

Appendix 1. An overview of evidence

Here I summarize observations and evidence relevant to the ideas presented in the main text. This is not an exhaustive summary, but rather illustrates the nature and limitations of such evidence.

My method was to define some hypotheses and identify relevant observations.

There are two fundamental hypotheses:

H1 – disturbance (reduced competition) permits species to occur at higher temperatures (lower elevations) than with greater competition.

H2 – disturbance (reduced competition) permits species to occur at lower temperatures (higher elevations) than with greater competition.

These hypotheses provide useful shorthand in classifying observations.

Distributions

Species common at high elevations in tropical mountains also occur locally, in disturbed areas, at much lower elevations (consistent with H1, see previous section). For example, the forest undergrowth around the Institute of Tropical Forest Conservation field station (where I worked until recently) at 2,300 m above sea level (a.s.l.) in the Bwindi Impenetrable National Park SW Uganda, burned in the late 1970s and now possesses vegetation typically associated with more pristine sites at higher elevations elsewhere in the region (Owiunji et al. 2005): e.g., tree heathers *Erica trimera* (Engl.) Beentje (more typically found close to the tree line at 3000-4000 m), *Hagenia abyssinica* (Bruce) J. F. Gmel. (a tree recorded up to 3600 m), and giant *Lobelias* (typical of the vegetation above 3000 m, pers. obs.).

Many species are cultivated outside their natural range. Several alpine species for example are grown as ornamentals at much lower elevations and higher temperatures than occur in their natural range (Birks and Willis 2008). Van der Veken et al. (2008) found 260 of 357 native European plants (73%) are sold well north (mean about 1000 km) of their natural range suggesting an ability to grow in colder conditions when suitably tended (supporting H2). Live collections offer a resource for future study but interpretation of such data must be treated with caution

due to uncertainties about local growing conditions, provenance and selection effects.

In the boreal forests of Scandinavia *Betula pubescens* Ehrh. is “early successional” at low elevations but sometimes form an apparent climax at higher elevations, e.g., in (Kullman 2013) (consistent with H1). Many other examples relate to the tropics.

Polyscias fulva, a common fast growing tree species of mountain forest, occasionally occurs in heavily disturbed forest and open sites at much lower elevations – this relationship is sufficiently well established that when its pollen is recorded in palynological reconstructions at lower elevations it is readily interpreted as an indicator of disturbance rather than of cooler conditions (Morrison and Hamilton 1974). Several Ericaceae typically found above 3000 m also occur in secondary regrowth at much lower elevations (Marchant and Hooghiemstra 2001).

Similar behavior occurs in other Araliads, Moraceae and Urticaceae in other regions (A Gillison pers. comm.).

Ocotea usambarensis Engl. is a large slow-growing dense-timbered tree of primary mountain forests in tropical Africa. Despite lacking pioneer characters this species indicates past disturbance when seen at low elevation sites. Lovett (1996) examined vegetation elevation relationships in the Tanzanian highlands and based on his observations comments that *O. usambarensis*, and by implication other species, are “restricted to higher elevations because of competitive community dynamics, and not as a result of physical factors such as temperature” (an implication of H1).

Elsewhere, in the high elevation oak forests of Costa Rica, regrowth after clearance leads to high species numbers due to the influx of species from above the treeline (Kappelle et al. 1995). These additional species do not otherwise establish and grow in closed forest (consistent with H1).

Bussmann (2004) noted that landslides on tropical mountains are frequently colonized first by species from higher elevations rather than those from the immediate surroundings. Other observations also indicate that disturbance can lower the elevations at which boundaries between vegetation communities occur. In East Africa burning has lowered the high elevation forest “tree line” on many mountains (Hamilton and Perrott 1981) and tree-cover patches remain in higher sites protected from fire (e.g., Wesche 2003). On Kilimanjaro the *Helichrysum* vegetation

that would otherwise occur above the potential tree-line at around 4000 meters, remains common in burned areas even 800 m lower (Hemp 2006). Such tree-line-lowering impacts occur worldwide (Smith and Young 1987, Korner 1998, Olivera et al. 2009, White 2013). All observations consistent with H1.

