BACKGROUND

This discussion represents the "more complete analysis of between-site variations and uncertainties in the major factors controlling ecosystem properties and processes across" a substrate age gradient that is promised in *Nutrient Cycling and Limitation: Hawai'i as a Model System*. In this discussion, I will assume familiarity with the general features of the substrate age gradient, and of the geology, organisms, and climate of Hawai'i, at the level of the book. Briefly, the substrate age gradient makes use of the increasing age of Hawaiian volcanoes with increasing distance from the hot spot, from southeast to northwest across the islands; it encompasses 6 sites that range in age from ~300 to ~4.1 million years. These include the 0.3 ky (ky = 1000 years) Thurston site on Kïlauea volcano, the 2.1 ky 'Öla'a site on Mauna Loa, the 20 ky Laupähoehoe site on Mauna Kea, the 150 ky Kohala site on Kohala Volcano, the 1400 ky Kolekole site on East Moloka'i volcano, and the 4100 ky Köke'e site on Kaua'i (Crews et al. 1995).

These sites were selected to be as alike as possible in the major factors that control the structure and functioning of ecosystems, while differing by more than 4 orders of magnitude in substrate age. Compared to most continental regions, "as alike as possible" is remarkably similar in Hawai'i – but it cannot be perfect. Here I outline the major factors that we attempted to keep constant in selecting sites, and then describe how in fact they differ for each individual site.

For climate, we are concerned both with the current climate of the sites, and their climatic history. All of the core sites are between 1120 and 1210 m elevation, and so all currently experience a mean annual temperature near 15.5˚C. In selecting sites, we sought a mean annual precipitation of 2500 mm/yr, based on the precipitation maps in Giambelluca et al. (1986). Hawai'i supports a dense network of rain gauges – but also extremely steep precipitation gradients, and the existing rain gauges tend to be located away from the montane forests we sampled. Accordingly, there is more uncertainty about current precipitation than current temperature. Past climates vary among the sites because they have experienced different amounts of subsidence, different exposures to climates outside the range of the current interglacial conditions, and different erosional histories upwind that have exposed them to the prevailing northeast trade winds for only portions of their history (Hotchkiss et al. 2000), as discussed in the book.

The parent material of all of the sites is all basalt, generally with lava flows overlain by volcanic ash. The youngest sites have developed in tholeiitic basalt, while the older ones developed in alkalic basalt from the rejuvenation stage of shield volcanoes. There have been no studies of the influence of this difference in parent material chemistry for the functioning of ecosystems. On one hand, it's a small difference relative to the distinctions among major rock types common in continental areas; on the other, alkalic basalt is substantially richer in P than is tholeiitic basalt. The older sites have accumulated inputs of continental dust from central Asia that the younger sites lack, as is described in the book.

The organisms that dominate the sites – at least the plants that do so – can be held relatively constant in Hawaiian rainforests – in large part due to the dominance of the native tree *Metrosideros polymorpha* across all the sites. Paleoecological studies suggest that vegetation differed during full-glacial conditions, in sites near those studied here; the influence of this past vegetation is unknown. More recent plant invaders occur in the sites as described below. Probably more importantly, animal invaders including feral pigs and earthworms have entered the sites and could influence nutrient cycling substantially.

Relief or topography also can be held quite constant in Hawaiian forests, as long as the original constructional surface of shield volcanoes can be utilized. However, late-stage volcanism can produce steeper constructional surfaces than occur during the shield-building phase, and there are hints of surface erosion on some of the surfaces, as discussed below.

The sites were selected to maximize variation in age – but as is discussed in the book, defining the age of a particular site is not always straightforward. A meters-thick volcanic deposit of tephra falling on a fresh lava flow clearly initiates soil development and plant succession – but a thin tephra deposit on an established forest has very different effects. Individual lava flows on younger mountains and the timing of mountain building on older ones are well-mapped and well-dated in Hawai'i, but the timing and effects of past tephra deposits are far less certain.

