Data Mining for Global Trends in Mountain Biodiversity
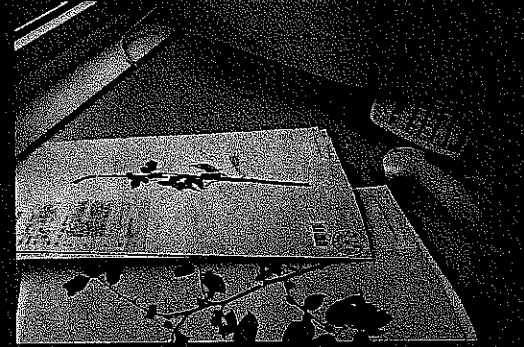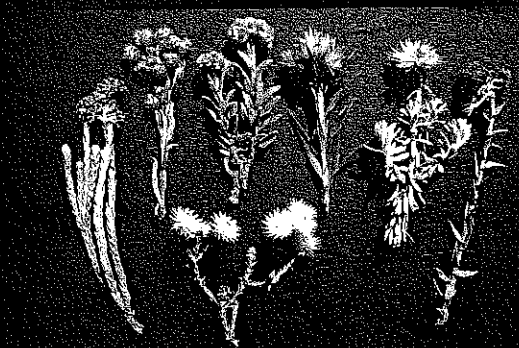

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Contents

5 A Possible Correlation between the Altitudinal and Latitudinal Ranges of Species in the High Elevation Flora of the Andes

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THE ALPINE LIFE ZONE AS A TEMPLATE FOR TESTING BIOGEOGRAPHIC THEORY

It is increasingly becoming recognized that the alpine life zone, defined as that vegetation occurring above the upper natural treeline on mountains (Körner, 2003), provides an impressive replicated, large-scale natural experiment, and thus an ideal system for studying macroecological patterns, and ecological and evolutionary processes. Although covering a relatively small proportion of the earth's terrestrial area (ca. 3%) (Körner, 2003), alpine vegetation is amply represented in both hemispheres, where it is found on all continents, and globally extends from subpolar to equatorial latitudes. Alpine vegetation in many parts of the world, unlike much subtending lowland vegetation, is still relatively well conserved (cf. Nogués-Bravo et al., 2008), thus providing greater assurance that any broad patterns detected in the alpine will reflect nonanthropogenic processes.

Characterized by the compression of the equivalent temperature conditions found along large distances of the latitudinal gradient into relatively short distances along steep altitudinal gradients, many macroecological patterns can be profitably investigated in the alpine life zone. For example, the physically compact alpine gradient provides an excellent system for detecting the effect of land area on patterns of species richness (Körner, 2000; Gorelick, 2008), and thus could go a long way in illuminating our understanding of the latitudinal species gradient, where differences in land area between the tropical and temperate zones becomes a major confounding factor. Because the mean growing season temperature theoretically should not vary significantly for alpine surfaces at different latitudes, comparative studies of species richness in

mountain ranges that span tropical to subpolar latitudes, such as the South American Andes, should enable sorting out the relative contributions of historical, evolutionary, and ecological causes of the latitudinal species gradient. The alpine gradient has already proven to be an excellent medium for unraveling the relationship between certain plant traits (e.g., breeding systems) and their evolutionary drivers (e.g., pollinators), as they are affected by the temperature regime and local weather conditions (Arroyo et al., 1982; Arroyo and Squeo, 1990) and for studying phenomena such as facilitation (Callaway et al., 2002; Arroyo et al., 2003; Cavieres et al., 2006).

Most large-scale macroecological work to date focuses either on latitudinal patterns or on altitudinal patterns, there being no attempts to link these two environmental gradients. Favorite themes currently are the latitudinal and altitudinal species gradient (cf. Lyons and Willig, 2002; Romdal and Grytnes, 2007; Chown et al., 2008) and Rapoport's rule (Rapoport, 1982; Stevens, 1989). Yet there are reasons to expect that the altitudinal range size is correlated with geographical range size. Predictably, the wider a species altitudinal range is, the greater are the species' chances for successful dispersal beyond its present geographical range. This stems from the following: Considering an adiabatic lapse rate of 6 k per 1,000 m elevation, the individual populations of a species distributed over 2,000 m of elevation straddle (and are adapted to) a range of temperatures differing by 12 k. By contrast, the populations of a species distributed over 500 m elevation under this same adiabatic lapse rate will span a mean annual temperature range of 3 k. Consequently, seeds dispersed by a species that covers 2,000 m elevation will be adapted to a much greater range of temperature conditions than those belonging to a species distributed over 500 m elevation.

