The Ecogeography of Andean Potatoes

Versatility in farm regions and fields can aid sustainable development

Karl S. Zimmerer

Spatial and environmental patterns, or ecogeography, are foundations of the evolutionary ecology of major food plants, such as rice, wheat, maize, and potatoes. Ecogeography offers key insights about the viability of agricultural biodiversity by analyzing the occurrence and the adaptive nature of diverse types of these primary crops.

Versatility and specialization

Adaptation to varied habitats confers ecological versatility and the capacity for coarse-grained distribution across heterogeneous habitats, whereas ecological specialization implies a restricted pattern. Ecogeography and adaptive traits help to determine whether farmers are able to adjust their diverse crops to socioeconomic and environmental changes (a process known as in situ conservation) or whether they are led to abandon them. Abandonment adds to the likelihood of local extinctions (genetic erosion). Versatility and specialization, and the corresponding ecogeography traits, thus require different strategies for the conservation of agricultural biodiversity, which is a primary goal of sustainable development.

The diversity and farming of Andean potatoes offer a useful example of food-plant ecogeography. These highly diverse potatoes display a wide ecogeographic range that is based on a moderate-to-high degree of ecological versatility. In this article, I use this case study to present a paradigm shift in the view of the ecogeography and adaptive traits of diverse food plants. This paradigm shift is an expanded focus on metapopulations, the interconnected groups of species and subspecies. This shift follows from advances in evolutionary ecology—reflected in the widely read work of Stephen Jay Gould, among others—that warn against the "adaptationist" or "just so" assumption of ecological specialization (Harper 1977, Gould and Lewontin 1979, Gould 1982, Futuyama and Moreno 1988, MacNally 1995, Linhart and Grant 1996).

Advancing the metapopulation paradigm with regard to agricultural biodiversity and recognizing its significance for sustainable development requires special attention to spatial scale (Slatkin 1987, Epperson 1993, Zimmerer 1996). Increasingly, it is at the scales of the farm region and the field that ecogeography is seen as crucial for understanding, using, and protecting diverse food plants. Most regions and fields that maintain the bulk of agricultural biodiversity are located in developing countries. Although recent socioeconomic changes, such as increased short-term migration, have caused the loss of some food-plant biodiversity, many farmers in developing countries still plant highly diverse types of staple crops. Before the 1970s, most studies of crop ecogeography were framed at the continent scale; consequently, the geographical structure of these plants at the regional and field scales is a relatively recent area of study, as are related farming techniques and knowledge.

Interest in ecogeography at the regional and field scales has been hastened by the fear of genetic erosion and the hope of countering it through in situ conservation. In the 1960s, a host of conservation-minded biological scientists, such as Erna Bennett, Sir Otto Frankel, John Hawkes, Jack Harlan, Hugh Iliris, and Garrison and Susan Wilkes, began raising alarms about the growing loss of agricultural biodiversity and the threat of a complete "genetic wipeout" (NAS 1972, Harlan 1975, Plucknett et al. 1983, Wilkes 1983, NRC 1991). Their worries focused attention on farm regions and on fields that were undergoing rapid change. Meanwhile, fears about threats to various noncrop organisms soon led others—including conservation biologists and landscape ecologists—to call for more analysis of ecogeography and of ecological adaptation at the spatial scales of
Table 1. Ecogeography of the cultivated Andean potatoes.