During periods of recurrent drought, when fires become more frequent, high elevation vegetation would – if consistent with H1 – be expected to expand into lower areas. Indeed, pollen cores reveal expansion of high-elevation vegetation in the East African Highlands (the upper Nile catchment) following periods when, according to ancient Egyptian texts, the Nile failed to flood for several consecutive years (Marchant and Hooghiemstra 2001).

Disturbances influence vegetation boundaries between types of forest too (as implied by H1). For example, the Caribbean pine forests of Hispaniola frequently occur just above mixed-species forests, but fires and landslides appear associated with lowered boundaries (Martin et al. 2011) with similar boundary dynamics reported from the Philippines (Kowal 1966 quoted in Martin et al. 2011).

Another example is East Africa's mountain bamboo *Yushania alpina*. Dominance at lower elevations appears associated with disturbance as noted on Kilimanjaro in Tanzania (e.g., Grimshaw 1999). Uganda's heavily disturbed Echuya Forest at 2260 to 2450 m is also dominated by bamboo though this occurs below the elevation range of the species elsewhere in the region (Morrison and Hamilton 1974). If disturbance "lowers" the mean per species elevation range (rather than broadening it near symmetrically as might occur if H1 and H2 are both true), then exploratory gradient analyses of the associated vegetation communities should indicate that the influence of elevation and disturbance on community composition are correlated. Such relationships do appear to occur, e.g. in Brazil's Atlantic forests (Eisenlohr et al. 2013), but further evaluation would be needed to exclude confounding factors.

Discussions with colleagues indicates that similar patterns of lower-elevation pioneers also occurring as higher-elevation late successional species are widespread, though the published literature remains sparse. For example, *Alphitonia* cf. *exce/sa* (Rhamnaceae) a short-lived pioneer in the lowland forests of Papua New Guinea, also occurs as a local dominant in an apparently climax community on at

some exposed low montane sites characterized by Eocene limestone (A Gillison pers. comm.).

While these relatively informal observations are suggestive, they are not conclusive: we remain uncertain concerning the role of soil, microclimates and other factors in generating the observed distributions. Furthermore, we recognize that occurrence is not evidence of viability and persistence – a problem also noted in formal studies of species coexistence where a species occurrence may result from a declining or randomly fluctuating population, or may depend on propagules from a source population elsewhere studies (Siepielski and McPeck 2010).

Successional traits

In the examples mentioned thus far, species from higher-elevations appear to behave as effective pioneers in disturbed areas at lower-elevations (suggesting a situation more like that in figure 1e than in figure 1f in the main text). Such species may be a subset of the community with more pioneer like characteristics such as good dispersal abilities, but there are also indications that higher-elevation species may be better adapted to colonization than are lower-elevation species. There are plausible evolutionary explanations. Tree replacement dynamics in closed forests is typically a tree-gap-scale, process while fires and perhaps other larger scale events, appear more frequent above the treeline (Smith and Young 1987, Wesche et al. 2000, Sherman et al. 2008, Martin et al. 2011). Ancestral states may also play a role: biogeographic isolation from similar environments increases with elevation so the ancestral dispersal events able to establish a species on a new but similar tropical mountain site become more extreme with increased elevation (as an example consider the Hawaiian lobeliads which evolved from one ancestor adapted to high elevation forest clearings, swamps or grasslands similar to its nearest extant relatives in Africa *Lobelia giberroa*, *L. columnaris* and *L. petiolata* (Givnish et al. 2009)). There is also ecological evidence of such a pattern.

A study of 234 boreal and temperate tree species indicated that a greater proportion of species had early successional traits as latitude increased (supporting H1) (Morin and Chuine 2006).

A more recent study of plant functional traits and the distribution of 250 North American tree species used quantile regressions and found that while these species distributions overlap over vast regions – clear distributional patterns arise at the boundaries. Denser wooded species and larger seeded species, characteristics considered typical of late succession, appeared to be excluded at more northerly (colder) conditions where only low density wood and small seeds (properties typical of pioneer species) occurred (Stahl et al. 2014). These patterns are consistent with H1.

Other evaluations of seed size with elevation and latitude – with smaller seeds implying pioneer type behavior – also fit the H1 pattern. For example, Baker (1972) found that per species seed weight declined with elevation on Californian mountains, while Moles et al. (2007) used a global data set to identify a 320-fold reduction in geometric mean seed mass from the equator to a latitude of 60 degrees. There are various possible explanations for these patterns but the outcome is that a comparison of higher elevation and lower elevation species communities will indicate more pioneer type characteristics in the former.