Because of the wider array of potential temperature niches represented among the dispersing seeds of the altitudinal widely distributed species, the probability that some of the dispersed seeds will encounter an adequate temperature niche outside the species' present geographical range should be higher than for a species with a narrow altitudinal range. Thus, altitudinally widely distributed species should be able to expand their geographical distributions (latitudinally and longitudinally) at a faster rate, and in a young mountain flora, come to occupy larger geographical areas than altitudinally narrowly distributed species. Consequently, in a young flora, size of altitudinal range and size of geographical range should be correlated. Apart from evident theoretical interest, this question has important connotations for understanding how successfully plant and animal species may respond

to climate change in high mountain floras, although on this occasion we will not dwell more on this theme.

Our primary aim here is to discuss the usefulness of electronic databases to preliminarily investigate whether altitudinal range and geographical range size are correlated in the north–south trending South American Andes, using the genus *Senecio* as a model. Data was obtained from electronic, specimen-based floristic databases, a source of information that is being increasingly employed in macroecological research when large geographical scales are considered. At this stage, we use latitudinal range as a surrogate for geographical range. In the north–south trending Andes, this finds some justification in a preliminary study such as this, although clearly is not as precise as one would like. For this and other reasons that will eventually be expounded, in the present paper, it is not our intention to come to any definitive scientific conclusions. Rather, having carried out a preliminary exercise for exploring the power of database work in a mountain ecological context (Körner et al., 2007); our main objective is to highlight some of the problems associated with using georeferenced databases for studying macroecological trends, especially when altitude is the variable of interest, as well as offering some suggestions as to how the problems might be overcome.

THE ALPINE LIFE ZONE IN THE SOUTH AMERICAN ANDES

The alpine life zone of the South American Andes, encompassing the páramo, puna, and southern temperate alpine, runs from approximately 11° N in Venezuela to the extreme tip of southern South America (55° S), with outlying patches of alpine vegetation found on the Cape Horn Islands close to 56° S. The páramo extends from 11° N to 8° S, followed by the puna to around 26 to 27° S, and from thereon south, the southern temperate alpine. A precise definition of the lower limit of the alpine life zone in the South American Andes is hindered by the lack of a treeline over a considerable extension of the puna and over part of the eastern side of the southern temperate alpine. In our work, we rely on the criterion of homologous vegetation belts. In the northern central Andes (northern and central Peru), the vegetation belt immediately above treeline corresponds to the puna, found at about (3,000) 3,200 to 3,500 m elevation. This vegetation type shows continuity with the páramo north of 8° S, which again occurs immediately above the treeline. Consequently, in the drier Andes where a treeline is absent, we use the lower limit of the puna as the lower bound of the alpine

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life zone. This limit is somewhat lower than the sporadic occurrence of *Polylepis* found within a matrix of typical high altitude puna vegetation from 18 to 22° S on the western side of the Andes. Using a 90 m resolution digital elevation model, we estimate the South American alpine life zone (including bare ground and ice above the upper vegetation limit), defined previously, to cover some 913,500 km², the equivalent of 5.1% of the land area of the continent.

Although the global trend for the alpine belt is to decrease in altitude with latitude, the altitude of the lower limit of the Andean alpine life zone experiences little elevational change from the tropics to 25 to 27° S on account of aridity in the central Andes. Aridity counteracts the global latitudinal decrease in temperature and at the same time forces vegetation belts upwards beyond the altitude expected for their latitude (Arroyo et al., 1988). Indeed, the elevation of the lower limit of the puna at its driest point on the western side of the Andes in Chile at 25° S is higher than further north (ca. 3,700–3,800 m compared with the more typical 3,200 to 3,500 limit). We specifically elaborate on this trend here, because, as will be seen later, it will be taken advantage of in order to avoid registering a spurious relationship between altitudinal and latitudinal range. The tendency for the vegetation, including tree species, in the arid area of the Andes to seek more adequate moisture at higher elevations has been pointed out by Braun et al. (2002) in their study of Andean treelines. From 27° S southward, as aridity ameliorates, the lower limit of the alpine zone descends gradually to around 2,000 to 2,200 m at 33° S to reach 300 to 400 m elevation on Hermit Island in the Cape Horn Islands.