<table>
<thead>
<tr>
<th>Common name</th>
<th>Species</th>
<th>Genetic ploidy</th>
<th>General ecogeographic rangea</th>
<th>Areal range in Paucartambob</th>
<th>Elevation range in Paucartambob</th>
<th>Yield peakc</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cut-Leaf Potato</td>
<td>Solanum stemotomum Juz. et Buk.</td>
<td>2n</td>
<td>Central Bolivia and Central Peru</td>
<td>Widespread</td>
<td>3600–4500 m</td>
<td>3800–4050 m</td>
</tr>
<tr>
<td>Ajawiri Potato</td>
<td>Solanum ajanhuiri Juz. et Buk.</td>
<td>2n</td>
<td>Northern Bolivia and Southern Peru</td>
<td>Not present</td>
<td>Not present</td>
<td>Not tested</td>
</tr>
<tr>
<td>Early Potato</td>
<td>Solanum phureja Juz. et Buk.</td>
<td>2n</td>
<td>Central Bolivia and Venezuela (Eastern Andes)</td>
<td>Northeast area (cloud forest)</td>
<td>2900–3500 m</td>
<td>3550–3800 m</td>
</tr>
<tr>
<td>Chaucha Potato</td>
<td>Solanum x chaucha Juz. et Buk.</td>
<td>3n</td>
<td>Central Bolivia and Central Peru</td>
<td>Widespread</td>
<td>3600–4050 m</td>
<td>3550–4050 m</td>
</tr>
<tr>
<td>Jujepczuk's Potato</td>
<td>Solanum x jujepczukii Buk.</td>
<td>3n</td>
<td>Central Bolivia and Central Peru</td>
<td>Widespread</td>
<td>3600–4100 m</td>
<td>4050 m</td>
</tr>
<tr>
<td>Irish Potato</td>
<td>Solanum tuberosum subsp. tuberosum L.</td>
<td>4n</td>
<td>Europe, North America, Asia, and worldwide temperate and tropical mountains</td>
<td>Widespread</td>
<td>2900–4000 m</td>
<td>Not tested</td>
</tr>
<tr>
<td>Andean Potato</td>
<td>Solanum tuberosum subsp. andigena Hawkes</td>
<td>4n</td>
<td>Northwest Argentina and Venezuela</td>
<td>Widespread</td>
<td>3600–4050 m</td>
<td>3550–4050 m</td>
</tr>
<tr>
<td>Short-Lobe Potato</td>
<td>Solanum x curtisobum Juz. et Buk.</td>
<td>5n</td>
<td>Central Bolivia and Central Peru</td>
<td>Widespread</td>
<td>3600–4100 m</td>
<td>4050 m</td>
</tr>
</tbody>
</table>

*bBased on field sampling results.
*cBased on experimental field results.

regions and smaller areas (Soulé and Wilcox 1980, Forman 1995). Subsequent concerns for the viability of both crop and noncrop organisms at these local scales have grown rapidly and in tandem (Brush et al. 1981, Nabhan 1983, Salick et al. 1997).

The principal taxonomic unit of food-plant ecogeography is the land race. Otherwise referred to as a native cultivar or as a primitive, folk, or traditional crop variety, each land race is a species subpopulation that is morphologically recognizable and genetically varied to at least some degree. Multiple land races are typically the chief units that are managed by diversity-cultivating farmers. Skillful farm management ensures that the staple food plants comprise a multitude of landrace types, the majority of which are still being grown in developing countries (Altieri and Merrick 1987, Oldfield and Alcorn 1987, Bellon 1991, Brush 1992, Brookfield and Padoch 1994, Cleveland et al. 1994, Zimmerer 1996). For instance, several thousand land races of rice are grown, mostly in Asia (Vaughan and Chang 1992), and more than 6000 potato land races are cultivated in the Andean countries of South America (Huamán 1986).

The ecogeography and the ecological adaptation of land races are still poorly understood. General summaries suggest that land races are ecological specialists adapted to particular microhabitats within local farm regions and even within individual fields (Harlan 1975, 1992, Brücher 1989). Their assumption that land races are ecological specialists implies that landrace ecogeography is fine grained, with each land race being restricted to a distinct microhabitat. This assumption may not be warranted, however, because of genetic relatedness and overlapping ecological traits.

Versatile ecological adaptation and coarse-grained distribution may, in fact, distinguish the land races of certain food plants. That is, the capacity of a landrace type for production in varied habitats (ecological habitat versatility, or fundamental niche breadth) would permit its cultivation across heterogeneous environments. Given sufficient seed dispersal and survival, this capacity would lead to the establishment of a wide (cosmopolitan) ecogeographic range. Although versatile and specialized crop types fall on a continuum of ecological adaptation, the actual extent of this adaptation is rife with implications for the design of sustainable development programs. By definition, such programs must accommodate various processes of socioeconomic and environmental change. Evaluating the details of the ecogeography of diverse food plants is, therefore, necessary.