Experiments

Woodward (1975) developed studies that indicated that the decrease of temperature associated with a 250 m variation in elevation is sufficient to reverse the competitive outcome between two *Sedum* species that can establish, grow and persist across this entire range in the absence of competition in Britain: *Sedum rosea* (L.) Scop, which dominates at higher elevations and *S. telephium* L., which is more common at lower elevations. A subsequent study that established populations at different elevations predicted that *S. rosea* and *S. telephium* would be excluded by competition at lower and higher elevation sites respectively: while this was born out for *S. rosea* (taking 5 years), *S. telephium* persisted for 15 years though the population declined over this period (Woodward 1992). These studies are all in agreement with H1 and H2.

A review of transplant studies has summarized the nature of the elevation limits implied (see main text) (Hargreaves et al. 2014). Direct examination of the impacts of warming of boreal communities in Norway indicate that increasing temperatures

also increase and modify competitive interactions consistent with H1 (Klanderud and Totland 2005, Olsen and Klanderud 2014). Looking to other systems I note one experimental study of biofilm-dwelling ciliates that found that disturbance reduced some effects of artificial warming on community change, again consistent with H1 (Marcus et al. 2014). Microcosm studies with single species and species combinations have highlighted that competitive hierarchies determine species-temperature distributions for fruit flies indicating that similar dynamics operate in these taxa under these conditions (Davis et al. 1998).

LITERATURE CITED

- Baker, H. G. 1972. Seed weight in relation to environmental conditions in California. *Ecology* **53**:997-1010.
- Birks, H. J. B., and K. J. Willis. 2008. Alpines, trees, and refugia in Europe. *Plant Ecology & Diversity* **1**:147-160.
- Bussmann, R. W. 2004. Regeneration and succession patterns in African, Andean and Pacific tropical mountain forests: the role of natural and anthropogenic disturbance. *Lyonia* **6**:93-111.
- Davis, A. J., L. S. Jenkinson, J. H. Lawton, B. Shorrocks, and S. Wood. 1998. Making mistakes when predicting shifts in species range in response to global warming. *Nature* **391**:783-786.
- Eisenlohr, P. V., L. F. Alves, L. C. Bernacci, M. C. Padgurschi, R. B. Torres, E. M. Prata, F. A. M. dos Santos, M. A. Assis, E. Ramos, and A. L. C. Rochelle. 2013. Disturbances, elevation, topography and spatial proximity drive vegetation patterns along an altitudinal gradient of a top biodiversity hotspot. *Biodiversity and conservation* **22**:2767-2783.
- Givnish, T. J., K. C. Millam, A. R. Mast, T. B. Paterson, T. J. Theim, A. L. Hipp, J. M. Henss, J. F. Smith, K. R. Wood, and K. J. Sytsma. 2009. Origin, adaptive radiation and diversification of the Hawaiian lobeliads (Asterales: Campanulaceae). *Proceedings of the Royal Society B: Biological Sciences* **276**:407-416.
- Grimshaw, J. M. 1999. The afro-montane bamboo, *Yushania alpina*, on Kilimanjaro. *Journal of East African Natural History* **88**:79-83.
- Hamilton, A., and R. Perrott. 1981. A study of altitudinal zonation in the montane forest belt of Mt. Elgon, Kenya/Uganda. *Vegetatio* **45**:107-125.
- Hargreaves, A. L., K. E. Samis, and C. G. Eckert. 2014. Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. *The American Naturalist* **183**:157-173.
- Hemp, A. 2006. Vegetation of Kilimanjaro: hidden endemics and missing bamboo. *African Journal of Ecology* **44**:305-328.
- Kappelle, M., P. F. Kennis, and R. J. de Vries. 1995. Changes in diversity along a successional gradient in a Costa Rican upper montane *Quercus* forest. *Biodiversity & Conservation* **4**:10-34.
- Klanderud, K., and Ø. Totland. 2005. Simulated climate change altered dominance hierarchies and diversity of an alpine biodiversity hotspot. *Ecology* **86**:2047-2054.
- Korner, C. 1998. A re-assessment of high elevation treeline positions and their explanation. *Oecologia* **115**:445-459.
- Kullman, L. 2013. Ecological tree line history and palaeoclimate—review of megafossil evidence from the Swedish Scandes. *Boreas* **42**:555-567.