Ongoing work by us, consisting of developing and refining a high altitude checklist, suggests that the South American alpine could house as many as 6,700 species in around 870 genera. It should be noted that many of these species are not restricted to the alpine zone per se, and some species records included at this point on the basis of a general altitudinal criterion could eventually be eliminated because of local variation in the elevation of the treeline. The alpine life zone is characterized by seven genera, with close to, or more than, one hundred species: *Calceolaria*, *Gentianella*, *Lupinus*, *Nototriche*, *Senecio*, *Solanum*, and *Valeriana*. Many additional genera are represented by close to, or more than, fifty species (*Adesmia*, *Astragalus*, *Baccharis*, *Calamagrostis*, *Carex*, *Diphlostephium*, *Draba*, *Elaphoglossum*, *Espeletia*, *Festuca*, *Geranium*, *Gynoxys*, *Halenia*, *Hypericum*, *Huperzia*, *Miconia*, *Oxalis*, *Pentacalia*, *Poa*, *Puya*, and *Viola*). Thus, the South American alpine flora is ideal for studies that require large

numbers of species. *Senecio* is by far the largest genus at high elevations in the South American Andes, with more than 300 species occurring totally or partially above the treeline. Species of *Senecio* are found in the páramo, puna, and southern temperate alpine.

THE *SENECIO* DATABASE TO SHOW ECOLOGICAL TRENDS ACROSS THE HIGH ANDES

Several subgeneric taxa are recognized in the South America species of *Senecio*, but here we have considered all species independently of their sectional placement in the absence of comprehensive phylogenetic work. We carried out separate analyses for species of *Senecio* occurring in the páramo and puna, so as to ascertain the generality of any emerging patterns. Toward this purpose, we extracted 1,209 puna and páramo *Senecio* records from a database of 95,000 specimens representing the entire South American alpine flora that we have downloaded from the open access TROPICOS electronic specimen-based database housed at the Missouri Botanical Garden (http://www.tropicos.org/) and 726 from Chilean sources. Twenty-two additional records were downloaded from the C.V. Starr Virtual Herbarium (http://sciweb.nybg.org/Science2/VirtualHerbarium.asp), an electronic gateway to the collections of the William and Lynda Steere Herbarium at the New York Botanical Garden (NYBG), to give a grand total of 1,957 records. TROPICOS is particularly well endowed with specimens from high elevations in Colombia, Ecuador, Peru, and Bolivia, and thus a valuable resource. Specimens from Argentina are now being actively incorporated in TROPICOS. However, most of the Argentine material presently found in TROPICOS lacks georeferences.

Many more nondatabased specimens of *Senecio* are found in Argentina's major herbaria, to the extent that the present information for Argentina (i.e., the eastern side of the southern part of the puna) is incomplete. Still more specimens are to be found in national herbaria in Venezuela, Colombia, Peru, Ecuador, and Bolivia. Overall, around 77.8% of the *Senecio* records downloaded from TROPICOS and NYBG contained either latitude and longitude coordinates or altitude data (including a few georeferences furnished by us) and thus are informative for the purposes here. However, only 58.6% of the records simultaneously contain both latitude and altitude in the same record. The Chilean data includes mostly specimens from Chile and is particularly rich in records for the southern half of the puna. Most herbarium specimens

collected in Chile from the 1950s onward contain georeferences and altitude data taken from topographical maps or with GPS and field altimeters. The major Chilean herbaria have retroactively provided georeferences for many older specimens, which, in any case, are few for the puna. All puna *Senecio* records contain latitude, and 98.6% contain both latitude and altitude. The records for each *Senecio* species include above and below treeline occurrences—i.e., their total altitudinal range.