Other processes besides the major state factors also could influence these ecosystems – including disturbance history, human uses, and atmospheric deposition. We know relatively little about disturbance history in these forests, whether natural or human-caused; we assume that human-caused disturbance has been minimal, in part because the sites are climatically unsuitable for the Polynesian's major crops. Natural disturbance no doubt has been important, including *Metrosideros* forest dieback (Mueller-Dombois 1992) and occasional hurricanes (Herbert et al. 1999), but its past influence is obscure. I will speculate about the recent disturbance below, based on what we see in the sites now. For atmospheric deposition, we assumed that sites at similar elevation with similar annual precipitation would have similar rates of deposition – but as described in the book, proximity to the active Kilauea Volcano has a substantial effect on deposition of N as well as S and other elements. The older sites may have had similar volcanic influences, when they were young and located on active volcanoes. In addition, both deposition measurements (Carrillo et al. 2002) and the chemistry of leachate and streams (Hedin et al. 2003) suggest that atmospheric deposition of marine aerosol varies as function of volcano size, perhaps reflecting distance from the ocean and the routing of air masses over land (see book).

DIFFERENCES AMONG SITES

Thurston – 0.3 ky

Climate

Current. With a weather station nearby at Park Headquarters, and 8 years of measurements even closer to the site in a location parallel to the rainfall isohyets, we are confident that average precipitation here is near 2500 mm/yr.

Past. The site is young enough to have subsided little, and not to have experienced glacial-interglacial cycles; past climate should be very similar on average to present climate.

Parent Material

The parent material at Thurston is a relatively thin (ca. 40 cm) layer of tholeiitic tephra over a tholeiitic pahoehoe lava flow.

Organisms

The site is dominated by *Metrosideros polymorpha*, with some *Ilex* in the canopy, and abundant *Cibotium glaucum* tree fern in the understory. *Myrica faya*, an introduced N fixer, was just starting to invade the site when our work started; we have kept it out. Introduced Kahili ginger (*Hedychium gardnerianum*) has been more successful. Earthworms and pigs are present but not abundant, the latter due to good hunting access.

Topography

The site is a gently sloping constructional surface, with little evidence of erosion.

Age

The age of the Thurston site was described in the book, as an illustration of the complexities of assigning substrate ages. To repeat that discussion here: the Thurston site is on the flank of a satellite volcanic shield of Kïlauea Volcano that erupted actively between about 1450 and 1500 AD (Clague et al. 1999). The lava is tens of meters thick; no vegetation or soil organic matter now on the site predates that eruption. In the first 250–300 years following the eruption, vegetation colonized the site and a thin soil developed, made up of organic matter and volcanic tephra from the nearby vents of Kïlauea. Finally, an explosive eruption in 1790 killed the forest (along with a Hawaiian army that was passing through the area), deposited a thicker layer of tephra, and re-initiated vegetation succession — this time with a legacy of some buried soil organic matter. The site is young, only hundreds of years old; we call it 300 years old (0.3 ky) because it must be between 200 and 500 years old, and we have to call it something.

Other

Disturbance. We have no evidence for disturbance in the Thurston site, although canopy dieback occurred near the site, on the same substrate, in the 1970s and 80s. It is young enough that the trees probably represent the first generation on-site, at least since the 1790 tephra deposit.

Atmospheric deposition. Atmospheric deposition is strongly influenced by proximity to active Kilauea Volcano; levels of S in particular, but also N, K, and other elements, are extremely high when wind reversals bring the plume from the current eruption (<15 km down-rift) and its ocean entry over the site. The central vent of Kilauea Volcano is even closer to the site, and atmospheric deposition must be high here whenever the volcano is actively erupting.

Olaa – 2.1 ky

Climate

Current. The weather station isn't as close to Olaa as to Thurston, but it is parallel to the rainfall isohyets; we believe that mapped rainfall is reasonably accurate.

Past. This site did not experience glacial climatic conditions, and has not subsided much in little over 2000 years.

Parent Material

The soil is made up of multiple deposits of tholeiitic tephra from Kilauea that sum to more than 2 m thick; the underlying flow is a tholeiitic pahoehoe flow from Mauna Loa.

Organisms

Most of the trees are *Metrosideros polymorpha,* and most individuals are substantially larger than those at Thurston (some exceeding a meter dbh); *Cheirodendron trigynum* is the second most abundant tree. The trees are scattered in this site, over a tall and continuous canopy of *Cibotium glaucum* tree fern, and there are numerous standing and downed dead trees. Earthworms are present in the site; pigs were at one time, but they have been excluded for decades.