The case study of the ecogeography of Andean potatoes described in this article furthers the metapopulation paradigm by showing that the wide ecogeographic range and the moderate-to-high ecological versatility of diverse Andean potatoes are characteristic of farming at the scales of regions and fields. Seed dispersal through farmers' techniques of field rotation and their networks of seed procurement strongly influences the geographical structure of these highly diverse potatoes. Conversely, ecological versatility has aided Andean farmers in maintaining their diverse potatoes in situ while they adjust their land use to socioeconomic and environmental changes. This major food plant and its farm-
ers offer new insights into the opportunities as well as the limits on prospects for sustainable development.

Ecogeography of the Andean potatoes

As domesticated plants, the Andean potatoes are closely entwined with the farmers and farming societies of regions where they are grown. The ecogeographic traits of the diverse potatoes are both a cause that helps to determine possible food-producing strategies and a consequence of past and present agriculture.

Potato diversity. The potato crop of the Andes is renowned for its immense diversity: It contains a complex of seven domesticated species and several thousand land races, as well as numerous closely affiliated wild relatives (Table 1). The so-called Irish Potato, designated taxonomically as Solanum tuberosum subsp. tuberosum, is of primary importance in Europe, North America, Asia, and Africa, leading it to rank as the world’s premier vegetable product.

The Irish Potato is, however, only one subspecies of this diverse complex. The biological diversity of the potato complex is spread across the Central Andes mountains of Peru, Bolivia, and Ecuador, the region in which early potato cultivation began approximately 7000 years ago. Today the diversity of potatoes is clustered in the eastern Andean valleys and uplands of south-central Peru and north-central Bolivia (i.e., from the Huancayo and Ayacucho highlands southward to the Cochabamba and Potosí sierras; Figure 1).

More than 1 million small-scale farmers—mostly Quechua and Aymara Indians—till the potatoes amid the abrupt relief of these tropical mountains. The varied types of their potato crop serve mainly as household staples and pillars of local cuisine. Most farmers pair this staple potato growing for their lar-ders with some combination of commercial cropping and nonfarm work. Since around 1950, many of these small-scale growers have also adopted genetically uniform high-yield varieties (HYVs) of “improved” potatoes. Most Indian potato farmers seek the dual benefits of a secure, desirable diet base that includes their own diverse native potatoes combined with the desire for economic betterment through the growing of HYV potatoes for markets.

In the farm region known as the Paucartambo Andes, a series of multidisciplinary studies is evaluating the ecogeography of the domesticated potato complex and the

Figure 1. The Central Andes of Peru and Bolivia. Small-scale farmers grow the world’s greatest concentration of diverse potatoes in this mountainous region. The elevational transect in the inset shows the rugged topography of the eastern Andean ranges, which include Cuzco and Paucartambo. Manu National Park and Biosphere Reserve stretches north and east of Paucartambo.
changing agriculture of the Indian peasants (Quiros et al. 1990, Zimmerer 1991a, 1991b, 1996, Zimmerer and Douches 1991, Brush 1992, Br...andigena), which as a group are described by the Paucartambo people as “boiling potatoes,” are sown from approximately 3600 m to nearly 4050 m; and Jużepekczuk’s Potato (Solanum x jużepekczukii) and the Short-Lobe Potato (Solanum x curtîloobum), both referred to as “bitter potatoes,” are sown between 3900 and 4100 m. Farmers create and reinforce the ecogeographic cohesiveness of all three species combinations by using techniques that preserve the mixtures through planting, harvest, storage, and selection (Zimmerer 1991a, 1991b, 1996, Brush 1992).

The land races of these diverse species also show a moderate-to-high degree of versatility. Ecological versatility is most notable in the land races of the highly diverse group made up of Cut-Leaf, Chaucha, and Andean Potatoes. Dozens of landrace types of these species are grown within the Paucartambo Andes, and these three species in fact contribute more than 90% of landrace diversity in the greater Central Andes (Hawkes 1990, Ochoa 1990, Quiros et al. 1990). In a sample of 77 landrace types of this group identified in Paucartambo potato fields, all but one were found across a range of elevations, from 3700 to 4050 m (Zimmerer 1991a). Statistical analyses indicated that only one land race was clustered in a narrower portion of this ample range. These findings thus attest to the versatility of the most potato land races.