PROBLEMS ASSOCIATED WITH THE USE OF DATABASES IN FINE-TUNED MACROECOLOGICAL WORK

To investigate the relationship between latitudinal range and altitudinal range, the first task was to obtain latitudinal and altitudinal limits for each *Senecio* species. This is easier said than done when using floristic databases and will always involve sources of error. Altitude on many herbarium specimens is given as a range (e.g., 3,500 to 3,800 m). Any field botanist knows that such ranges can refer to the general range over which a series of specimens representing diverse species would have been collected on a particular collecting trip or day, and not necessarily the altitudinal range over which the particular species occurs at that collecting site. Unfortunately, determining when ranges on specimens in electronic databases refer to a species' real range versus a general collecting range is virtually impossible without going back to original field notes, and then might not work anyway. Secondly, in order to obtain the altitudinal range of a species from database records, one usually has no other choice than to use the data obtained from several specimens collected from different localities.

To estimate a species' altitudinal range, we employed two criteria: Criterion (1) The range was considered the number of 100 m bands calculated from the difference between the highest point elevation represented among the collections of the species under consideration (or highest upper limit among the altitudinal ranges), and the lowest point elevation represented among the collections (or lower limit among the ranges); Criterion (2) Prior to searching for the upper and lower elevation recorded for the species, all range data on individual specimens was averaged so as to provide one altitude point per specimen. Under both criteria, when a species had been collected once, its altitudinal range was considered to be 100 m. To be consistent, 100 m was added to the difference between the maximum and minimum altitude at which each species was collected. In other words, when a species was

reported for, say, 3,400 m, it was assumed that it occurred at least between 3,400 to 3,500 m. The first criterion effectively assumes that the ranges given in individual database records are meaningful for the particular species, which, of course, we know is not always true. The second measure of altitudinal range is more conservative. The truth will lie somewhere between. The latitudinal range of each species was expressed as the number of 1° latitudinal bands obtained from lowest and highest latitudes registered for the species. When a species had only been collected once, it was considered to be distributed in one latitudinal band.

A second and more serious problem concerns spurious effects, which will arise if the localities from which an altitudinal range is deduced cover a very large latitudinal range. In a north–south trending mountain range such the Andes, a species distributed, say, from the latitude of the páramo into the southern temperate alpine will naturally be found at much lower elevations at the southern extreme of its latitudinal range, on account of the latitudinal reduction in temperature. The further south such a species extends (therein increasing its latitudinal range), the wider will be its altitudinal range based on the upper and lower altitudinal limits taken from database records throughout its latitudinal range. We attempted to avoid this kind of spurious effect in terms of the hypothesis we wish to test in the present study, as far as possible, by limiting our analysis to those species of *Senecio* found in the páramo and the puna, and whose maximum latitudinal distribution terminated in the 25th parallel south. In this way, we were able to consider around 36° of latitude in the Andes, where there is little latitudinal variation in the lower limit of the alpine zone. The altitudinal increase in the lower limit of the puna (ca. 200 to 300 m) at 25° S is fairly inconsequential, because the upper limit of the alpine vegetation does not increase accordingly.

Under these restrictions, the altitudinal range calculated on the basis of the highest and lowest records available should be fairly representative of a species' altitudinal range through the study area. Discarding 16 puna species whose distributions extend beyond the 25° latitudinal band limit and numerous other species for which the available data was noninformative, we obtained distribution data for 112 *Senecio* species, of which 14 are found in both the páramo and puna. For the purposes of the present analysis, these last species were assigned to that sector of the Andes corresponding to where the midpoint of their respective latitudinal ranges is found (< 8° S = páramo; ≥ 8° S = puna). The total number of species of *Senecio* in the páramo and puna, including those species that are distributed south of the 25° latitudinal band, is around 220.

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Thus, the electronic databases available to us allowed consideration of around 50% of the species.

