone (1000–2000 m), feral pigs have been a major source of disturbance for at least a century, despite efforts to reduce their numbers (Tunison et al., 1994). Introduced