One cause of this ample range is seed dispersal owing to field rotation. In the Paucartambo Andes, as in many farming regions of developing countries, growers rotate their potatoes and other crops among scattered field plots. The Paucartambo farmers typically sow their landrace-rich potato fields for 1–3 years before rotating the planting to another site; field rotation serves to renew soil fertility and may lessen the load of soil-borne viruses and nematodes. The ecological versatility of land races is thus vital because a farmer’s fields typically traverse a range of elevations of at least 200 m and, in many cases, more than 400 m (Figure 2). Field habitat variation includes soil type (from sandy loams to clays), slope (from slightly inclined...
to steep), drainage (from well drained to boggy), and exposure (all slope aspects). In general, therefore, farm management is able to benefit from landrace ecological versatility; conversely, coarse-grained distributions of land races are created and reinforced by these farm management techniques.

Interestingly, the ecological versatility of landrace types does not ensure that all distributions are widespread in terms of area. Nearly half of all landrace types cluster as local endemics in one of several distinct subregional areas, known as “landrace areas” or “cultivar areas” (Zimmerer 1991a). As shown in Figure 3, each landrace area (Northwest, West, and South) is composed of a high-elevation farming upland and its adjoining slopes. The three landrace areas are represented by the farm communities of Majopata, Colquepata, and Mollomarca, respectively.) These distinct landrace clusters are shaped by the farmers’ seed procurement networks of barter, gifts, and purchases. Most often, farmers secure seed of diverse potatoes from nearby uplands. More than 50% of the seed in each community is of this upland provenance (Figure 3). Distributions of many land races are thus clustered within the upland-slope area, where seed procurement is common.

By contrast to the “landrace area” endemics, 25 land races, approximately one-third of the sample from the Paucartambo fields, are grown widely, in cosmopolitan or cross-regional distributions. Cosmopolitan land races are generated by seed exchange, thus providing evidence that the distribution of potato land races is not strictly local or isolated. At the gene level, many alleles of these cosmopolitan land races have been found to occur widely across elevations, subareas, and taxa. In one study, alleles at 10 polymorphic gene loci of six cosmopolitan land races turned up widely, across elevations and areas (Zimmerer and Douches 1991); similar results were demonstrated at four other polymorphic loci (Brush et al. 1995).

Total allele diversity also does not vary with the environment because the tubers of varying field habitats contain a similar degree of allelic diversity. In the cosmopolitan land races, most allelic diversity (99% of the total) can be found within each subregional area (Zimmerer and Douches 1991, Brush et al. 1995). The wide-ranging distribution of the alleles suggests an absence of habitat-related genetic differences. Equally notable, a single type among the six cosmopolitan types was found to contain 70% of the total allelic diversity (Zimmerer and Douches 1991). This result strongly suggests that land races belong to interconnected genetic systems rather than to closed subpopulations.

The ecogeography of particular genotypes of the tested potatoes suggests that genotypes spread less widely than the individual alleles. In a field-based sample of 139 tubers, 30 unique genotypes were identified at 10 loci (Zimmerer and Douches 1991); in a similar sample of 610 specimens (Brush et al. 1995), 30 genotypes were also identified at four loci. Distributions of genotypes do not, however, match specific sorts of agricultural habitats. Genotype ecogeography thus fails to show evidence of ecological specialization. Nevertheless, several unique geno-
types were restricted to single subregional areas (Zimmerer and Douches 1991). This finding suggests that genetic recombination is common enough to create local differences in individual genotypes, even in the presence of frequent extra-local seed flow.

Further evidence of marked ecological versatility comes from the results of factorial experiments designed to test the elevation-based adaptation of potato species and land races (Zimmerer 1991a). Treatments in these experiments consisted of five agroecosystems—highly distinct fields at the elevations of 2800, 3300, 3550, 3800, and 4050 m—that were marked by the steep gradients of climate (mean temperature) and soils (texture) that are characteristic of Andean regions (Figure 4). Experiments replicated growing conditions that were similar to the farm management of Andean Indians. These conditions included tillage techniques and the management of soils and pests. To estimate the degree of adaptation to an elevation-related habitat, each tuber’s yield was measured. This trait is emphasized in seed selection by the Andean farmers (Brush et al. 1981, Zimmerer 1991b, Brush 1992).