TRENDS IN ALTITUDE VERSUS LATITUDE IN SENECIO

The correlation coefficients between altitudinal range and latitudinal range for *Senecio* species are summarized in Table 5.1. Results obtained under Criterion 1 are shown graphically in Figure 5.1. High altitude *Senecios* may be distributed over a very narrow altitudinal range (100 m) to as much as 3,890 m elevation, and over a single, 1° latitudinal band to up to twenty-four latitudinal bands (Figure 5.1). Our original prediction of a relationship between altitudinal and latitudinal range is borne out for both the páramo and puna *Senecios* (Table 5.1, Figure 5.1). In both high Andean vegetation zones, significant correlations were obtained between these variables independently of the criterion used to represent altitudinal range. The median altitudinal and latitudinal ranges, respectively, tend to be larger in the páramo than in the puna, although the differences are not significant (Mann Whitney U tests) (Table 5.2).

While these results are auspicious, they need to be considered critically. Aside from the problem of correctly

depicting the exact altitude at which a particular database entry was collected, rare species are possibly influencing the results. In general floristic surveys, the source of most database records, rare species will tend to be collected on fewer occasions than common species. Nevertheless, there will be cases where botanists studying a particular genus will seek to collect rare species. Given these caveats, the true altitudinal and latitudinal ranges of rare species in geographical regions still at the phase of general exploration, as is the case in the high Andes, will tend to be underrepresented in relation to more common species. As a consequence, rare species will tend to cluster relatively more closely to the origin on both axes of a plot of latitudinal versus altitudinal range than their true distributions dictate, in comparison with more common species. When rare species are very numerous in the data set, they could conceivably force a positive correlation between altitudinal and latitudinal range. Variation in the level of exploration (in different parts of the páramo and puna, in this particular case) also will affect results. That is, when the level of exploration is more limited, the probability of representing the full altitudinal and latitudinal ranges of a species will be diminished. One way of assessing whether rare species are influencing the analysis is to eliminate them entirely and repeat the analysis

TABLE 5.1

Correlation Coefficients for Altitudinal Versus Latitudinal Range of Species of Senecio in the Puna and Páramo, South American Andes, as well as for the Subset of Puna Species Occurring in Chile

		Criterion 1		Criterion 2	
	Number of species	Correlation coefficient (r)	P	Correlation coefficient (r)	P
Full set of species					
Puna (Chile)	33	0.516	0.01	0.444	0.05
Puna	88	0.540	0.01	0.522	0.01
Páramo	24	0.433	0.05	0.436	0.05
Restricted set of species					
Puna (Chile)	31	0.508	0.01	0.434	0.05
Puna	56	0.408	0.01	0.289	0.05
Páramo	15	0.097	NS	0.063	NS

Note: Criterion 1: Absolute limits obtained from all range data given on all database records; Criterion 2: When the altitude on an individual database record was given as a range, the midpoint was calculated as the representative altitude for the specimen (see text for further details); Full set of species: All species included regardless of the size of their latitudinal ranges; Restricted set of species: Species found in only one altitudinal band eliminated.
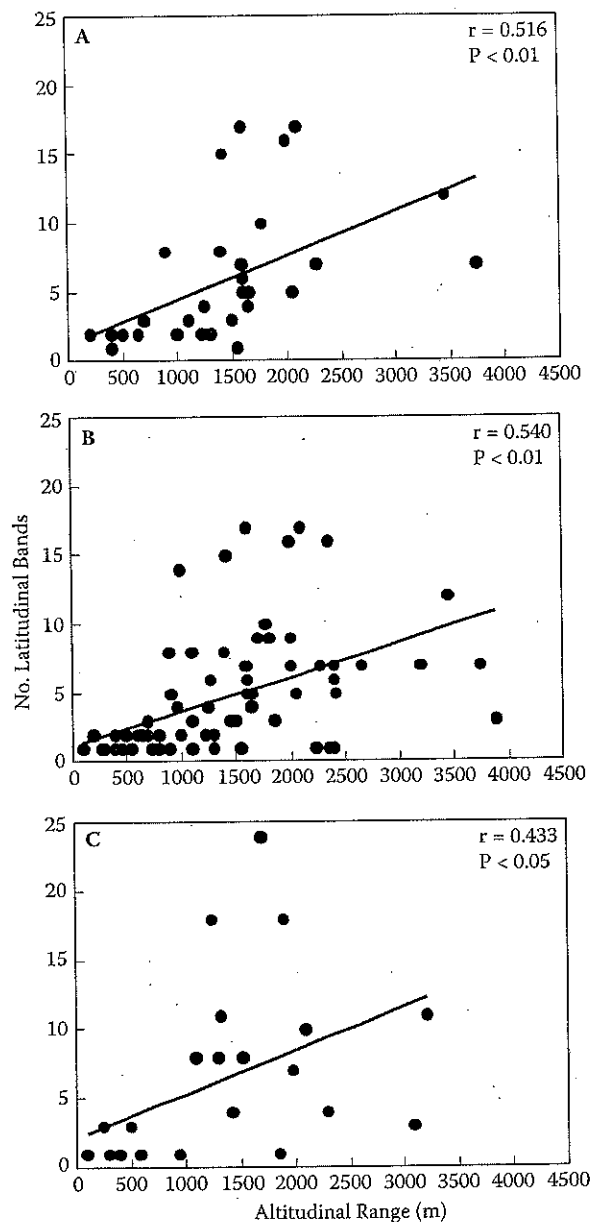
FIGURE 5.1 Relationship between altitudinal range and latitudinal range in species of Senecio (Asteraceae), South American Andes. (A) Puna of Chile only (n = 33 species); (B) puna of Chile, Peru, Argentina (n = 88 species); (C) páramo (n = 24 species). The lines show the tendencies in the data. r = product–moment correlation coefficient.