Topography

The site is on a gently sloping constructional surface, like Thurston; there are some small depressions that have been observed to carry surface runoff during intense rains (> 25 cm/day).

Age

The age of this site is more complicated than that of Thurston. In the book, I reported that Don Swanson (USGS) determined that ‘Öla‘a is covered with a thicker blanket of the same 1790 tephra that covers Thurston. Here this 1790 tephra overlays deep layers of older tephra, the oldest and thickest of which is ~2100 yrs old. Trees at ‘Öla‘a are much larger than at Thurston; we believe that many survived the 1790 tephra fall, and in any case their roots reach into the deep tephra layers. We define this site to be 2.1 ky old, although most of our soil measurements in fact took place within the 1790 tephra layer.

Other

Disturbance. The sparse canopy in this site reflects an episode of *Metrosideros* dieback that killed many of the trees in this site, in the 1960s – 1980s; dead trees from that dieback remain on the site.

Atmospheric Deposition. The Ola’a site also is affected by volcanic fumes from Kilauea, although it is enough farther from the central vent that the influence of volcanic inputs is likely to be smaller.

Laupahoehoe – 20 ky

Climate

Current. There is no weather station near this site, at anything like the same elevation. The map in Giambelluca et al is therefore a bit of a stretch, but it suggests the site is somewhat wetter than Thurston (3000-3200 mm/yr). The composition of the vegetation suggests the site isn’t that wet – the native legume Acacia koa is present (though sparse) in the area, and becomes dominant 3 – 4 km to the northwest (farther into rain shadow). At this elevation, it generally occupies sites drier than 2500 mm. However, one year of precipitation measurements near the site (Herbert unpublished) yielded >3000 mm/yr – more rain than fell that year in Thurston, Kohala, or Kokee.

Past. The site has experienced past climates (during the last glacial period) that we believe were somewhat cooler and substantially drier than present; it has also subsided more substantially than the younger sites, and so has a cooler past than present for that reason as well. Much of its history is within the present interglacial, however.

Parent Material

The soil has developed in alkalic basalt, from later-phase eruptions of Mauna Kea; it consists of a thick layer of volcanic tephra (reflecting multiple episodes of deposition) over aa lava.

Organisms

The vegetation is dominated by *Metrosideros polymorpha*; a few large individuals of the native legume *Acacia koa* occur in and around the site. *Cibotium* tree ferns (both *C. glaucum* and *C. chammissois*) are abundant and vigorous, but not so dense as at Olaa or Thurston. Pigs and earthworms both are abundant – reaching their peak abundance (or at least apparency) in this site compared to any other along the gradient.

Topography

The Laupahoehoe site is on a steeper slope than Thurston or Olaa, as is typical of the alkalic cap of older Hawaiian volcanoes. The surface around the site also is more dissected; there is an incised stream on one side of the site, and some topography within it that I believe reflects both the underlying aa flow and some redistribution of material within the site by water.

Age

Geochemical evidence (especially Sr isotopes) suggest that there is a ca 20 cm thick deposit of younger ash overlaying older soil in this site. When we started working here, we thought that the dominant material in the site was the so-called Pahala ash, actually an accumulation of tephra deposits that is widespread over the Island of Hawai'i, that accumulated between 10 and 30 ky ago – hence the 20 ky age. There must be a meter or more of that material on site – but we believe that the deposit on the surface is younger, perhaps coming from the large eruption of Kanakaleonui cone (on the flank of Mauna Kea) about 5000 years ago. There is an aa flow close to the site derived from that cone, and it does have tephra on it, supporting that possible source.

Other

Disturbance. There has been Metrosideros dieback in the area relatively recently, but not in the site itself. The area downslope of the site, below 700 m elevation, has been used intensively for agriculture for many years, originally by Polynesians, but we see no evidence of forest harvesting in this site.

Atmospheric Deposition. We can see some evidence for volcanic influence in the sulfate in lysimeters and streams here, but it is extremely subtle compared to Thurston and Olaa. Concentrations of elements derived from marine aerosol are low, as is observed on the younger sites.