Ecological versatility of Andean potatoes ranged from moderate to high in the experiments (peak yield in Table 1). Yields of the Juzepczuk’s Potato and the Short-Lobe Potato were highest at the uppermost site (4050 m). The Cut-Leaf Potato displayed a moderately broad yield peak between 3550 m and 3800 m, and the Chaucha, Early, and Andean Potatoes produced maximally across the wide range between 3550 and 4050 m. The 18 landrace types tested in the experiments also displayed moderate to high ecological versatility. With only one exception, the yield-elevation peaks of the landrace types resembled those of the species to which they belong. Insignificant differences between the yield-elevation responses of conspecific landrace types offer additional evidence that moderate to high ecological versatility is common in these land races.

Together, the sampling, genetics, and experimental results described above indicate that the species, land races, and alleles of diverse Andean potatoes possess a moderate-to-high degree of ecological versatility and gain ecological versatility through introgression with weedy species. Several weedy potatoes that interbreed readily with the related diploid domesticates thrive in a sizable spectrum of Andean environments (Ugent 1970, Johns and Keen 1986, Hawkes 1990, Ochoa 1990, Rabinowitz et al. 1990, Fernández 1994). Two such wild potato relatives, Solanum sparsipilum and Solanum leptophyes, span an array of diverse habitats of 2200-4200 m and 2600-4000 m, respectively (Hawkes and Hjerting 1989, Hawkes 1990, Ochoa 1990).
Local farming techniques further promote and take advantage of the ecological versatility and coarsely-grained eco­geography of Andean potatoes. Customary field rotation among a range of sites and seed procurement networks undoubtedly expose the potatoes to an ample spectrum of the region’s agroecosystems. In addition, the farmers select seed of the diverse potatoes by culling most tubers through en masse mixtures (Figure 5; Zimmerer 1991b, 1996). Because the diverse land races are not selected individually, each type must be sufficiently ecologically versatile to grow on the wide range of possible field sites.

The field scale. The farm field is a second scale at which the eco­geography of diverse Andean potatoes can be evaluated. Figure 6 shows maps of three typical fields of boiling potato. These fields, which are the most abundant type of diverse field, contain the Cut-Leaf, Chaucha, and Andean Potatoes.

Each field typically sprouts a mixture of species. As shown by the frequency of species in Figure 6 (the key includes the species classification of each land race), the Andean Potato usually predominates. The Cut-Leaf and Chaucha Potatoes occur in most fields, although in smaller numbers. The Limeña potato (Sola­num stenotomum subsp. gonio­calyx), which was until recently classified as a separate species but is now identified as a Cut-Leaf Potato subtype, tends to be rare. This hierarchy of relative commonness among potato species is also typical of other Andean regions of Peru and Bolivia (Jackson et al. 1980, Brush et al. 1981, Quiros et al. 1990).

The boiling potato fields harbor an impressive richness of potato land races. Maps of 100-125 plants in Figure 6 illustrate a range of diversity of between 10 and 20 land races. (This varietal diversity of a single Andean potato field exceeds the diversity of nine-tenths of the entire potato crop of the United States.)
Larger samples of 225 plants per field show as many as 30 land races, with a mean near 21 (Zimmerer 1991b). Curiously, these estimates, which are based on random sampling, differ sharply from findings of other studies. Inventories of stored potatoes in the Paucartambo Andes have suggested averages of 9.6 and 10.6 land races per farm family (Quiros et al. 1990, Brush 1992, Brush et al. 1995). Similar inventories made in neighboring regions of the Southern Peruvian Andes conclude that the average family cares for between 6.0 and 13.9 land races (Dueñas et al. 1992). The reasons for this disparity are not yet known.

A pair of distinct patterns distinguishes the within-field ecogeography of potato land races. Most commonly, the landrace types are sown in an interspersed pattern. In sowing an interspersed field, the farmer does not plant landrace types as separate groups. By contrast, the second pattern of within-field ecogeography does involve the clustering of land races. In many fields of this second mode, farmers plant their predominant landrace type in a clustered, block-like pattern, as shown by the suyt'u land race of the Majopata field (Figure 6).

Neither interspersion nor clustering, however, involves the matching of particular land races to certain microhabitats. Figure 6, which shows examples of typical farm fields with at least one distinct topographic microhabitat, demonstrates this point. These microhabitats may be especially prone to the familiar hazards of mountain farming: frost hits hardest in topographic depressions, the microbial diseases are most damaging in waterlogged soils, and drought and low fertility be et the plants in shallow soils. However, the maps in Figure 6 illustrate that the distributions of both potato species and of land races cross-cut, rather than conform to, the contrasting Andean microhabitats.