so as to determine if the correlation between altitudinal and latitudinal range still holds up. We performed the analyses again, eliminating all species recorded from a single latitudinal band (n = 9 in the páramo; n = 32 in the puna) (Table 5.1, restricted set of species). The correlation

TABLE 5.2

Mean and Median Altitudinal and Latitudinal Ranges for Species of Senecio in the Puna and Páramo, South American Andes

	Number of species	Mean altitude (m)	Median altitude (m)	Mean latitude (No. bands)	Median latitude (No. bands)
Criterion 1					
Puna	88	1194	1100	4.2	2
Páramo	24	1270	1275	6.2	3.5
Criterion 2					
Puna	88	980	835	4.2	2
Páramo	24	1127	1158	6.2	3.5

Note: Differences between species in the puna and páramo not significant (Mann Whitney U Test); Mann Whitney. U Test. Altitude: Criterion 1: $p = 0.499$; Criterion 2: $p = 0.745$; Latitude: $p = 0.128$.

between altitudinal range and latitudinal range continued to be significant for the puna, but not for the páramo, where the number of species was now very low (Table 5.2). With respect to differing levels of exploration, the Chilean puna has been extensively collected, there being only two species restricted to a single latitudinal band, according to the data at hand. It can be seen that the relationship between altitudinal range and latitudinal range holds up in this well-collected area (Figure 5.1, Table 5.1).

DISCUSSION

The study of large-scale macroecological patterns is dependent on the existence of sufficient and accurate plant and animal data. Our preliminary results in Senecio are in line with the hypothesis that altitudinal range and geographical range, as proxied by latitudinal range, are correlated. However, numerous uncertainties have appeared with the use of raw georeferenced database records, in particular because of the need of precise altitudinal data. Consequently, we feel that it is too early to come to any definitive conclusions.

DEALING WITH THE PROBLEMS

How to deal with altitudinal ranges in electronic database records constitutes a major challenge for macroecologists. If abundant specimens are available, those fo

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which altitude is cited as a range could be eliminated. For the *Senecio* data set, this would be tantamount to eliminating 27.5% of the informative specimens obtained from TROPICOS and NYBG, signifying a huge loss of information. In order for such valuable resources as TROPICOS to reap maximum value, field botanists might endeavor to report the precise altitude where a collection is made. If a species is sighted beyond that point on an altitudinal gradient, its additional range could be explicitly noted on the herbarium specimen label and be included in the general habitat data that the best databases included. At the same time, ecologists should be explicit regarding the limitations of any databases employed.