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- Lovett, J. C. 1996. Elevational and latitudinal changes in tree associations and diversity in the Eastern Arc mountains of Tanzania. *Journal of Tropical Ecology* **12**:629-630.
- Marchant, R., and H. Hooghiemstra. 2001. A Response to “Climate of East Africa 6000 14C yr B.P. as Inferred from Pollen Data” by Peyron et al. (2000). *Quaternary Research* **56**:133-135.
- Marcus, H., J. K. Wey, H. Norf, and M. Weitere. 2014. Disturbance alters the response of consumer communities towards warming: a mesocosm study with biofilm-dwelling ciliates. *Ecosphere* **5**:article 10.
- Martin, P. H., T. J. Fahey, and R. E. Sherman. 2011. Vegetation zonation in a neotropical montane forest: environment, disturbance and ecotones. *Biotropica* **43**:533-543.
- Moles, A. T., D. D. Ackerly, J. C. Tweddle, J. B. Dickie, R. Smith, M. R. Leishman, M. M. Mayfield, A. Pitman, J. T. Wood, and M. Westoby. 2007. Global patterns in seed size. *Global Ecology and Biogeography* **16**:109-116.
- Morin, X., and I. Chuine. 2006. Niche breadth, competitive strength and range size of tree species: a trade-off based framework to understand species distribution. *Ecology Letters* **9**:185-195.
- Morrison, M. E., and A. C. Hamilton. 1974. Vegetation and climate in the uplands of south-western Uganda during the later Pleistocene Period: II. Forest clearance and other vegetational changes in the Rukiga Highlands during the past 8000 Years. *The Journal of Ecology*:1-31.
- Olivera, M. M., J. F. Duivenvoorden, and H. Hooghiemstra. 2009. Pollen rain and pollen representation across a forest-páramo ecotone in northern Ecuador. *Review of Palaeobotany and Palynology* **157**:285-300.
- Olsen, S. L., and K. Klanderud. 2014. Biotic interactions limit species richness in an alpine plant community, especially under experimental warming. *Oikos* **123**:71-78.
- Owiunji, I., D. Nkuutu, D. Kujirakwinja, I. Liengola, A. Plumptre, A. Nsanzurwimo, K. Fawcett, M. Gray, and A. McNeilage. 2005. The biodiversity of the Virunga Volcanoes. Unpublished report, Wildlife Conservation Society, New York.
- Sherman, R. E., P. H. Martin, T. J. Fahey, and S. D. Degloria. 2008. Fire and vegetation dynamics in high-elevation neotropical montane forests of the Dominican Republic. *Ambio* **37**:535-541.
- Siepielski, A. M., and M. A. McPeck. 2010. On the evidence for species coexistence: a critique of the coexistence program. *Ecology* **91**:3153-3164.
- Smith, A. P., and T. P. Young. 1987. Tropical alpine plant ecology. *Annual Review of Ecology and Systematics* **18**:137-158.
- Stahl, U., B. Reu, and C. Wirth. 2014. Predicting species' range limits from functional traits for the tree flora of North America. *Proceedings of the National Academy of Sciences* **111**:13739-13744.
- Van der Veken, S., M. Hermy, M. Vellend, A. Knapen, and K. Verheyen. 2008. Garden plants get a head start on climate change. *Frontiers in Ecology and the Environment* **6**:212-216.
- Wesche, K. 2003. The importance of occasional droughts for afroalpine landscape ecology. *Journal of Tropical Ecology* **19**:197-208.
- Wesche, K., G. Miehe, and M. Kaeppeli. 2000. The significance of fire for afroalpine ericaceous vegetation. *Mountain Research and Development* **20**:340-347.
- White, S. 2013. Grass páramo as hunter-gatherer landscape. *The Holocene* **23**:898-915.
- Woodward, F. 1975. The climatic control of the altitudinal distribution of *Sedum rosea* (L.) Scop. and *S. telephium* L. *New Phytologist* **74**:335-348.
- Woodward, F. 1992. Predicting plant responses to global environmental change. *New Phytologist* **122**:239-251.