One explanation for the coarse-grained distribution and within-field ecological versatility of diverse potato land races is local farm management. The main hazards often strike unpredictably in terms of timing and which microhabitats they affect. Frost and drought, for example, frequently inflict damage irrespective of field topographic features. Such unpredictability favors versatile crop types because it leads local farmers to try to stabilize their yields by mixing land races in a general fashion rather than by locating each type individually. This risk-reducing strategy in turn exerts a clear pressure in favor of versatility, because each land race of the Andean potatoes must be viable across the gamut of field microhabitats.

Even when they cluster each landrace type separately within the field, farmers still select for versatility. Although this arrangement is less common than interspersed seeding, it is practiced throughout the Central Andes (Brush et al. 1981, Zimmerer 1991b). Within-field clustering might seem symptomatic of the ecological specialization of landrace types, but neither these block-style fields nor farmers’ accounts of them show evidence that the potato land races are sown according to within-field microhabitat. Instead, the Andean farmers typically elect this technique as a means to more accurately proportion the amount of each landrace type, sometimes in response to market opportunities.

Farmers’ own classification systems further favor the ecological versatility of potatoes (Hawkes 1947, Jackson et al. 1980, Brush et al. 1981, Quiros et al. 1990, Zimmerer 1991b, 1996). Andean farmers do not distinguish among each domesticated species, especially among the three boiling potato species. This omission from their extensive folk taxonomy is analogous to scientific taxonomies that rely on minor morphological traits in distinguishing among these species. Andean farmers are therefore likely to depend on the shared, versatile adaptation of these undifferentiated taxa to the breadth of field habitats.

Potato alleles and genotypes may also be marked by ecological versatility and coarse-grained ecogeography at the field scale. Although substantial allelic and genotypic diversity exists within most single landrace types (Quiros et al. 1990, Zimmerer and Douches 1991, Brush et al. 1995), the varied genotypes of a potato land race are either identical or strongly similar in morphology. Farmers typically do not distinguish the genotype variants of a land race. This lack of separate management means that all genotypes must be sufficiently versatile to deal with the full suite of environments that may occur within the Andean potato field.

Versatility and sustainable development

The results of field experiments, genetic analyses, and field sampling and mapping show the moderate-to-high versatility and coarse-grained ecogeography of potato land races at two scales, the farm region and the field. Such versatility is conspicuous in the species, land races, and alleles of the Andean potato complex. Ecological versatility enables the establishment of ecogeographic ranges that are shaped strongly by the dispersal flows that result from seed procurement networks.

Ecological versatility and coarse-grained ecogeography of potatoes call into question the still common assumption that diverse crops are, ipso facto, ecological specialists that are restricted to fine-grained microhabitats. The findings I have described indicate a paradigm shift, from a narrow, “adaptationist” view of agricultural biodiversity to one that is integrated with a metapopulation perspective. The metapopulation view frames the analysis of potato land races as open systems rather than as genetically isolated and inevitably specialized variants. The metapopulation paradigm also brings into focus the reciprocal relations of biodiversity and farm management: Potato growers’ techniques are both the cause and the effect of ecological versatility and coarse-grained ecogeography.

The shift to the metapopulation view has several implications for sustainable development. First, sustainable development efforts must pay close attention to the existing ecogeography of diverse food plants. The tested assumption of specialization had implied that the variety of potato-growing microhabitats would determine the pattern in which land races grow and would provide the blueprint needed for crop con-
servation. Instead, however, many Andean potato land races are clustered in landrace areas, intraregional spatial units that are formed by seed procurement networks. Cosmopolitan land races result from cross-regional seed exchange. Both spatial patterns are strongly shaped by metapopulation gene flows.