Controlling for spurious effects between altitudinal and latitudinal ranges insofar as our interests are concerned is even more challenging. The situation in the Andes, whereby the lower limit of the alpine life zone does not vary much over its northern 36 degrees of latitude, and if anything, increases with latitude, would seem unique worldwide. Notwithstanding taking advantage of this fortuitous situation, the *Senecio* altitudinal ranges will not be totally accurate because of local differences in the lower limit of the alpine zone.

We suggest that the best way of getting around this problem, in terms of the hypothesis of interest here, is to convert the altitudinal ranges of each species into an equivalent mean growing season temperature range, thereby abandoning altitude, per se (cf. Körner, 2007). This procedure, besides leading to greater accuracy in depicting the breath of a species' temperature niche in the present study, would have enabled the inclusion of many more species of *Senecio* found in the southern temperate alpine, thereby increasing statistical power. However, to be able to reach this point, regional climate models capable of discriminating between temperatures over small spatial scales on altitudinal gradients must be available. Even then, some difficulties will remain. At any given altitude, significant small-scale variation in temperature and other environmental variables, associated with opposite facing slopes, exposed versus windy slopes, and different substrate types, is typical at high elevations (Squeo et al., 1983; Rozzi et al., 1997; Körner, 2007). Additionally, in large-scale studies involving many degrees of latitude, latitudinal ranges should be converted into linear distances, thereby overcoming the problem that latitudinal bands are of different widths.

A procedure is needed to deal with the distributions of rare species, which by their very nature will tend to be undersampled in most floristic databases. It should be born in mind that databases of museum records reflect the accumulated effort of generations of plant and animal collectors, such that unequal sampling of rare and common species and between different geographical areas will always be a problem when using this kind of data. Resampling the database to obtain a standard number of collections per species provides a possible solution to this problem, always that a sufficient number of species in the group of organisms under study is represented by a large number of collections. However, except for a few groups of organisms, such as birds and mammals, reality has it that the tropical latitudes still lag behind temperate latitudes in terms of collection density. Another uncertainty that tends to be disregarded in these kinds of studies concerns the misidentification of closely related allopatric species, which will lead to an exaggeration of the latitudinal or latitudinal range of a species. Of course, the best test of the hypothesis would consist of systematically sampling the altitudinal gradient at 100 m intervals and 1° intervals along both sides of the entire Andean chain. Until more formal work is carried on these various issues, the most appropriate avenue would seem to be to work with very large numbers of species drawn from many plant genera. Greatly increasing the number of species studied would allow implementation of some of the procedures suggested above, without a significant loss of statistical power. For the Andes, needless to say, inclusion of herbarium records in national herbaria could lead to significant changes in the distributions of many *Senecio* species and thus is critical.

UNDERLYING CAUSES OF THE PUTATIVE PATTERN

Assuming for the moment that the pattern revealed in this preliminary study of a single large taxon in the South American Andes could conceivably hold up with the inclusion of additional data and better altitudinal range control, to our knowledge, such a pattern has not been previously revealed for any other plant or, for that matter, animal group. The closest parallel we have been able to find is Brown and Mauer's (1987) demonstration of a strong correlation between the length and width of geographical ranges expressed as km north–south versus km east–west in North American and European land birds, which, of course, is not exactly the same. At some level, the underlying process leading to the macroecological pattern of interest here is akin to the notion that species with larger geographical distributions will tend to provide larger numbers of dispersing propagules and hence be more likely to succeed better in long-distance dispersal. However, here

we are talking not only about more diaspores, but about a set of diaspores that are adapted to many different temperature conditions. Thompson et al. (1999) showed that a measure of niche breadth is the best predictor of range size in the herbaceous flora of England.

Species with wide altitudinal distributions effectively have wide temperature niche breadths. As a corollary, among species with equal-sized geographical distributions, those species spread out over a steep altitudinal gradient should be more successful as long-distance colonizers than species with narrow altitudinal ranges. In passing, it is worthwhile pointing out that some of the most striking cases of long-distance dispersal concern dispersal from the northern hemisphere into the South American Andes (e.g., *Halenia*, *Valeriana*; Von Hagen and Kadereit, 2000; Bell and Donoghue, 2005). Dispersal into alpine areas is usually considered easy because of the less competitive, open nature of the alpine habitat. However, the high probability of temperature niche matching could also be a factor here.