Kohala – 150 ky

Climate

Current. Again there is no rainfall gauge close to the site – and here the map in Giambelluca et al. (1986) suggests that the site is relatively dry, around 1700 mm/yr. However, there is a clear pattern of rainfall zones that diagonals up the leeward slope of Kohala Mountain, and rain gauges higher on the mountain suggest that the forest edge (about 1 km below the site) receives >2000 mm/yr. Moreover, the vegetation becomes boggy within a few hundred meters upslope of the site, and the one year of measurements yielded precipitation near 2500 mm. We believe that 2500 mm is a reasonable estimate for this site.

Past. The site has been through a full glacial-interglacial cycle – and the best glacial-interglacial climate record we have is for Kohala Mountain, showing substantially drier conditions just before the last full glacial (when there is a hiatus in the record, probably because conditions were too dry for peat to form, and hence for pollen preservation)

(Hotchkiss 1998). Moreover, Kohala Mountain has subsided substantially through its history. For most of its history, this site must have experienced cooler and drier conditions than at present.

Parent Material

The Kohala site is developed in alkalic tephra that overlies an alkalic aa flow. The late-stage eruptions of Kohala produced lava that is unusually rich in P, even for alkalic basalt, and this parent material could contribute to the P-rich soils and vegetation of this site.

Organisms

The forest on this site is dominated by Metrosideros polymorpha; *Cheirodendron trigynum* and *Melicope clusiifolia* are also relatively abundant. The understory is predominantly tree ferns (both *Cibotium* species), but they are noticeably less abundant than at Laupahoehoe and younger. Pigs and earthworms are present in this site, and feral cattle probably were at one time as well. Pig populations were low through most of our studies, but have increased recently.

Topography

The slope of the Kohala site is not as steep as that of Laupahoehoe, and while there is topography that reflects the underlying aa flow, there appears to be less surface redistribution of soil at Kohala than Laupahoehoe. There are small incised streams adjacent to the site on both sides.

Age

The alkalic eruptions of Kohala occurred about 140 – 220 ky ago; the lava flows and tephra on this site date to that period. Some preliminary work on ash deposits in bog cores elsewhere on Kohala Mountain suggests that one or more recent ash deposits (ca 10 ky ago) have reached the site from other volcanoes, although the amount of tephra involved is small, < 10 cm. Continental dust also is abundant in Kohala soils.

Other

Disturbance. There is no evidence for recent dieback in the area of the age gradient site, although dieback is extensive in wetter areas of Kohala Mountain. However, the forest is relatively short-statured compared to other forests on fertile substrates along the gradient, and it has the highest NPP on the gradient. These observations are consistent with the idea that the Kohala forest is recovering vigorously from a past disturbance some decades ago; dieback, introduced animals, and a hurricane that is known to have passed over the area in 1871 all represent potential causes of such a disturbance. Further evidence consistent with a history of disturbance is the low N status of the forest (relative to P, and relative to Laupahoehoe – though not relative to the younger sites), and the fact that losses of N via leaching are lower in Kohala than in any of the other sites other than Thurston or Olaa (and much lower in streams). We suspect that forest regrowth represents a substantial sink for N in this site.

Atmospheric Deposition. The Kohala site is the youngest of our sites on a relatively small volcano, one where air masses move across the summit and down to the sea rather than in diurnal upslope/downslope patterns. Perhaps for that reason, the concentrations of marine aerosol-derived elements in leachate are substantially higher in Kohala (and later) than in the younger sites, suggesting that deposition is similarly concentrated.

Kolekole – 1400 ky

Climate

Current. Again there is no rain gauge near the Kolekole site, and the rainfall gradient in this area is extremely steep. During one year of measurements adjacent to the site, Herbert recorded 3500 mm of precipitation – and the site may indeed be wetter than others on the gradient. Based on vegetation and soils, we suspect it's not as much as 1000 mm/year wetter.

Past. Kolekole, like the rest of Maui Nui, has a more complex history than the rest of the Hawaiian Islands. The current islands of Maui, Molokai, Lanai, and Kahoolawe have been combined into a single island for most of their history, and continue to be combined when sea levels are lower at full-glacial. Maui Nui has subsided up to 2000 m during its history – and it is difficult to be at all confident about its full-glacial climate, because the size and geometry of the (larger) island is unlike anything extant today. Hotchkiss et al. (2000) speculated that this site has been cooler and drier for most of its history – and that as much water would leach through this site in 240 ky under present climatic conditions as have leached through it in its 1400 ky history. This is speculation, of course, but it's more plausible than assuming that conditions have been constant through the history of the site.