The metapopulation view thus recommends a case-by-case study of the ecogeography of crops and its implications for sustainable development. Determining the degree of ecological versatility of crops and the geographical structure of distributions and gene flows should be priorities in the general advance toward "second generation" research on agricultural biodiversity (Brush 1989, NRC 1991, Cleveland et al. 1994, Vandermeer 1995, Louette et al. 1997, Wood and Lenné 1997). In the case of Andean potatoes, ecological versatility and coarse-grained ecogeography of land races can aid sustainable development by delivering a helpful dose of flexibility. At least 90% of potato land races have remained in one area of the Paucartambo Andes since the 1920s, despite major agricultural changes, including the expansion of farm commerce and the relocation of landrace cropping (Zimmerer 1996). Many small-scale farmers in Peru and other developing countries are similarly seeking to manage their diverse crops in conjunction with expanded commerce, including the adoption of HYV crops (Altieri and Merrick 1987, Oldfield and Alcorn 1987, Bellon 1991, Brush 1992, Brookfield and Padoch 1994, Cleveland et al. 1994, Zimmerer 1996). Future research should define how the capacity for management flexibility and in situ conservation conferred by the ecological traits of diverse food plants are compatible with some sorts of rural development but not others. The loss or reduction of seed procurement networks, for example, would severely weaken the overall diversity and viability of Andean potatoes.

Sustainable development prospects are also conditioned by how Andean potatoes and other diverse crops are capable of responding to environmental change. The response of some diverse crops, including potato, may be particularly limited with respect to soil degradation. Several Paucartambo farmers have ascribed the reason for their curtailing of the diverse potatoes to be the loss of soil fertility and the ensuing yield declines (Zimmerer 1996). The impacts of climate change on agricultural biodiversity also hinge on the extent of ecological versatility. Because high tropical mountains such as the Andes may be especially sensitive to climate change, the coping capacity of these farmers will depend on the ecological versatility and ecogeography of their diverse food plants.

The new paradigm also has implications for the relationship between sustainable development, on the one hand, and crop breeding and agricultural biotechnology, on the other. Useful traits, such as disease resistance and taste factors, are likely to be contained in a potato genotype or land race that possesses general ecological versatility and coarse-grained ecogeography. In fact, the desired genotype or land race may be found within a relatively undifferentiated, diverse field mixture. Although desirable types may be identified in the field or laboratory, the evolution of those types needs to be seen as an outcome of both field- and regional-scale adaptations and ecogeography rather than through purely local processes of optimal adaptation. Consequently, in situ conservation is crucial for crop breeding and agricultural biotechnology.

These findings also encourage the reevaluation of a widely held assumption about biodiversity and its potential role in sustainable development. The a priori tenet of specialized adaptation reflects a central preoccupation with the potential role of the environment in controlling the evolution of biodiversity. By the 1880s, adaptation to distinct habitats was already known to determine the distinctness of wild plant subspecies, especially variants of lowland and alpine plants that were first studied by European botanists in the French Pyrénées and Tyrolean Alps and later by leading American ecologists, including Frederick Clements, in the Rocky and Sierra Nevada Mountains. By contrast, Andean potatoes demonstrate how ecological versatility and coarse-grained ecogeography may prevail in certain domesticated plants. Recognizing the reduced environmental control in the case of potato biodiversity in comparison with at least some wild plants helps to broaden thinking on a central idea of sustainable development.

Finally, adaptation and ecogeography of the Andean potatoes can be briefly compared with those of two other major food plants: maize (Zea mays) and manioc (Manihot esculenta; also called cassava). Diverse maize land races of Mexico and the Andean countries appear to fit local climate and soils more exactly than potato types and thus appear to be more narrowly specialized (Alcorn 1984, Bellon 1991, Zimmerer 1991b). For example, phenological traits, such as maturation time, tend to differ among land races of maize and thus are used by farmers to fit cropping to locally varied growing seasons. Such observations on the ecogeography of maize land races, which suggest a notable degree of genetic differentiation, remain to be reconciled with other results, which demonstrate the high magnitude of gene flow and the ensuing genetic similarity of diverse maize land races (Louette et al. 1997).

The manioc crop appears to have a level of ecological versatility that is intermediate between potatoes and maize (Boster 1985, Salick et al. 1997). In the tropical lowlands of the Western Amazon Basin, manioc land races appear to possess versatility at the field scale, where vegetative propagation and highly diverse within-field mixtures resemble those aspects of Andean potato farming. However, unlike potato land races, manioc land races may be ecologically specialized with respect to regional-scale habitat variation, such as elevation-related environments. The isolation of farming communities and resulting restrictions on seed flow probably help to produce and maintain this eco-genetic differentiation in the manioc crop (Salick et al. 1997).

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