Evolutionary history and differences in dispersal capacity also may influence the putative correlation between altitudinal range and latitudinal extension in the genus *Senecio*. All other things being equal, the more recently evolved species in a genus could be expected to have smaller altitudinal and latitudinal distributions, whereas earlier branching species would have had more time to colonize into the alpine, both altitudinally and latitudinally.

Assessing the effect of evolutionary history on the size of latitudinal and altitudinal ranges requires access to appropriate phylogenetic information, as yet not available for *Senecio*. Although we are not totally versed in the relevant literature, we note that much recent phylogeographic research on alpine plants focuses on their glacial history (e.g., Holderegger and Abbott, 2003; Schoenswetter et al., 2003). Insofar as dispersal is concerned, poorly dispersing species could be expected to have smaller altitudinal and latitudinal ranges, simply because they are not well-adapted for getting around. The achenes of *Senecio* bear a pappus and are wind dispersed. However, considerable variation in achene size is seen among species, which could make for differences in dispersal capacity among species. In the genus *Celmisia* (Asteraceae) in New Zealand, altitude is significantly and negatively correlated to seed dry weight (Fenner et al., 2001), suggesting that establishment at higher elevations favors smaller and, presumably, more easily dispersed seeds. A comparison of the latitudinal and altitudinal ranges of Andean taxa characterized by different dispersal types would be very enlightening in this respect.

Finally, it should be noted that our hypothesis presupposes that new evolved species will be able to colonize altitudinal gradients relatively rapidly, after which time lateral spread will occur. Very little seems to be known about how alpine species extend their geographic ranges. The unwritten dogma is that tracking the same temperature latitudinally constitutes an easier option than the spawning of new populations adapted to increasingly colder temperatures at the higher altitudes. Nevertheless, clinal variation in seed longevity over a compact alpine gradient in a fairly continuously distributed species has been reported by Cavieres and Arroyo (2001). For species distributed at high elevations, tracking the same temperature latitudinally (and longitudinally) will often involve crossing significant barriers from one mountain peak to another. Thus, lateral temperature tracking may not be as easy as intuitively assumed. But, of course, in reality, both processes are likely to occur simultaneously.

In conclusion, the use of electronic databases to detect large-scale patterns in alpine ecosystems poses numerous challenges, yet at the same time opens the door for taking further advantage of one of the best replicated natural experiments on Earth for detecting and understanding fundamental macroecological patterns. Just as altitude compresses large temperature differences into short distances, imprecise altitude data will signify magnified errors in macroecological analyses. Yet with caution, ecologists should use the highly valuable information contained in electronic databases while ensuring maximum rigor.

SUMMARY

Understanding the determinants of large-scale biodiversity patterns depends on access to sufficient and accurate georeferenced collection data. Macroecological patterns can be profitably studied in the alpine zone, a replicated, large-scale natural experiment that extends over large regions and exists at all vegetated latitudes of the globe. In our study, we take a look at the relationship between latitudinal range and altitudinal range for species of the genus *Senecio* occurring in the páramo and puna of the South American Andes. We compared latitudinal ranges of species measured as the number of 1° latitudinal bands and altitudinal ranges depicted as the number of 100 m elevational bands, over which a species is distributed, along an area of the Andes where temperature does not become markedly depressed with latitude, and found that these two variables to be positively correlated. We discuss the caveats of the method: the problem of rare species; variation in levels of exploration; the effect of

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misidentification of closely related allopatric species. We highlight several problems associated with the use of georeferenced data when altitude is the variable of interest, pointing out that use of mean growing temperature range instead of altitudinal range is biologically more realistic. Comparisons of altitudinal and latitudinal ranges will help to disentangle historical, evolutionary, and ecological causes. With appropriate phylogenetic information (not yet available for *Senecio*) one could assess the effect of evolutionary history on macroecological patterns. Differences in dispersal capacities on the size of latitudinal and altitudinal ranges also needs to be considered. The pattern uncovered in the genus *Senecio* in high elevation habitats in the South American Andes needs to be tested across a wide range of taxa in order to determine whether it is a general macroecological pattern.

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