Parent Material

The soil at Kolekole developed in alkalic ash deposits on an alkalic aa flow; we don't know if there have been recent ash falls in the area.

Organisms

The site is dominated by *Metrosideros polymorpha*, with *Cheirodendron trigynum* the second most abundant tree. The Metrosideros canopy is more of a monolayer in this site than the others, with the individual trees having umbrella-like growth forms and crowns that abut on each other – rather than the columnar forms in most of the sites. Tree ferns (both *Cibotium* species) are present but less abundant than at Kohala, and the staghorn fern *Dicranopteris linearis* is more abundant in this site than the others. The N fixing lichen *Pseudocyphellaria crocata* is abundant in the canopy, much more so than in any of the other sites. Pigs and earthworms are present; pig populations are low due to hunting.

Topography

The slope of the Kolekole site is relatively steep, much like Laupahoehoe – and I suspect erosion has been more important here than in most of the sites. There is a small stream on one side of the site, and a larger one on the other. Still, the site itself slopes more or less continuously, and there is little dissection of the surface.

Age

The age we use for the site reflects the alkalic phase of eruption for East Molokai volcano; we do not know if there have been later ash deposits, but if so they have not been large or recent.

Other

Disturbance. There is no evidence of human disturbance of the site, or of recent *Metrosideros* dieback.

Atmospheric Deposition. Atmospheric deposition was not measured in this site; concentrations of elements derived from marine aerosol are relatively high here as in Kohala and Kokee, probably reflecting higher concentrations in deposition.

Kokee – 4100 ky

Climate

Current. Most rain gauges in the area are to the lee of the Kokee site. The Giambelluca et al map suggests that rainfall is near 2500 mm/yr, and the year of measurements by Herbert yielded close to this rainfall. Later measurements summarized by Lohse found lower rainfall (ca 1700 mm/yr) over a two-year period; however, these measurements were made during a severe drought.

Past. While we can speculate reasonably about the climate of Kokee during the last half of its history, during the Pleistocene, we have little idea of what the climate might have been during the first half of this site's history. The deep weathering of rainforest soils on Kauai relative to Kolekole might suggest that it was wetter in the Pliocene.

Parent Material

The Kokee site is old enough that we don't know whether it represents old tephra over lava, or just weathered lava flows – but by analogy with places we do know, we suspect that it represents alkalic tephra over alkalic lava flows.

Organisms

This site also is dominated by *Metrosideros polymorpha*; other trees in the site are far more diverse than in the younger sites, including *Cheirodendron spp*, *Syzigium sandwichense*, *Tetraplasandra oahuense*, and others. Tree ferns are nearly absent from the site; many shrubs occupy the understory, and there is a layer of *Elaphoglossum* fern on the ground. An introduced *Rubus* and *Hedychium gardnerianum* are abundant in the site, and both pigs and earthworms are present. The earthworm populations are relatively small, and the pigs are suppressed by hunting.

Topography

The site occupies what many suggest was the caldera of the Kauai shield volcano (though there is much discussion as to whether Kauai formed from one volcano, or two); it lies on the flat top of a gently sloping ridge. While there are deep valleys on both sides of this ridge, the top of the ridge itself is remarkably smooth. We suspect erosion has not been a major force in shaping this site.

Age

Our age for the site is that of the alkalic phase of volcanism on Kauai; we do not know if rejuvenation stage volcanoes (one of which erupted only 500 ky ago) deposited any substantial tephra on the site. The pattern of soil development shows that most of the soil material in the profile, maybe almost all of it, is very old.

Other

Disturbance. The Kokee site has been affected by two recent hurricanes, in 1982 and 1992; the one in 1992 (Iniki) was a major storm. Darrell Herbert evaluated the effect of this hurricane on stand structure; he found that while much of the canopy was lost, few trees were snapped or uprooted. The earlier, weaker hurricane (Iwa) might have been more damaging, in that more trees might have been vulnerable to wind damage then. There is no evidence of human disturbance in the site, and no dieback – but the forest must be responding to hurricane damage.

Atmospheric Deposition. There is a short-term record of the chemistry of precipitation on Kauai; it's somewhat richer in marine aerosols than Thurston, and of course nearly or entirely lack volcanic influence.